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CABI

The Encyclopedia of Animal Nutrition

The Encyclopedia of Animal Nutrition

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And to the following individuals for waiving editing fees: Professors Robert Blair, University of British Colombia, Guoyao Wu of Texas A&M University, and Clive J.C. Phillips, Estonian University of Life Sciences and Curtin University Sustainability Policy Institute.

Comments

As a food scientist who is not a nutritionist, but does work with both humans and animals, … (the Encyclopedia is) quite comprehensive in its coverage of topics and has both short, focused blurbs, while other blurbs have a much more comprehensive exposition when their importance justifies it… 'nutrition' seems to be defined broadly so a lot of topics are covered, including background information on important biological compounds … It is certainly the 'go to' place to get started on almost any nutritional topic.

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Joe M. Regenstein
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The new edition of the *Encyclopedia of Animal Nutrition* contains an expanded amount of information that now not only includes information about farm, zoo, laboratory and companion animals, but also includes information concerning human nutrition. Entries provide descriptions, definitions and diagrams/figures to help the reader understand the types of materials used for feed/food ingredients, what nutrients are required for growth and health, and the physiological processes involved in the acquisition and utilization of those nutrients. The scientists and editors responsible for preparing and editing the content include many world-renowned individuals who are leaders in their fields. This publication will be a valuable source of information for those seeking to learn more about nutrition, how the field developed, and how issues such as climate change, pollution, food security and animal welfare are influencing the science of animal nutrition.

Nancy D. Turner, PhD
Professor
Nutrient Information Editor – *Advances in Nutrition*
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Preface to the Second Edition

Knowledge is available today in more forms than ever before. In an instant we can get an answer to any question we pose about animal nutrition, often from authoritative sources. But what is increasingly becoming clear in this internet-driven world is that it is not what we know, it is the organisation of this knowledge and how it is presented to us that matters most if it is to be effectively used. An encyclopaedia is a large collection of works on a particular theme; as such it should synthesise available knowledge and present that which is thought to be most relevant for the theme. This encyclopaedia is the first to gather all the information thought to be most relevant to animal nutrition, including humans, wildlife, companion, zoo and farm animals.

The first book I ever bought was a Victorian encyclopaedia,

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entitled *Cassell's Encyclopaedia: A Storehouse of General Information*. Its eight volumes delighted its young reader, encouraged me to want to learn more, teaching me about things I knew nothing about, made me wonder at the world around me. This *Encyclopedia of Animal Nutrition* aims to do exactly that for you. Animal nutrition is an advanced field of science that is fundamental to our very existence. It is at the very heart of modern debates on food security and animal health and welfare, and it has important considerations for climate change. Constructing an encyclopaedia is a vast work, which should survive the passage of time. My encyclopaedia was already 70 years old when I bought it, but it still contained many gems of knowledge that made me want to understand and use that knowledge for the benefit of society. It is hoped that the current encyclopaedia will do exactly that for many years – encourage readers, young and old, to take this knowledge and use it to improve the way we manage our feeding systems, feeding farm animals, laboratory animals, zoo animals, sport animals and ourselves.

Nutrition is the key to all life: it sustains our bodies, nurtures our life processes and governs our health and wellbeing. We face unprecedented challenges to our ability to feed both ourselves and the other animals on the planet: rising human and animal populations, growing demand for animal products, increased environmental impact from farm livestock, unacceptable welfare of intensively farmed livestock, and rising costs of the necessities for feeding animals. The world is entering an unprecedented period when more prudent use of food and feed resources is required to

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maintain its populations of humans and other animals. This encyclopaedia, which is open to all nutritionists and consumers alike, should help us to manage animal nutrition better.

Essential as it is, animal nutrition has been increasingly questioned for its impact on health – our health, other animals' health and our planet's health. Does utilising so many resources for growing animal feeds impact on our ability to feed humans? Do animal feeding habits transmit diseases to other animals, including humans? Is it ethical to feed cereal grains to farm animals when some human societies do not have enough for themselves? Do our current methods of feeding intensively reared farm animals affect their welfare?

These are important questions, and this volume includes short and long articles that attempt to enlighten us so that we can solve these issues. The knowledge itself will not solve any problems; it is how we use it that will produce the answers. Hence this volume aims to entice animal nutritionists to read more, to learn about these key issues. Researchers, students, lecturers, advisors, government scientists – they will all find something to interest them in this book. Some entries are necessarily long because of the complexity of the issues, others short because they are more tangential to the main theme, not as important or on topics about which less is known. This encyclopaedia edition differentiates from its predecessor, *The Encyclopedia of Farm Animal Nutrition*, by broadening its scope to include all animals, including humans, and the inclusion of several long articles, addressing some of the questions posed above. These include entries on the effects of

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nutrition on the quality of farm animal products, the history of nutritional sciences, GM foods and organic farming.

Farm animal nutrition has been comprehensively studied for several centuries, even compared with human nutrition, because of the economic importance of maximising the efficiency with which our farm animals are 'produced'. The extension of our scope to include all animals, including ourselves, was a logical step, since nutritional principles are common to all species. Humans are treated as just another animal, although there is more focus on food security than for the other animal species. As the world develops, it is imperative that we manage the feeding systems more efficiently to guarantee food security and prevent starvation and malnutrition in any species. However, it is the human species whose population has expanded beyond anything considered possible just a few hundred years ago.

As in the first edition, readers are invited, and requested, to submit their suggestions for amendments or for additional entries for the third edition. These can be emailed direct to me at clive.phillips58@outlook.com. I would also be delighted if you could contribute financially so that the third edition can also be open access. In preparing the second edition, feedback from the first edition was carefully considered by the team of editors, which led to some of the changes you will find incorporated into this volume. I pay tribute to the enormous efforts of the first edition editor-in-chief, the late Malcolm Fuller, in leading a team of scientists to produce that first edition, which gave us the solid foundation for the second edition. I myself am extremely grateful

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to my team of editors who have made my work easy, and all the many authors who have contributed. I acknowledge the hard work of Bob Blair and Guoyao Wu, writing entries, raising funds to make the volume open access and checking facts to make the current edition as up-to-date as possible. Without their support my task would have been Herculean. Working at a time of a major world pandemic, we inevitably had issues with limited availability of some editors and authors, and the original editors for several sections in this second edition of the *Encyclopedia* had to withdraw. I am grateful to Alex Lainsbury at CABI for giving me the freedom to steer this project and for the staff at CABI for their work in editing the final version. I take full responsibility for selection of illustrations and am grateful to Wordpress for access to their library of photographs. I also take responsibility for the cross-referencing. Whilst every effort has been made to ensure its accuracy, a few words, such as 'lead' have been omitted from cross-referencing because of the obvious other meanings of the word. I particularly thank my understanding and long-suffering family, and especially my wife, Alison, for putting up with my absences at key times, and for my absconding to the Estonian University of Life Sciences to finish the book.

Please pause a while to peruse the work without any particular objective in mind; encyclopaedias should stimulate the intellectual palate and titillate the mind, leaving you wanting to come back for more. In the end, it is not what you know that matters, it is how you use it and whether you have a curiosity to go deeper.

Clive Phillips

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Queensland, Australia
November 2023

Preface to the First Edition

An encyclopedia should properly encompass the totality of human knowledge, or at least of some particular sector of it. Not so many years ago it would have been possible to contain all that was known of animal nutrition in a book the size of this, for the science of nutrition is young, but such has been the pace of its growth that that is no longer possible. The nutrition of farm animals is a complex subject, reaching into biochemistry, physiology, pathology, veterinary medicine, animal husbandry and agriculture and even, as evidenced in the following pages, beyond those disciplines. The subject matter of farm animal nutrition is covered in a large number of text books – most are referred to in the entries of this encyclopaedia – but their arrangement does not lend itself to the rapid recovery of specific pieces of factual information and it was with that object in view that this encyclopaedia was devised and written. Its aims are completeness, accuracy, succinctness and ease of access. The aim of completeness – to include as much factual

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information as possible – was addressed by embracing all the ramifications of nutrition just mentioned. Yet, no doubt there are omissions. To achieve a high degree of accuracy authors were chosen for their expertise in specialized areas of nutrition. But mistakes there surely are and for those that I have failed to spot I would plead, as that pioneer lexicographer Dr Johnson famously pleaded, when asked by a lady why he had defined 'pastern' as 'the knee of a horse', 'Ignorance, Madam, pure ignorance'. To encompass the whole of farm animal nutrition in this space obviously requires succinctness and all the contributors were enjoined to be as brief as possible – though some found it harder than others. Finally, ease of access is ensured by the alphabetical arrangement of the entries and the system of cross-references. There is more on this in the note that follows.

Although there have been other encyclopedias of nutrition they have been more in the nature of collections of review articles, valuable certainly, but not providing the ready access to specific facts and figures that is the essence of this work. This is the first encyclopedia to be devoted exclusively to the nutrition of farmed animals, including birds and fish. It contains some 2000 entries, written by about 100 specialists and reviewed by an international editorial panel. The entries range from short definitions of terms to extended descriptions of subjects of major importance. The entries are illustrated by figures (e.g. chemical structure, anatomy, graphs), tables (e.g. families of nutrients, feed composition) and photographs (of things that can best be appreciated visually). Entries are supported by references to important original papers

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and reviews, with suggestions for further reading. The encyclopedia includes definitions of terms commonly used in nutrition; chemical structures and functions of nutrients, important metabolites, toxins, etc.; explanations of nutritional processes; their physiological and metabolic bases; descriptions of the major farmed species, their metabolism and practical feeding; composition and nutritional value of important crops and feedstuffs; feed processing; feeding systems. It is intended as a book that users will regularly refer to for information because they know it will be there.

Because this is the first time that such an encyclopedia has been published, it must also be seen as a work in evolution, not yet complete. To further its evolution, so that future editions can be more nearly complete, more accurate and more informative, readers are invited, and requested, to submit their suggestions for amendments. Just as the first editor of the Oxford English Dictionary relied upon a host of contributors to submit material, it seems appropriate to ask the readers of this volume, some of whom undoubtedly have specialized knowledge, to contribute, if they will be so kind. Suggested amendments should be addressed to the Editor-in-chief, care of the publisher.

This book represents the combined efforts of many people and I would like to thank, first, the authors, who have distilled their many years of learning into a very few words. I owe a great debt of gratitude to my fellow editors who have not only secured the services of the many contributors but helped me to edit the resulting writing so as to achieve some kind of uniformity of

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presentation. In addition to the editors whose names are on the title page, I am most grateful to those who, for various reasons, were unable to complete their roles; to the late Dr John Topps, to Dr Angus Russell, Dr Colin Fisher and Dr Julian Wiseman.

I wish to express particular appreciation to Rebecca Stubbs, Development Editor (Books and Reference Works) at CAB International. Her patience in the face of numerous delays and her helpfulness have made an enjoyable experience of what could have been an irksome chore. I am also most grateful to Sarah Williams for her careful work on the manuscript and to Rachel Robinson for production. Finally, I thank my wife Margaret for her tolerance of all the hours in which I have neglected her, the house and the garden.

Malcolm Fuller
Stony Brook, New York
September 2003

Notes on Using the Encyclopedia

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The entries are in alphabetical order, using English, not American, spelling. Where there are two or more names for the same subject, the entry appears under the most common name, alternative names appearing as blind entries, directing the reader to the common name under which the entry appears. For example '**Gossypose:** *see* Raffinose'.

Within an entry, a bold typeface highlights a word that is an entry in its own right. For example, in the entry '**calorimetry**' the passage 'Distinction must be made between **direct calorimetry**, which is the physical measurement of heat given off by the animal, and **indirect calorimetry**, in which the measurements are of the chemical quantities involved in metabolism' indicates that there are also entries on **direct calorimetry** and **indirect calorimetry**.

Where information related to the content of an entry is to be found elsewhere, but where the cross-reference is not indicated by a highlighted word in the text, there may be a footnote beginning '*See also*' to direct the reader to that other material. For example, the entry '**absorption**' does not contain the word '**digestion**' but the entry '**digestion**' nevertheless includes information on **absorption,** so '*See also* Digestion' is added at the end.

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Abalone

A large marine snail or gastropod of the mollusc family *Haliotidae*. More than 50 species have been identified. Abalone have a hard shell and a muscular foot. They inhabit rocky shorelines, from shallow water up to depths of approximately 40 m. Their shells are rounded or oval with a large dome towards one end. The shell has a row of respiratory pores. The muscular foot has strong suction power, permitting the abalone to clamp tightly to rocky surfaces. Abalone have succulent meaty bodies with a naturally salty and buttery flavour and chewy texture. Abalone meat is known for its texture and composition changes throughout the abalone's lifetime. Seasonal variations show that the **collagen** content in *Haliotis discus* is highest in winter and lowest in summer, affecting the texture of the flesh. They have been widely used by indigenous populations in Australia, New Zealand, East Asia and North America as an important subsistence food. Known in ancient times as 'elixir of life', abalones are believed to symbolize wealth and power and to have a unique flavour. Abalone are in high demand in China, Japan and other Asian countries. With capture fisheries in serious decline, abalone farming is expanding in Taiwan, South Korea, Chile, Iceland, Mexico, USA, Australia, Thailand and several countries in South-east Asia, in particular China (the world's largest producer and consumer of cultured abalone) with over 2000 farms

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that produced 163,169 t in 2018. In the natural environment abalone graze on benthic (bottom-growing) algae, but formulated diets from a combination of animal and plant **protein source**s have been developed for feeding farmed abalone. (SPL; QS; DB)



Australian dried abalone. Photo courtesy of Avlxyz and Australia Fortune Company. Licensed under CC BY-SA 2.0.

Further reading

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Abdominal fat

In most domesticated species, deposits of abdominal fat can be divided between peritoneal and inguinal regions; the exception is the duck, in which subcutaneous fat deposits, required for thermal insulation, comprise the largest single depot and are a special development in this species. The fat of the peritoneum is located within the abdominal cavity and extends ventrally over the visceral mass, being attached to the peritoneal membranes lining the abdominal wall. Inguinal fat lies along the interior femoral and tibiotarsal region and extends from the sartorius muscle to approximately two-thirds the length of the tibiotarsus. Consistency and appearance of fat in terms of its chemical and physical nature can vary between species, reflecting not only genetic traits but also diet. For example, abdominal deposits of fat in horses and certain Channel Island breeds of cattle are yellow while those of sheep are hard and white and those of pigs soft and greyish in colour. Body temperature is important, with fat being almost semi-fluid compared with that at cooler temperatures. **Brown adipose tissue** is not found in abdominal fat stores. (MMax)

Abomasum

The fourth compartment of the ruminant stomach. It communicates anteriorly with the **omasum** through the omaso-

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abomasal opening, and posteriorly with the **duodenum** via the pyloric orifice. The abomasum is analogous to the simple stomach of **monogastric** animals. Like the stomach of non-ruminants, it is lined with a glandular epithelium that secretes mucus, **hydrochloric acid** and enzymes, including pepsins and **lipase**. (RNBK; GMcLD)

Abortion

Abortion is defined relative to the stage of pregnancy when the embryo or fetus is lost. In cattle, early embryonic death refers to deaths occurring from the day of conception until about 42 days of gestation (the end of the embryonic period), which coincides with the end of differentiation. Embryos lost during this period may be either resorbed or aborted. A normal rate of early embryo **resorption** (0–45 days) is 9–12% and abortion or resorption after 45–60 days is usually rare (1–2%). Higher rates are attributed to disease. Bovine fetuses discharged from day 42 until approximately 260 days are generally called abortions, and from day 260 until normal term (281 ± 3 days), premature births.

Dietary causes of embryonic death, abortion or premature birth include poisonous plants, fungi and synthetic toxicants. Plants associated with abortion or premature birth include *Pinus* species (*P. ponderosa*, *P. radiata*, *P. taeda*, *P. cubensis*), *Juniperus communis*, cypress (*Cupressus macrocarpa*), snakeweeds (*Gutierrezia sarothrae* and *G. microcephala*), locoweeds (***Astragalus*** spp. and *Oxytropis* spp. containing swainsonine), hairy vetch (*Vicia villosa*), darling pea in Australia (*Swainsona* spp.) and **leucaena** (*Leucaena leucocephala*). **Mycotoxin**s

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include **ergot** alkaloids from grains and grasses infected with *Claviceps* and *Balansia* spp., loline **alkaloid**s from endophyte-infected tall fescue, **trichothecene**s from *Fusarium* spp., grains and maize silage infected with *Aspergillus* and *Penicillium* spp., and hay, straw and mouldy sweet clover (**dicoumarol**) contaminated with *Stachybotrys* spp. Xenobiotics believed to contribute to embryo or fetal loss include nitrates and nitrites, high-protein diets (excess **urea**), carbon monoxide, oestrogenic compounds, **glucocorticoids**, lead, phenothiazines, **oxytocin**, chlorinated pesticides (DDT, dieldrin, heptachlor) and warfarin (coumarins). (KEP)

Absorption

The process by which nutrients are transported from the lumen of the **gastrointestinal tract** to the blood or lymphatic system. Absorption of most nutrients occurs predominantly in the **jejunum**. Absorption of intact macromolecules is very limited. Most are degraded into their constituents by digestive enzymes in the intestinal lumen: proteins to **amino acid**s and small **oligopeptide**s; **glycogen** to **maltose**, **isomaltose** and small **oligosaccharide**s; triglycerides to **fatty acid**s, 2-monoglycerides and **glycerol**. Further degradation of proteins and carbohydrates occurs at the **brush border** surface under the influence of a large number of specific enzymes for degradation to their mono-constituents, amino acids (small amounts of peptides may pass to the blood) and the hexoses **glucose**, **fructose** and **galactose**. Degradation products from **lipids** are emulsified by bile salts and **lecithin** and organized in micelles which diffuse through the

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unstirred water layer to the membrane of the brush border, where the nutrients are absorbed. In the distal **ileum**, about 95% of the bile is absorbed into the blood during one turn of the enterohepatic circulation.

Absorption of macromolecules can occur in specific instances; for example, absorption of immunoglobulins from colostrum in newborn mammals is performed by **pinocytosis**, mainly in the ileum.

Absorption of some minerals and of degradation products from microbial **fermentation**, such as **short-chain fatty acid**s (SCFA), also takes place in the **large intestine**. In the horse, up to 70% of the absorbed **energy** is absorbed as SCFA in the **colon**. In ruminants, absorption of these products formed in the **rumen** or derived from diets mainly takes place in the fore-stomach.

Little water is absorbed from the stomach, but it moves across the **mucosa** via aquaporins in both directions in the **small intestine** and large intestine and generally the osmolality in the intestinal lumen is close to that of plasma. In the colon, sodium is pumped out and water moves passively with it. (SB; GW)
See also: Digestion; Intestinal absorption

Acceptability:
see Palatability

Acetaldehyde
An **aldehyde**, $CH_3 \cdot CHO$. It can be produced chemically by **oxidation** of **ethanol** $CH_3 \cdot CH_2OH$. In cellular **metabolism**, acetaldehyde is an intermediate produced in the conversion of

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ethanol to acetic acid. After activation in the cell, acetic acid can be used as a source of energy. Acetaldehyde can be toxic. (NJB)

Acetate

$CH_3{\cdot}COO^-$. Acetic acid, $CH_3{\cdot}COOH$, is one of the three (acetic, propionic, butyric) common short-chain **volatile fatty acid**s found in intestinal contents. This fatty acid accounts for a major proportion (more than half) of the **short-chain fatty acid**s produced by anaerobic fermentation in the **rumen** or in the **large intestine**. In cellular **metabolism**, acetate is converted to acetyl-**coenzyme** A (CoA) prior to being used in catabolic or anabolic processes. **Acetyl-CoA** is a major metabolic intermediate in the **catabolism** of fatty acids and carbohydrates to carbon dioxide and water and of **amino acid**s to carbon dioxide, water and nitrogen end-products in the production of cellular energy in the form of ATP. In cellular biosynthetic activities, acetate as acetyl-CoA is the precursor for all of the carbon in **long-chain fatty acid**s (16–18 carbons), **ketone**s and **cholesterol**. (NJB)

Acetic acid:

see Acetate

Acetoacetate

$CH_3{\cdot}CO{\cdot}CH_2{\cdot}COO^-$, one of the three **ketone** bodies (acetoacetate, β-**hydroxybutyrate** and **acetone**) produced in the incomplete **oxidation** of **fatty acid**s. In the liver, fatty acids, via their metabolism to acetyl-**coenzyme** A, can produce acetoacetyl coenzyme A which in turn can be converted to the other two ketone

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bodies. Acetoacetate and β-hydroxybutyrate can be taken up by other tissues and used for **energy**. (NJB)

Acetone

$CH_3{\cdot}CO{\cdot}CH_3$, one of the three **ketone** bodies (acetoacetate, β-**hydroxybutyrate** and acetone) produced in the incomplete **oxidation** of **fatty acid**s. Because acetone is volatile and has a unique sweet odour, it can sometimes be detected in the breath of ketotic animals. Acetone is not further metabolized and is lost from the animal. (NJB)

Acetyl-CoA

Acetyl-coenzyme A, $CH_3{\cdot}CO{\cdot}SCoA$, the metabolically active form of **acetate**. It is produced in the metabolism of **carbohydrates**, **fatty acid**s and **amino acid**s. Free acetate is converted to acetyl-CoA in the cytoplasm of cells and utilizes **coenzyme** A and ATP in its production. (NJB)

Acetylcholine

A **neurotransmitter**, $(CH_3)_3N^+{\cdot}CH_2{\cdot}CH_2OOC{\cdot}CH_3$. It is formed in nerve endings by combining **acetyl-CoA** with **choline** and is found in synaptic vesicles. These vesicles are released into the synapse in response to nerve impulses and initiate a response in another nerve or muscle. (NJB)

Acid–base equilibrium

The balance between acids (elements or compounds that increase H^+ concentration) and bases (elements or compounds that

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decrease H^+ concentration). Neutrality (equal balance of acid and base) is at a pH of 7.0 (H^+ concentration = 1×10^{-7} mol l^{-1}). However, homeostatic mechanisms in living organisms tend to maintain an extracellular fluid pH between 7.35 and 7.45. Survival of the organism is not possible outside of the range of a pH between 7.0 and 7.7. Acidosis is defined as a blood pH < 7.35 and occurs with prolonged **starvation**, severe **diarrhoea**, asphyxia, **ketosis** and **lactic acidosis**. **Alkalosis** is defined as a blood pH > 7.45 and is associated with hyperventilation, vomiting of gastric acid and diuresis. Multiple systems within the body are primarily responsible for maintenance and regulation of acid–base equilibrium. These include the physiological buffers, the respiratory system and the renal system. These systems are interrelated and provide relatively rapid responses to shifts in acid–base equilibrium. The **gastrointestinal tract** also plays important roles in acid–base equilibrium but the responses are of greater consequence to long-term regulation and involve shifts in absorption and excretion of mineral ions.

Major physiological buffers include **bicarbonate**, phosphate and proteins. Bicarbonate ions (HCO_3^-) and hydrogen ions (H^+) are in equilibrium with carbonic acid (H_2CO_3), a weak acid. Carbonic acid is produced by enzymatic action of carbonic anhydrase from CO_2 and H_2O. The formation and end-products of bicarbonate can be easily eliminated via respiratory or renal systems without an effect on pH. Since mechanisms exist to maintain a constant extracellular concentration of bicarbonate ions (which are an excellent **buffer** for physiological fluids), the

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bicarbonate buffer does not provide a means for net elimination of acidic or basic loads imposed on the body. In terms of acid–base equilibrium, the bicarbonate buffer is considered a **futile cycle** since net elimination of bicarbonate as CO_2 via the lungs is eventually compensated for by renal synthesis of bicarbonate by the kidneys with no net change in H^+. Phosphate ions buffer H^+ in physiological fluids and contribute to the net equilibrium of acids and bases in the body. Within physiological pH ranges the concentration of dibasic (HPO_4^-) phosphate ions is approximately four times the concentration of monobasic ($H_2PO_4^-$), but the kidneys can concentrate H^+ in urine to a pH as low as 4.5. As urine pH decreases, the dibasic phosphate ions provide a buffer by accepting H^+ to form monobasic phosphate, thus providing net elimination of H^+ from the body.

Another major route for a net elimination of H^+ from the body involves renal production and secretion of ammonium ions from **glutamine** catabolism. Under acid loads, the expression of phosphate-activated glutaminase in renal mitochondria is increased, resulting in enhanced degradation of glutamine and excretion of H^+ as ammonium (NH_4^+).

The strong ion difference (SID), which is the sum of all strong cations (mol l^{-1}) minus the sum of all strong anions (mol l^{-1}), also impacts on the regulation of acid–base equilibrium. The SID affects the partial pressure of blood CO_2 and renal electrolyte excretion. Shifts in SID impact renal compensation by changes in the relative amounts of ammonium and phosphate ion excretion. The pH of the

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rumen is controlled through the actions of salivary phosphate and biocarbonate buffers, and absorption of the **volatile fatty acid**s produced by microbial fermentation. (TDC, GMcLD)

Acid detergent fibre (ADF)

The detergent fibre analysis scheme was introduced to overcome inadequacies in the use of the traditional acid–alkali **crude fibre** estimation when applied to fibrous **forage** feeds for ruminants (see table).

Classification of forage fractions using the detergent fibre methods of Van Soest and Wine (1967).

Fraction	Components
Cell contents (soluble in neutral detergent)	Lipids Sugars, organic acids and water-soluble matter Pectin, starch Non-protein N Soluble protein
Cell wall constituents (fibre insoluble in neutral detergent)	Hemicelluloses Fibre-bound protein
1. Soluble in acid detergent 2. Acid-detergent fibre	Cellulose Lignin Lignified N Silica

The determination of ADF involves the extraction of food (1 g)

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by boiling (1 h) in acid-detergent solution (100 ml; 2% cetyltrimethylammonium bromide (CTAB) in 0.5 M H_2SO_4). The insoluble residue is filtered, washed with **acetone**, dried (8 h, 100°C) and weighed. This residue, which includes **cellulose**, **lignin** and some inorganic elements such as **silica**, is described as ADF. The residue can be used for subsequent measurement of cellulose after **oxidation** of lignin by saturated **potassium** permanganate solution and removal of **manganese** dioxide by oxalic acid (Van Soest and Wine, 1968). (IM)

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Acid detergent insoluble nitrogen

(ADIN; also called acid detergent fibre nitrogen, ADFN). The

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amount of **nitrogen** retained in the **acid detergent fibre** residue. ADIN is relatively indigestible, and it has been used to determine heat damage to proteins in feedstuffs. Excessive heating of foods containing protein and carbohydrate leads to **Maillard reaction**s, which cause the formation of covalent bonds between **aldehyde** groups in carbohydrates and free amino group residues on **amino acid**s, especially **lysine**. ADIN is an **indicator** of these heating effects, which decrease the **digestibility** of the protein. (IM, GMcLD)

Acid treatment of feeds

Acids are generally applied to forages either to improve the degradability of poor-quality cereal crop residues or to enhance pH reduction during ensiling. They are also used as dietary supplements to help maintain blood pH. The addition of either hydrochloric or **sulphuric acid** to cereal straws reduces **hemicellulose** content but has little effect on either **cellulose** or **lignin**. However, **digestibility** and intake improve and so, like alkali treatment, acid treatment may hydrolyse the **ester** bonds between lignin and the other cell wall **polysaccharide**s. Again like alkali treatment, acid treatment improves degradability in the rumen, but sufficient dietary protein must be supplied to ensure that this potential can be realized. Animals consuming cereal straw treated with acid and **urea** have been shown to have both an enhanced flow of **microbial protein** to the **small intestine** and increased **nitrogen retention**. An additional benefit identified with this combined treatment is that acidification appears to enhance the degree of **ammoniation** of straw by the urea. When

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sulphuric acid is used, the **sulphur** content of the treated material increases, which may be beneficial as sulphur is a vital element in the production of microbial protein. It is generally recommended that where additional nitrogen is supplied, sulphur should be provided at a ratio of S:N of about 1:12. Short-term treatment of cereal straw with **organic acid**s such as **formic acid** has no effect on either digestibility or intake, with the acids being degraded in the rumen to **methane** and **carbon dioxide**.

The most common use of acids is their incorporation into the herbage mass to enhance the rate of pH reduction during ensiling. Successful preservation of plant material as **silage** depends on rapidly achieving a controlled fermentation under anaerobic conditions and the conversion of water-soluble carbohydrates to **lactic acid**. At pH 3.8 to 4.3, microbial activity is inhibited, resulting in well-preserved, stable silage. When the crop and conditions within the silo permit, no additives are needed; but where either these are inadequate or to minimize losses in fermentation, the desired pH can be partly achieved by direct acidification. This promotes a lactic acid fermentation and lowers the energy **cost** of fermentation. A.I. Virtanen of Finland first developed the use of acids in this way in the 1930s. In what became known as the AIV method, combinations of sulphuric and hydrochloric acids were added to forages at ensiling to encourage the rapid reduction of pH (< 4) so as to suppress proteolytic activity. A number of acid-based **silage additive**s are now available. For safety and to limit their corrosive effect, weaker organic acids such as formic acid are used, either alone or in

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combination with fermentation inhibitors such as formalin. The application of acids has been shown to increase animal performance, due to reduced losses of nutrients as well as improved **protein quality**, **palatability** and intake. (FLM)

Acidification

Acids are sometimes added to animal feed ingredients or diets to protect the material against microbial deterioration or to reduce the pH in the animal's stomach. **Propionic acid** can be added to hay or cereal grains to prevent the growth of moulds and the formation of **mycotoxin**s. This allows such feed materials to be stored safely with a higher moisture content than is normally recommended. Short-chain **organic acid**s (e.g. formic, propionic, fumaric and citric) can be added to diets for newly weaned piglets to reduce digestive upsets. The young piglet has an immature gut, where enzymatic activity for the **digestion** of plant materials and **hydrochloric acid** secretion are not sufficiently developed; piglet feeds often have a high acid-binding capacity and are fed in relatively large meals. Organic acids reduce the incidence of **diarrhoea** in piglets post-weaning by their antimicrobial action on the feed itself, by reducing stomach pH and by acting as **energy source**s. **Lactic acid** can be added to **dried milk** powder for artificial rearing of calves. Lactic acid preserves reconstituted milk, allowing *ad libitum* feeding of cold milk; it also reduces the pH of the calf's **abomasum**, thereby assisting clot formation. (PCG)

Acidity of the gastrointestinal tract

The quality of being acid describes a solution with a pH less than

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7.0. The contents of the stomach or **abomasum** are normally acid because of the secretion of 0.15 M hydrochloric acid by the **parietal cell**s in the gastric **mucosa**. This acid is bacteriocidal for many ingested organisms; it also provides the necessary pH for the conversion of pepsinogen to **pepsin** and for the latter to start the digestion of dietary protein. The gastric mucosa is protected from self-digestion by an unstirred layer of mucus, made alkaline with **bicarbonate**.

Because of its high content of bicarbonate, the **pancreatic juice** secreted into the **duodenum** is alkaline, e.g. pH 8.0. In addition, **bile** and intestinal juice both tend to be alkaline and so these three secretions soon neutralize the gastric contents entering the duodenum and raise the pH of the duodenal contents to 6.0–7.0. By the time the **chyme** reaches the **jejunum**, its reaction is neutral or may become alkaline, depending on the species. This has an important bearing on the solubility of **calcium phosphate** and the absorption of calcium ions from the upper part of the **small intestine** (*see* Hyperparathyroidism).

The pH of the contents of the **large intestine** is close to neutrality; however, in the horse, and other species in which there is a good deal of **cellulose** fermentation in the **caecum** and **colon** with the production of **volatile fatty acid**s, the pH of the gut contents in these regions is nearer 6.0 than 7.0. (ADC)

Acidosis:
see Lactic acidosis

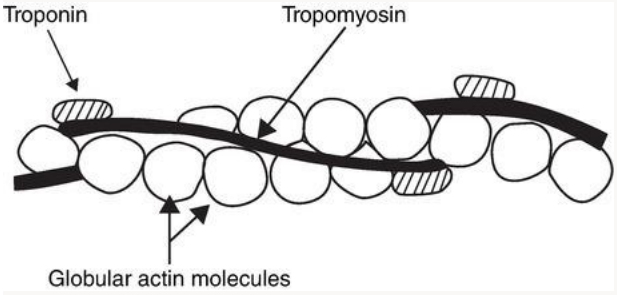
Acorn

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The fruit of the oak tree (*Quercus* spp.). Acorns can be dehulled but are more frequently fed whole, as, for example, to Iberian pigs in southern Europe to produce highly prized hams. These hams are considered to have special flavour due to the **tannins** and **fatty acid**s in the acorns. The tissues of pigs fed acorns have high concentrations of α-**tocopherol**, which reduces oxidative damage to the tissue. The **crude protein** of acorns is low (about 60 g kg^{-1}) and their **digestible energy** for pigs is 11–12 MJ kg^{-1}. Acorns contain hydrolysable tannins which degrade to produce pyrogallol. The consumption of acorns has been responsible for pyrogallol toxicity in cattle. (TA)

Actin

A water-soluble protein (molecular weight 43,000) containing 376 **amino acid**s. It is found in muscle and other tissues with motile function. It provides the thin filament backbone and combines with **myosin** to produce muscle contraction in the presence of **adenosine triphosphate** (ATP). Actin is the second most abundant protein in muscle, making up 10% of the total protein. (NJB)



The arrangement of actin, tropomyosin and troponin in the thin filament.

Activity, of enzymes:

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see Enzyme activity

Activity, physical

Activity is brought about by muscular contractions in which chemical **energy** stores are converted into mechanical energy, which in turn is converted into heat as the work is performed. In this sense it is wasted energy but some activity is essential – for example, **foraging** by free-range animals, which involves further **energy expenditure**. This has led to the development of intensive production systems for egg layers and for growing chickens, pigs and calves, where activity is minimized.

Although chemical energy can be mobilized very quickly for vigorous work, this may not be reflected immediately in the animal's **oxygen consumption**, but the delay is only of short duration and the so-called oxygen debt is usually made up in a few minutes by increased respiration. Changes in oxygen consumption of an animal thus provide a good indication of the heat produced by activity. Even mild exercise can cause a considerable increase in oxygen consumption, and therefore in **heat production**, and at higher levels of activity increases of up to ten times the resting oxygen consumption can be sustained for prolonged periods, e.g. in draught animals, sheep being herded, racehorses and animals in flight from predators.

There have been few direct measurements of the metabolic cost of activity in farm animals. Most estimates take the form of comparisons of heat produced under different conditions, such as standing vs. lying, walking vs. standing still, walking uphill vs. walking on the level. These comparisons are surprisingly

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consistent, even between species. When cattle and sheep stand up, the effort involved in getting up causes increased oxygen consumption of some 30% over a few minutes, after which the standing:lying ratio is of the order of 1.12–1.20:1. The metabolic cost of continued standing over lying has been estimated as 0.07 to 0.14 watts kg^{-1} body weight (6–12 kJ kg^{-1} per day). In horses, which have the ability to sleep whilst standing, there is little difference in oxygen consumption between standing and lying.

The cost of movement on treadmills has been measured for animals and humans. The results for horses, cattle and sheep may be very crudely summarized as the increase in heat production per kg body weight in moving a distance of 1 m; it is 1.5–3 J kg^{-1} m^{-1} for horizontal movement and 25–35 J kg^{-1} m^{-1} for vertical upward movement. Speed of the movement has little effect on these estimates of total **energy cost**, because the effort of rapid movement has to be sustained for less time to cover the same distance. All these treadmill measurements may seriously underestimate the practical energy cost to animals of moving over soft or otherwise difficult ground. Experiments on animals dragging loads suggest that the mechanical work performed (i.e. force × distance) multiplied by three provides an approximate estimate of the extra heat produced by the animal. The metabolic cost of activities of humans, who are cooperative subjects, has been extensively studied and may provide a guide as to what may be expected in animals. (JAMcL)

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Acylglycerol
A form of **lipid** made up of one **glycerol** molecule combined with one to three individual (not necessarily identical) **fatty acid** molecules attached to the glycerol by **ester** bonds. Acylglycerols form part of the neutral lipid fraction. (NJB)

***Ad libitum* feeding**
Feeding at will. Unlimited access to feed allows animals to satisfy their **appetite**s at all times. Synonymous with full feeding. Their intake when feeding *ad libitum* is termed **voluntary food intake**. (MFF)

Adaptation
Term implying that there is some sort of norm from which the body or system deviates in response to changes in the normal environment. Within the normal population, a range of values is seen for any particular criterion that is examined, whether it be, say, activity of an enzyme, a blood parameter or body weight. Thus there is the statistical concept of the normal distribution. Adaptation implies a shift in the normal distribution or in the values for a particular individual. The former may be a long-term phenomenon in response to, for example, climatic change where those animals best suited genetically to the change will survive. Short-term adaptation implies that the physiological systems can respond to changes in external factors. These factors include **environmental temperature**, **light** cycle or intensity, stocking

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density, the physical environment and **nutrition** (particularly in relation to energy or protein intake). In general, the term can relate to a modification that lessens the negative impact of imposed change or takes advantage of an opportunity afforded.

One major aspect relates to changes in environmental temperature. Homeothermic animals tend to have a defined range of temperature – the thermoneutral zone – within which core body temperature remains constant without any change in **heat production**. The thermoneutral zone varies for different species and stages of development and may also be modified by adaptation of an animal to prolonged exposure to an environment that falls outside the thermoneutral zone. However, within the zone, different species have a wide range of mechanisms by which they can adapt to maintain **homeostasis**. For example, poultry can increase heat loss in warm environments by increasing **blood flow** to the comb, wattles and shanks and, conversely, can reduce heat loss by reducing blood flow, changing posture and piloerection, thus improving body insulation. Pigs, individually housed, alter posture to increase or decrease heat loss and, in groups, can significantly reduce heat loss by huddling together. Environmental temperatures below the thermoneutral zone result in shivering, which is a rapid noradrenaline-induced mechanism for increasing heat production. Prolonged exposure to low temperature results in an increase in basal **metabolic rate**, due to **non-shivering thermogenesis**. This adaptation takes several weeks to complete in response to a permanent reduction in environmental temperature.

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Feed intake is increased at low temperatures and reduced at temperatures close to or above the upper limit of the thermoneutral zone. In the case of domestic fowl, food intake declines linearly across the normal range of environmental temperature (15–30°C). Stocking density and availability of trough space can also lead to marked changes in food intake. In pigs, for example, it has been observed that intakes are 10–15% higher with individually housed animals compared with those in groups. It is unclear whether this is a behavioural adaptation to boredom on the part of individual pigs or depression of intake due to **competition** in groups. However, there is a wide range of behavioural adaptations associated with changes in the physical environment, etc. For example, stereotypic behaviours such as bar-**biting** by sows tethered in stalls and reductions in tail-biting and aggression by pigs provided with the opportunity to root are negative and positive examples of such adaptations.

Of particular importance is the ability of the body systems to respond to changes in nutrition, especially in relation to energy and protein. One of the most extreme examples of response to **undernutrition** relates to studies by McCance and Mount (1960) on young pigs. These pigs were maintained for long periods on just sufficient quantities of a normal diet to maintain body weight. Whereas the **maintenance** requirement (MR) of normal piglets would be around 550 kJ kg^{-1} metabolic body weight ($W^{0.75}$), these undernourished pigs showed an MR of 250 kJ kg^{-1} $W^{0.75}$. The speed with which such changes occur in response to energy or protein deprivation was demonstrated by McCracken and

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McAllister (1984), who observed a reduction of approximately 25% in calculated maintenance requirement over a 3-week period. Changes in organ size relative to body weight have been observed during undernutrition of a wide variety of species, including poultry, pigs, cattle and sheep, and can be considered as contributing to the improved economy of the system. Conversely, increases in **energy intake** during **lactation** are associated with increased digestive organ capacity and increased metabolic rate. Similarly, offering a high-fibre (less digestible) diet to non-ruminants results in increased digestive organ size and weight, particularly in the hindgut, and increased energy supply from microbial **fermentation**.

In summary, the human or animal body has a wide range of mechanisms for coping with external stressors and a multitude of short-term and long-term adaptations have been reported, of which only a few examples have been discussed above. (KJMcC)

See also: Energy intake; Thermoregulation; Voluntary food intake

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Additives, feed

Feed additives are so numerous and heterogeneous that they almost defy precise definition. In general terms, however, a feed additive refers to low-inclusion products used in diet formulations for purposes of improving the nutritional quality of feed or the animal performance and health. A much broader description has been provided in EC regulation 1831/2003, wherein feed additives are defined as substances, microorganisms or preparations (other than feed material and pre-mixtures) which are intentionally added to feed or water to favourably influence *inter alia*: (i) the characteristics of feed or animal products; (ii) the environmental consequences of animal production; (iii) performance, health or welfare through their influence on gut microflora profile or feed **digestibility**; or (iv) to have a coccidiostatic or histomonostatic effect. Accordingly, feed additives are assigned to one or more of the following categories, depending on their functions and properties.

Technological additives (e.g. antioxidants, emulsifiers, acidifiers)
Sensory additives (e.g. flavours, pigments)
Nutritional additives (e.g. vitamins, trace minerals, amino acids, non-protein N sources)
Zootechnical additives (e.g. digestibility enhancers, gut flora stabilizers)

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Coccidiostats and histomonostats.

These additives have now become vital components in livestock and poultry diets. Lists of commonly used non-nutritional feed additives in poultry and ruminant diets are presented in Tables 1 and 2.

Table 1. Non-nutritional feed additives commonly used in poultry feeds

Additive	Examples	Reasons for use
Enzymes	Carbohydrases, phytase, protease	To overcome the anti-nutritional effects of arabinoxylans (in wheat and triticale), β-glucans (in barley) or phytate (in all plant feedstuffs) and to improve the overall nutrient availability and feed value.

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Additive	Examples	Reasons for use
Antibiotics[a]	Avilamycin, flavomycin, zinc bacitracin	To control Gram-positive, harmful bacterial species in the gut and to improve production efficiency; as a prophylactic measure against necrotic enteritis
Coccidiostats	Monensin, salinomycin, narasin	To prevent and control the clinical symptoms of coccidiosis
Pigmenting agents	Xanthophyll (natural and synthetic)	To improve the skin colour and appearance of carcasses
Antioxidants	Butylated hydroxy toluene (BHT), butylated hydroxy anisole (BHA), ethoxyquin	To prevent auto-oxidation of fats and oils in the diets

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Additive	Examples	Reasons for use
Antifungals		To control mould growth in feed; to bind and mitigate the negative effects of fungal toxins
Antibiotic replacers[b]		
i. Direct-fed microbials	Probiotics	Provision of beneficial species such as lactobacilli and streptococci
ii. Prebiotics	Fructo oligosaccharides (FOS), mannan oligosaccharides (MOS)	Binding of harmful bacteria
iii. Organic acids	Propionic acid, potassium diformate	Lowering of gut pH and prevention of the growth of harmful bacteria
iv. Botanicals	Herbs, spices, plant extracts, essential **oils**	Prevention of the growth of harmful bacteria

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Additive	Examples	Reasons for use
v. Antimicrobial proteins/peptides	Lysozyme, lactoferrin, α-lactalbumin	Prevention of the growth of harmful bacteria

[a] The use of in-feed antibiotics is banned in the European Union and several other countries. Antibiotics are included in the above list because they are still in restricted use in other countries.

[b] A multitude of compounds (individually and in combination) are being used or tested as alternatives for antibiotic growth promoters (AGP).

Table 2. Additives used in ruminant animal feeds

Additive	Examples	Reasons for use
Non-protein N sources	Urea, biuret	Added to roughage feeds which have low rumen degradable protein contents as sources of ruminally available N to promote the growth and activity of rumen microorganisms

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Additive	Examples	Reasons for use
Minerals	Limestone, dicalcium phosphate, monoammonium phosphate	Improving the mineral content of feeds (often those based on cereal grains or low-quality roughages)
Surfactants	Poloxalene, vegetable oil	To reduce the foaming capacity of rumen contents and reduce the risk of frothy bloat
Protected nutrients	Formaldehyde-treated protein, Ca soaps	A way of protecting amino acids (e.g. methionine) and unsaturated fatty acids from microbial destruction in the rumen
Antibiotic	Virginiamycin	This antibiotic helps to protect the animal against acidosis and laminitis

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Additive	Examples	Reasons for use
Direct-fed microbials	Probiotics	Provision of beneficial species such as *Lactobacillus* spp., *Bacillus* spp., *Saccharomyces cerevisae*
Prebiotics	Fructo oligosaccharides, mannan oligosaccharides, yeasts	Nutrient sources for probiotic organisms

The use of feed additives in poultry feeds is expected to increase in the future and this will be driven by ongoing changes in world animal agriculture. In particular, three groups of additives, namely exogenous enzymes, replacements for antibiotic **growth promoter**s (AGP) and synthetic amino acids, are expected to play key roles.

The potential **nutritive value** of feedstuffs is often not realized at the animal level because of the limitations imposed by the presence of a range of anti-nutritional factors and the insufficiency (or lack) of digestive enzymes to break down specific chemical linkages. The need to improve nutrient utilization is the principal rationale behind the acceptance of feed enzymes. A wide range of feed enzymes, targeting different substrates in ingredients,

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is commercially available (see the Table 3). The poultry industry is now the largest user of feed enzymes.

Table 3. Type of feed enzymes and target substrates

Enzyme	Target substrate	Target feedstuffs
β-Glucanases	β-Glucan	Barley, oats and rye
Xylanases	Arabinoxylans	Wheat, rye, triticale, barley, fibrous plant materials
α-Galactosidases	Oligosaccharides	Soybean meal, grain legumes
Phytases	Phytic acid	All plant-derived ingredients
Proteases	Proteins	All plant protein sources
Amylase	Starch	Cereal grains, grain legumes
Lipases	Lipids	Lipids in feed ingredients, lipid supplements
Mannanases, cellulases, hemicellulases, pectinases	Cell wall matrix (fibre components)	Plant-derived ingredients, fibrous plant materials

Because of the AGP ban, the poultry industry has moved

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towards alternative strategies to prevent proliferation of pathogenic bacteria, thus maintaining health and performance status and optimizing digestion in poultry. A range of alternatives have been tested to directly affect microbial communities in the digestive tract. Although these additives all have been shown to 'mimic' the working effects of AGP on gut microbiome, none of the current generation of AGP alternatives, on their own, are capable of fully replacing them. Furthermore, the reproducibility of most AGP alternatives appears low and there is a lack of consistency in performance response. Available AGP alternatives are also costlier than conventional AGP programmes.

Protein is the second costliest item in animal diets, so maximizing the efficiency of protein and amino acid utilization is important. Geneticists have done their part in providing modern strains of poultry and pigs that can produce protein gain at greater efficiencies than ever before. The challenge to the nutritionists is to sustain these improvements in genetic potential by refining the amino acid nutrition. In this context, the commercial availability of synthetic amino acids has enabled the nutritionists to meet more precisely the ideal amino acid profile and to sustain high performance levels. Currently four synthetic amino acids, namely DL-methionine, L-lysine HCl, L-threonine and L-tryptophan, are available at competitive prices. **Valine**, **leucine** and **isoleucine**, the next limiting amino acids in poultry diets, have recently become commercially available. (VR; GMcLD)

Further reading

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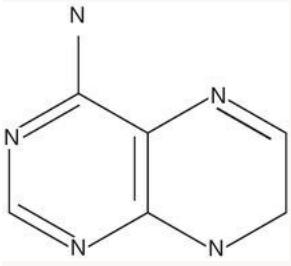
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Adenine

6-Aminopurine $C_5H_5N_5$, one of the two **purine** (adenine, **guanine**) **nucleic acid** bases found in DNA and RNA. It is also part of molecules that are essential cofactors in **metabolism**, including ATP (**adenosine triphosphate**), ADP (adenosine diphosphate), NAD (**nicotinamide adenine dinucleotide**), NADP (nicotinamide adenine dinucleotide phosphate), FAD (flavine adenine dinucleotide) and CoA (**coenzyme** A). (NJB)



Adenosine diphosphate (ADP):

see Adenosine triphosphate

Adenosine monophosphate (AMP):

see Adenosine triphosphate

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Adenosine triphosphate (ATP)
A water-soluble compound critical to cellular **metabolism**. It can store chemical **energy** for a short time (seconds to minutes) and then release that energy to support cellular processes (ATP → ADP + work + heat). The energy is derived from the electrons removed during the cellular **catabolism** of **carbohydrates**, **fatty acid**s and **amino acid**s. These electrons are used to reduce oxygen to water in the mitochondrial electron transport chain. In this process energy is stored in the terminal phosphate bond when adenosine diphosphate (ADP) is reconverted to ATP. (NJB)

Adenylate cyclase
A cytoplasmic enzyme involved in the production of the second messenger cyclic AMP (cAMP) from ATP. The cellular concentration of cAMP is increased or decreased by the action of hormones on adenylate cyclase activity. Cellular responses are modified by changes in the concentration of cAMP. (NJB)

Adhesion receptors
Receptors (which may have other functions) by which bacteria adhere to epithelial cells in the **gastrointestinal tract**. Adhesion is mediated by a specific **lectin** on either the receptor or the bacterium. (SB)
See also: Chemical probiosis; Gastrointestinal microflora; Probiotics

Adipocyte
A fat cell, a specialized cell in particular regions of the body in

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which neutral fats (**triacylglycerol**s) are stored. Adipocyte diameter can vary over threefold, depending on **lipid** content, which varies between the **adipose tissue** sites in the body. (NJB)

Adipose tissue

There are two types of adipose tissue: white and brown. White adipose tissue (WAT) is the main site of fat deposition in the animal body. Its main function is as an energy store, which accumulates in times of positive **energy balance** and is mobilized in times of negative energy balance. In addition, it protects certain internal organs against physical damage and provides thermal insulation.

The main WAT depots are subcutaneous, perinephric (perirenal), pericardial, abdominal (mesenteric and omental, sometimes also called gut and channel fat), intermuscular and intramuscular. In some **newborn animal**s there is very little WAT. It is a late-developing tissue that accumulates as animals approach their mature body size.

The main cell type found in adipose tissue is the **adipocyte**. Adipocytes range in size from 20 to 200 μm. The size and number of adipocytes vary between adipose tissue depots. Intermuscular adipose tissue contains a large number of small adipocytes whereas perinephric adipose tissue contains a small number of large adipocytes.

The main metabolic processes in adipose tissue are: (i) **fatty acid synthesis** and **triacylglycerol** synthesis, jointly known as **lipogenesis**; and (ii) **lipolysis**, the breakdown of triacylglycerols

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to yield **glycerol** and non-esterified fatty acids (NEFA). Adipose tissue is the major site of *de novo* fatty acid synthesis in ruminant species. In some non-ruminant mammals, fatty acid synthesis occurs in both adipose tissue and liver; whereas in avian species, adipose tissue is not an important site of fatty acid synthesis and triacylglycerols are synthesized from fatty acids of dietary origin or synthesized in the liver. In ruminant adipose tissue, **acetate** is the primary substrate for fatty acid synthesis. In non-ruminant mammals and birds, **glucose** is the major substrate.

Brown adipose tissue
(BAT) is a specialized form of adipose tissue. Its function is the generation of heat by the oxidation of fatty acids by the process of **non-shivering thermogenesis**. It is particularly important in neonatal animals. In some species (e.g. lambs) the ability to generate heat by non-shivering thermogenesis is lost within 2–3 days of birth; in others (e.g. rats) this property persists into adult life. Some species, such as the pig, do not have BAT and are particularly susceptible to cold immediately after birth. BAT is pale brown in appearance, due to the well-developed blood supply and to the presence of numerous mitochondria in adipocytes. It is found in a number of anatomical locations, for example in interscapular, axillary and perinephric regions. Its ability to generate heat is due to the 'uncoupling' from ATP synthesis of mitochondrial electron transport by uncoupling proteins (UCPs). These proteins cause the disruption of the proton gradient across the inner mitochondrial membrane. (JRS)

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Adrenal

The adrenal gland is located above the anterior portion of the kidney. It is made up of two distinct anatomical and functional parts: the cortex and medulla. The cortex secretes three types of hormones: **glucocorticoids**, mineralocorticoids and androgens. The medulla produces and releases the catecholamine hormones, **dopamine**, **norepinephrine** and **epinephrine**. (NJB)

Adrenaline:

see Epinephrine

Adverse effects of food constituents

Any of the major food constituents (protein, carbohydrate, fat, mineral, vitamin, fibre, water) can induce adverse effects if they are not balanced for the requirements of the consumer. If the constituents are not balanced, the food may be avoided or, if it is the sole food available, intake will be low. One example is fibre which, being indigestible or only slowly digested (by microbes in the digestive tract), imposes physical work on the digestive tract as well as limiting the capacity to eat food. Other examples are specific plant toxins that interfere with **metabolism**, reducing the overall satisfaction the animal derives from each unit of food eaten. Many plants have evolved these to avoid being eaten. Another way in which food can have adverse effects is by the heat produced by its ingestion, **digestion** and metabolism, especially in a hot environment in which this extra heat is difficult to lose. A diet excessively high in protein can have such adverse effects due to the heat produced in the **deamination** of the excess **amino acid**s.

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Excessive concentrations of individual minerals, particularly in plants that accumulate the minerals as a means of protection, can induce specific toxicity symptoms or adverse effects by disturbing the mineral balance. Plants with a high water content, such as young herbage, may adversely affect the intake of dry matter, particularly if requirements are high and intake capacity is limited. (JMF)

Aerophagia

The consumption of excessive air during the eating of food. This may happen when food is eaten too quickly or the consumer vocalises while eating. (CJCP)

Aflatoxins

A family of bisfuranocoumarin **metabolite**s of toxigenic strains of *Aspergillus flavus* and *A. parasiticus*. The name derives from *Aspergillus* (a-), *flavus* (-fla-) and toxin. The major aflatoxins (AFs) are AFB1, B2, G1 and G2. The AFs are bioactivated by hepatic enzymes to toxic metabolites including AFB1-8,9-epoxide, and AFM1 (in milk). The AFs occur in the field in seeds (maize, cottonseed, groundnuts) and in storage of grains (maize, soybeans).

Biological effects are liver damage (acute and chronic) and liver cancer (chronic), reduced growth, impaired **lipid absorption**, with induced deficiencies of vitamins A, D and K, causing impaired blood coagulation, haemorrhage and bruises (poultry), and adverse reproductive effects. Differences in susceptibility between species of animals relate to the activity of hepatic **cytochrome** P450 enzymes, which bioactivate AF to the toxic metabolites. Rabbits,

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ducks and turkeys are highly susceptible to AF toxicity, while rats and sheep are less sensitive. Chronic AF intoxication is caused by 0.25 ppm (dietary) in ducks and turkeys, 1.5 ppm in broilers, 0.4 ppm in swine and 7–10 ppm in cattle. AF metabolites in liver cross-link DNA strands, impairing cell division and **protein synthesis**. AFB1 metabolites form DNA adducts, causing liver cancer. AF has immunosuppressive effects, impairing cell-mediated **immunity**. (PC)

See also: Mycotoxins

Age at weaning

This term is applied to young mammals, and it can be used in two ways: to mean either the age at which the young animal is separated from its mother, but may still be given milk or milk substitute; or the age at which any natural or artificial milk is withdrawn from the ration. (PJHB; GMcLD)

Agglutinins:

see Haemagglutinins

Agroforestry/silvopastoral system

A combination of trees with agricultural crops and livestock can have significant benefits for the environment and water use. When trees are combined with grazing in silvopastoral systems, this can provide benefits to parasite control in the animals, shade and diversification of feed resources. However, establishment of **legumes** and other **forage** for grazing can be hindered by low light levels under the canopy of the trees, particularly if it is almost

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closed. If properly managed, agroforestry can ensure good agricultural yields while maintaining biodiversity and promoting social equity. Agroforestry is seen as an alternative to large-scale conventional agriculture with the potential to deliver transformational agricultural practices. (CJCP; DM)

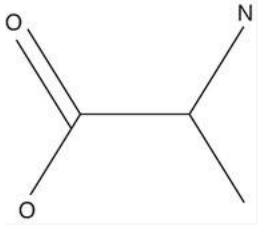
Further reading

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Alanine

An **amino acid** ($CH_3{\cdot}CH{\cdot}NH_2{\cdot}COOH$, molecular weight 89.1) found in protein. It can be synthesized in the body from **pyruvate** and an amino donor such as glutamic acid. Substantial quantities of alanine are synthesized in gut **mucosa** and muscle, and the alanine not used for **protein synthesis** is transported to the liver where the enzyme alanine **aminotransferase** converts alanine to pyruvate. Mitochondrial pyruvate in the liver can either be used in the **TCA cycle**, or it can be converted (carboxylated) to **oxaloacetate**, some of which is subsequently reduced to **malate**, some transaminated to aspartate, and some decarboxylated to phosphoenolpyruvate. All three of these compounds can escape the mitochondrion and enter the cytosol to be used for **gluconeogenesis**. Integration of these processes involving muscle and liver tissue is often referred to as the glucose–alanine cycle. (DHB)

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See also: Gluconeogenesis; Pyruvate

Albumin

Originally classified as protein that was soluble in a 50% saturated solution of ammonium sulphate. Albumins (five separable proteins) account for approximately half of the protein in **blood plasma**. Plasma albumin plays an important role in regulation of osmotic pressure. Bilirubin, free **long-chain fatty acid**s and a number of steroid hormones are found bound to albumin. (NJB)

Alcohols

Having a functional ·COH group. The group includes primary, secondary and tertiary alcohols, with one, two and three ·COH groups. Long-chain alcohols (up to 30 carbons) are found as esters with **palmitic acid**. **Glycerol** and **cholesterol** are alcohols. **Ethanol**, $CH_3{\cdot}CH_2OH$, is an alcohol produced by **fermentation** and can be used as a source of metabolic energy. It has a caloric value of 29.7 kJ g^{-1} or 23.4 kJ ml^{-1}. (NJB)

Aldehydes

Having a functional ·CHO group. Many six-carbon (e.g. **glucose**), five-carbon (e.g. ribose) or four-carbon **sugars** (e.g. erythrose) have a functional aldehydic carbon. Aldehydes are intermediates when a functional alcohol carbon is converted to an acid carbon.

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Aldehydes such as **formaldehyde** and **acetaldehyde** are highly toxic and react with tissues. (NJB)

Aldosterone
A 21-carbon steroid hormone synthesized in the **adrenal** cortex and classified as a mineralocorticoid. It plays a role in sodium retention and potassium excretion by the kidney. (NJB)

Aleurone
The single outer layer of living cells surrounding the **endosperm** of cereal grains. Rich in protein, these cells synthesize the enzyme α-**amylase**, which is responsible for the breakdown of the stored starch in the endosperm into **maltose** and **glucose** during **germination**. The aleurone layer remains attached to the bran during milling. (ED)
See also: Cereal grains

Alfalfa:
see Lucerne

Algae
Plant-like diverse aquatic photosynthetic, and nucleus-bearing organisms that lack the true roots, stems, leaves and specialized multicellular reproductive structures of plants. They possess **chlorophyll** in combination with accessory photosynthetic pigments and have minimal differentiation into defined tissues or organs. They occur in a variety of forms and sizes and range from single microscopic cells (picoplankton that are between 0.2 to 2 micrometres in diameter) to among the tallest organisms known

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(giant kelps, c. 60 m in length) and are mainly aquatic, with some tolerating periodic or prolonged exposure to air. Algae are found in a range of aquatic habitats, both freshwater and saltwater, and they have potential as food and fuel in the future. Increasingly algae meal is used in aquatic animal feeds, for example in the diets of abalone, sea cucumber, marine shrimp, marine fish fry, etc., since it contains a high level of sticky algal **polysaccharide**s (Barsanti and Gualtieri, 2014) and a high level of protein (Li and Wu, 2020) in most single microscopic cells. The nutritional potential of algae additives in poultry nutrition includes improvement of the **antioxidant** activity of the blood, increase of immunoglobulins and strengthening of the immune system of the host, and use as a valuable phytogenic additive for partially replacing in-feed antibiotics (Tufarelli *et al*., 2021; Feshanghchi *et al*., 2022).

Some algae can reduce the output of **methane** from the rumen and hence greenhouse gases, without any negative effects on the productivity and health of ruminants. This could be one strategy to help prevent global climate change, but there is a need for more studies of suitable species of algae for commercialization and the determination of the optimal dosage in feeding domestic animal (McCauley *et al*., 2020). (CB; DB; QS; AS; BH-G; CJCP)

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Algal toxins

Toxins of algal origin (also called phycotoxins) are most often produced by unicellular marine flagellates, particularly dinoflagellates, but also by members of other major flagellate algal groups, such as raphidophytes, haptophytes and pelagophytes. A few species of the diatom genus *Pseudo-nitzschia* synthesize a potent neurotoxin, domoic acid. In fresh and brackish waters, cyanobacteria ('blue-green algae') are often implicated as toxic algal contaminants in drinking-water supplies for humans and livestock. In the **marine environment**, cyanobacterial toxins are responsible for 'net-pen **liver disease**' in caged salmonids. When present in high abundance or during periods of rapid growth

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('blooms'), algae can cause water discolorations known as 'red tides', usually in fresh or coastal waters – these phenomena are not always associated with toxicity. Toxic events associated with algae may be divided into two types: (i) those caused by the production of specific toxic **metabolite**s; and (ii) those resulting from secondary effects, such as post-bloom **hypoxia**, **ammonia** release, or other artefacts of decomposition on marine flora and fauna. Phycotoxins and their causative organisms are globally distributed in marine coastal environments, from the tropics to polar latitudes, and few areas are exempt from their effects, which may be expanding in geographical extent, severity and frequency on a global basis. In a few cases, this may be linked to eutrophication, but there is no general hypothesis to explain all such events.

Among the thousands of extant species of marine microalgae, only several dozen produce highly potent biotoxins that profoundly affect the health of marine ecosystems, as well as human and other animal consumers of seafood products (see table). As an operational category, certain toxic microalgae are often called 'fish-killers' because of their potent direct effects on fish, particularly in **aquaculture** systems. Such toxins are poorly characterized and the mechanism of action is often not well understood, although the toxic effects are typically mediated through the gills. In contrast, the toxins associated with human illnesses by consumption of contaminated finfish (e.g. ciguatera fish **poisoning**, clupeotoxicity) and paralytic, amnesic, neurotoxic and diarrhoeic shellfish poisoning (PSP, ASP, NSP and DSP, respectively) caused by ingestion of **shellfish** are much better known. The phycotoxins

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responsible for these syndromes constitute a heterogeneous group of compounds, affecting a variety of receptors and metabolic processes, acting as Na^+-channel blockers, Ca^{2+}-channel activators, **glutamate** agonists, phosphatase inhibitors, etc. These pharmacologically active compounds also include the emerging problems associated with 'fast-acting toxins' of poorly defined human health significance, such as gymnodimine and spirolides. Many of the phycotoxins can be propagated within marine food webs from **phytoplankton** through **zooplankton** (copepods, **krill**), then from ichthyoplankton to large carnivorous fish, and even marine birds and mammals. Toxin accumulation within fish stocks (e.g. anchovies) harvested for fish meal production may even be a risk for aquaculture of certain species. Except in bivalve shellfish, where oxidative and reductive transformations mediated by both enzymatic and non-enzymatic processes have been determined, and in the case of biotransformation within fish tissues of ciguatoxin precursors from dinoflagellates, metabolism of phycotoxins is poorly understood. (AC)

Acute toxicity (LD_{50}) of selected phycotoxins after intraperitoneal injection into mice. Only major toxin analogues found in shellfish or finfish, and/or the corresponding toxigenic microalgae, for which the pathology in mammals is known or highly suspected are included. Note that multiple derivatives of varying toxicity are common for most toxin groups. Data summarized from citations in Hallegraeff *et al*. (2002).

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Toxin group	Analogue	**Toxicity** (μg kg^{-1})	Primary pathology
Azaspiracid	AZA	200	Gastrointestinal
	AZA2	110	Gastrointestinal
	AZA3	140	Gastrointestinal
	AZA4	470	Gastrointestinal
	AZA5	1000	Gastrointestinal
Brevetoxin	BTX-B1	50	Neurological
	BTX-B2	300	Neurological
	BTX-B3	> 300	Neurological
Ciguatoxin	CTX1	0.25	Neurological
	CTX2	2.3	Neurological
	CTX3	0.9	Neurological
Gambiertoxin	GTX-4B	4.0	Neurological
Maitotoxin	MTX1	0.05	Neurological
	MTX1	0.05	Neurological
	MTX2	0.08	Neurological
	MTX3	0.1	Neurological

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Toxin group	Analogue	**Toxicity** (μg kg^{-1})	Primary pathology
Okadaic acid	OA	200	Gastrointestinal; tumour promotion
Dinophysistoxin	DTX1	160	Gastrointestinal
	DTX3	500	Gastrointestinal
Gymnodimine		96	Neurological(?)
Pectenotoxin	PTX1	250	Hepatotoxic
	PTX2	230	Hepatotoxic; gastrointestinal
Saxitoxin	STX	11	Neurological
	NeoSTX	12	Neurological
Gonyautoxin	GTX1	11	Neurological
	GTX2	32	Neurological
	GTX3	16	Neurological
	GTX4	13	Neurological
Spirolide	B	200	Neurological (?)
	des-methyl-C	40	Neurological (?)

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Toxin group	Analogue	**Toxicity** (μg kg^{-1})	Primary pathology
Yessotoxin	YTX	100	Cardiotoxic

See also: Marine environment; Marine toxins

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Alimentary tract:

see Gastrointestinal tract

Alkali disease

A chronic form of selenosis, which occurs in cattle and horses after prolonged consumption of plants with high **selenium** concentrations. It is characterized by alopecia, hoof dystrophy, lack of vitality, emaciation, poor quality hair, sloughing of the hooves and stiff joints. Although not widespread, it is of major importance in some localized areas, such as parts of the Great Plains of North

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America. (CJCP)

Alkali treatment of feeds

A method of treating feeds to improve their **digestibility** and/or storage life. It is used with cereal grains, and with low-quality (i.e. highly lignified) forages such as cereal straws. The principle behind the treatment of fibrous materials with alkali is that it hydrolyses **ester** bonds between the cell wall **hemicellulose** and **lignin**, thus reducing the capacity of lignin to protect the cell wall **polysaccharide**s and rendering the material more susceptible to rumen microbial degradation.

Early techniques in the late 19th century were industrial processes requiring both heat and pressure. However, in the **Beckmann process**, the first on-farm methodology, cereal straw was soaked for up to 2 days in a dilute (1.5%) sodium hydroxide solution, then washed to remove any excess alkali. This technique improved degradability but considerable soluble (i.e. potentially degradable) material was lost during the washing process. The use of more concentrated solutions, either sprayed on to chopped or shredded straw, or applied by dipping baled **straw** into vats which was then allowed to 'mature' for up to a week prior to feeding, reduced these losses. The delay ensured that residual sodium hydroxide had reacted with carbon dioxide, to form sodium carbonate.

The response to treatment varies inversely with the quality of the untreated straw. To realize the potential improvement in degradability, sufficient **ruminally available nitrogen** (RAN) and sulphur must also be provided when the treated straw is fed.

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Sodium hydroxide is the most commonly applied alkali, though potassium hydroxide (often as wood ash), calcium hydroxide, alkali **hydrogen peroxide** and calcium oxide (lime) have all been used. There are some disadvantages of this technique. Animals fed these treated materials increase their water consumption (a potential drawback in arid regions), leading to increased urine output, which generates a problem with quantity and disposal of bedding. The high urinary output of sodium may damage soil structure. Unreacted sodium hydroxide can cause ulceration around the mouth.

Alkalis applied to cereal grains disrupt the integrity of the seed coat, increasing the accessibility of the starch to the **rumen microorganisms** without the requirement for physical processing. Conventionally harvested grain is blended with sodium hydroxide, water is then added and the material mixed. This reaction produces considerable heat, following which the grain should be remixed prior to storage. The amount of sodium hydroxide required for optimum digestibility varies with the fibre content of the grain husk. About 25 kg t^{-1} is used with wheat and 40–45 kg t^{-1} for oats. Treated grain can be fed direct or after mixing with water, which causes the seed coat to swell and rupture. The slower release of starch relative to that from ground or rolled grain interferes less with fibre degradation, allowing higher intakes of **roughage** to be maintained. Residual alkali helps to maintain rumen pH, reducing the incidence of acidosis when high levels of grain are offered. An additional benefit is that sodium hydroxide treatment has a preservative effect on high-moisture grain,

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reducing both bacterial and fungal growth. Offered to cattle, treated grain maintains a higher rumen pH, tends to increase the acetic:**propionic acid** ratio, and reduces the incidence of rumenitis in comparison with cattle fed conventionally processed material. Similarly, when high levels are offered to dairy cows, depressions in milk fat content are minimized and roughage intake is maintained. (FLM; GMcLD)
See also: Ammonia treatment

Alkaline phosphatase
An enzyme found in intestinal contents that catalyses the release of phosphate from a wide variety of phosphorylated cellular **metabolite**s and cofactors (e.g. sugar phosphates, **nucleotides**, ATP). It is also found in tissues such as liver, bone and kidney, which are sources of plasma alkaline phosphatase. In bone it is thought to contribute to crystal formation. (NJB)

Alkaloids
A class of **plant secondary compound**s generally characterized as containing at least one basic heterocyclic nitrogen atom and usually possessing some type of physiological activity. They are found in approximately 15% of all vascular plants. Alkaloids are a heterogeneous group of compounds, subdivided and further classified by a similar basic chemical structure containing the nitrogen atom. Alkaloids comprise several thousand different structures and possess a wide variety of physiological activities and potency. Some of the key sources of plant material containing alkaloids affecting animal **nutrition** are listed in the table.

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(DRG)

Key sources of plant alkaloids

Alkaloid class	Plant or organism	Physiological effect
Diterpene	*Delphinium*	Neurotoxic
Indole	*Claviceps*, *Peganum*, *Phalaris*	Neurotoxic, vascular
Indolizidine	*Swainsona*, *Astragalus*, *Physalia*	Glycosidase inhibitor, teratogenic
Piperidine	*Conium*, *Lupinus*, *Nicotiana*	Neurotoxic, teratogenic
Pyridine	*Nicotiana*	Neurotoxic
Pyrrolizidine	*Senecio*, *Crotalaria*, *Heliotropium*	Hepatotoxic, pneumotoxic, photosensitization
Quinolizidine	*Lupinus*, *Thermposis*, *Cytisus*, *Baptisia*	Teratogenic, myotoxic, neurotoxic
Steroidal	*Solanum*, *Veratrum*, *Zigadenus*	Teratogenic, cholinesterase inhibitor
Tropane	*Datura*, *Atropa*, *Hyoscyamus*	Neurotoxic, blindness

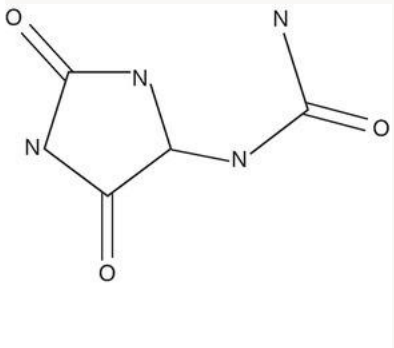
Alkalosis

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A pathological condition in which the arterial plasma pH rises above 7.4. The range of alkalosis that is compatible with life is 7.4–7.7. An example is metabolic alkalosis resulting from excessive loss of gastric acid during prolonged vomiting. This also involves considerable loss of potassium in the urine. Treatment is by intravenous infusion of isotonic saline containing supplementary **potassium chloride** to correct both the chloride and potassium deficits. The bicarbonate excess corrects itself. (ADC)

All-*trans* retinoic acid
A metabolic derivative of **vitamin A** (all-*trans* retinol) or β-carotene via the intermediate formation of all-*trans* retinol. Retinoic acid interacts with nuclear retinoic acid receptors (there are at least six) to affect appropriate genes, which results in cellular differentiation. (NJB)

Allantoin
$C_4H_6N_4O_3$, a degradation product of **purines**. It is an intermediate in the production of allantoic acid from uric acid that can be converted in part to urea except in birds and reptiles. (NJB)



Allowance nutrient requirements The best estimates for the

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particular species, age and production system based on the available scientific evidence. The term 'allowance' takes account of the need to include a **safety factor** on top of 'requirements' to allow for variations in environmental conditions and individual variability in requirements. Allowances are usually set at 5–10% above requirements. (KJMcC)

Aloe (*Aloe vera*)

A plant with thick (fleshy) and long leaves, recognizable spots, blades at the end of the leaf, yellow-green flowers that grows in temperate and tropical conditions.



Aloe vera as a cultivated crop. Photo courtesy of Mathias Isenberg. Licensed under CC BY-ND 2.0.

This plant contains a small amount of essential **oil** with a

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special smell belonging to aloes. It contains 12–13% resin. A special compound in aloe vera is called aloe emodine, with the molecular formula $C_{15}H_{10}O_5$, which is also known as frangula emodine, a methyltrioxyanthraquinone. The common name of the active compound of this plant is aloin (Zargari, 1997). This plant is one of the oldest medicinal plants, but in the 1990s the industrial use of this plant led to the expansion of its production, so that in 2018 the trade value of this plant in the world was estimated at US$1.6 billion. The presence of more than 75 bioactive compounds such as **polysaccharide**s (the most important of which is acemannan), **phenolic compound**s, anthraquinones and phytosterols indicate the value of this plant (Thakare , 2020; Martínez-Burgos *et al*., 2022). The application of aloe vera is wide; it can be mentioned in cosmetic moisturizers, toothpaste, food flavouring, compounds and preservatives of medical products. The properties of this plant include wound healing, anti-inflammatory, immunogenic, anti-diabetic, natural antioxidant, laxative, antibacterial, antifungal, antiviral and anti-tumour effects (Martínez-Burgos *et al*., 2022). A review of scientific literature shows that supplementing poultry diets with aloe vera (0.1–1%) can increase body weight by 7–25%, improve and strengthen the immune system by 10–50%, and reduce the number of intestinal bacteria by 24% and 30%, while increasing the population of beneficial bacteria in the gut. These results indicate the usefulness of aloe vera extracts as a natural supplement without side effects to maximize poultry productivity (Ebrahim *et al*., 2020). (AS, BH-G, CJCP)

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Alpaca meat, effects of nutrition:
see South American camelids, effects of nutrition on meat quality

Aluminium

The most abundant metal in the earth's crust. Its low solubility ensures that the concentration in most plant and animal tissues remains low. The only evidence of toxicity in farm animals comes from its interaction with essential nutrients, in particular phosphorus and magnesium in ruminants and iron in poultry, possibly leading to deficiencies in those elements in range livestock. Neurobehavioural disorders have been demonstrated at high aluminium intakes in laboratory animals by those seeking to determine the role of aluminium in the development of Alzheimer's disease in humans. (CJCP)

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Amadori products

Intermediates in the reaction of phenylhydrazine with monosaccharides (e.g. glucose) to form glucose phenylosazones. Amadori products are undefined intermediates in Amadori rearrangement in the production of, for example, **glucose** phenylosazone from glucose phenylhydrazone. (NJB)

Amaranth

There are 75 species in the *Amaranthus* genus. According to the report of the Food and Agriculture Organization (FAO), amaranth could contribute significantly to meeting human nutritional requirements (Li *et al*., 2018). The World Health Organization (WHO) considers amaranth a neglected and underutilized species (NUS), which could improve food security and contribute to climate change mitigation (FAO, 2018).



Cultivated crop of *Amaranth opopopeo*. Photo courtesy of Photofarmer. Licensed under CC BY 2.0.

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Several species have edible leaves, such as *Amaranthus tricolor*, *A. dubius* and *A. lividus*. In addition to leaves, some species have valuable edible grain, such as *A. hybridus*, *A. cruentus*, *A. caudatus*, and *A. hypochondriacus* (Cai *et al*., 2004). The amaranth grain has a high protein content relative to many other plant-sourced foods and has a **metabolizable energy** value similar to that of cereals (Hosseintabar-Ghasemabad *et al*., 2020). Amaranth grain protein consists mainly of albumin (48.9–65%) and glutelin (22.4–42.3%), **globulin** (13.7–18.1%) and prolamin (1–2.3%). It is a good source of some **amino acid**s such as **lysine**, **methionine** and **arginine** in animal nutrition (Cai *et al*., 2004). In recent years, the diversity and abundance of amaranth's bioactive compounds have attracted the attention of researchers and the health benefits of amaranth have been investigated (Tang and Tsao, 2017). Due to the challenges of providing squalene from marine sources (whales and ocean sharks), amaranth is of interest as a rich source of squalene in plants. Squalene has significant roles in medicine, as well as in chemical (in the formulation of lubricants) and pharmaceutical industries (in the formulation of cosmetics and corona vaccines). Amaranth is **gluten**-free, which makes it useful for coeliac patients. It is also recommended in the formulation of baby food and for high-risk communities affected by AIDS, hepatitis and malaria (Cai *et al*., 2004; Tang and Tsao, 2017). The anti-cancer properties of the amaranth grain are attributed to the presence of compounds such as lunasin, amaranthine, isoamaranthine, some **tocopherol**s and **tocotrienol**s, squalene, **lectin**, **resistant starch** (RS) and phytasmic compounds. The

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leaves contain **carotenoid**s, such as **lutein** and beta-carotene with anti-cancer properties. Anti-obesity properties and reduction of **cholesterol** and atherogenic index (LDL/HDL) are attributed to the fibre, squalene, **vitamin E** and B **isomer**s and isoprenoids in amaranth (Paśko *et al*., 2011; Tsao and Tang, 2017). Anti-diabetic properties of amaranth are thought to be due to the presence of dipeptidyl **aminopeptidase** IV (DPP IV) and 20-hydroxyecdysone (20HE) (O'Harte *et al*., 1999; Tsao and Tang, 2017). In 1975, the National Academies of Science, Engineering and Medicine of the USA listed amaranth as a feed ingredient in animal nutrition, supported by research on poultry (broilers, laying hens, turkeys and quails), ruminants and **aquaculture** (Peiretti, 2018). (AS, BH-G, CJCP)

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Amide

A compound with the specific carbon–nitrogen linkage R·CON·R. The peptide bond between amino acids in proteins is an amide linkage. Familiar amides are the amino acids **asparagine** and

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glutamine in which an **amino nitrogen** (·NH_2) is linked to a carboxyl-carbon, e.g. asparagine, $NH_2CO{\cdot}CH_2{\cdot}CH(NH_2){\cdot}COOH$. (NJB)

Amine

A compound with the specific carbon–nitrogen linkage R·CNH_2. The simplest amine is **methylamine** ($CH_3{\cdot}NH_2$) in which one of the hydrogens of ammonia has been replaced by a methyl ($CH_3{\cdot}$) group. Free **amino acid**s can be considered as amines. Some amines produced by **decarboxylation** of amino acids or modified amino acids are precursors of active substancees (e.g. **histidine** to **histamine**, 5-hydroxy-**tryptophan** to **serotonin** etc.). (NJB)

Amino acid

Organic substance containing both amino and acid groups. All amino acids consist of the elements C, H, N and O, and some have the elements S, P, I and Se. An acid group in a natural amino acid can be the carboxyl (-COOH; e.g. **alanine**), sulfonic acid (-SO_3H; e.g. **taurine**), phosphoric acid (-PO_4H_2; e.g. phosphoethanolamine), or phosphonic acid (-PO_3H_2; e.g. 2-aminoethylphosphonte) group. Amino acids are readily ionizable in an aqueous solution to form a structure known as a dipolar ion or zwitterion, with both positive and negative electrical charges. The different carbon atoms of amino acids are named in sequence according to the Greek alphabet. If the amino group is linked to the ß-, γ-, δ-, or ε-carbon, the amino acid is designated a ß-, γ-, δ-, or ε-amino acid, respectively. Examples of natural α-, ß-, γ-, δ-, or ε-amino acids are **alanine**, β-alanine, γ-**aminobutyric acid**, 5-

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aminovaleric acid and 6-aminocaproic acid, respectively. (GW)
See also: individual amino acids

Amino acid metabolism

Although there are hundreds of naturally occurring amino acids, only 20 are normally found as constituents of protein. Other amino acids not found in protein are products (e.g. **taurine**) or intermediates (e.g. **ornithine** or **citrulline**) in essential metabolic processes. Proteinogenic amino acids have the general formula $R{\cdot}CH(NH_2){\cdot}COOH$. In solution they are 'zwitterions', meaning that the $\cdot COO^-$ is negatively charged and the $\cdot NH3^+$ is positively charged. The metabolism of amino acids involves their incorporation into a wide variety of proteins, their release from protein during **protein turnover**, their use in the production of essential peptides (e.g. **glutathione**) as precursors of other amino acids and essential **metabolite**s, and as a source of energy via **gluconeogenesis** or ketogenesis. In the body approximately 1% of all amino acids are found as free amino acids, while 99% are integrated into protein, with a small fraction found as polymers such as peptides and **hormone**s.

The main source of amino acids for animals is the **diet**, though in some animals (especially ruminants) amino acids are also produced by gut microflora from dietary amino acids (i.e. one amino acid is metabolized to a different amino acid by the microbes) and non-amino acid precursors during fermentative **digestion**. In **foregut** fermenters, the microbially synthesized protein continues through the digestive tract, and is subject to

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digestion and the amino acids absorbed in the same manner as dietary protein. In hindgut fermenters, **microbial protein** synthesis takes place after the gastric **stomach**, and therefore microbial protein digestion and amino acid utilization by the animal is limited. Some animal species (e.g. rabbits, hamsters and guinea pigs, among others) engage in caecotrophy to further extract the amino acids from microbial protein and other nutrients (*see* Coprophagy). Amino acids are absorbed from the **small intestine** as free amino acids or as di- and tripeptides and released into the **blood** mostly as free amino acids but some peptides. Cellular uptake of amino acids is dependent on both **sodium**-dependent and sodium-independent transporters.

For non-ruminant animals, dietary amino acids are classified as being dispensable (or nutritionally non-essential; i.e. can be synthesized at rates sufficient to meet the metabolic need), conditionally indispensable (i.e. can be made from the basic carbon skeleton with **amino nitrogen** provided by reactions such as **transamination**) or indispensable (or nutritionally essential; i.e. the carbon skeleton cannot be synthesized by the animal and must normally be supplied fully formed in the diet). The dispensable amino acids are **alanine** and aspartate, because their precursor carbon skeletons are unlikely to be limiting under normal metabolic conditions. The conditionally indispensable amino acids are **arginine** (indispensable for birds, fish and young mammals), **aspartate, glutamine**, **glutamate**, **glycine**, **proline,** and **serine**. The indispensable amino acids are **histidine**, **isoleucine**, **leucine**, **lysine**, **methionine**, **phenylalanine**, threonine,

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tryptophan and **valine**. Often included in this category are the semi-indispensable amino acids, **cysteine** and **tyrosine**, which can be synthesized by animals from methionine and phenylalanine, respectively. For **ruminant animal**s, the same classification applies but a large proportion of the amino acids required can be derived from microbial synthesis in the rumen.

The limitation to synthesis of indispensable amino acids is the ability to synthesize the carbon skeleton, or to transaminate the alpha-**keto acid**. Within the body, glutamate is synthesized by the reaction of α-ketoglutarate with ammonium or an existing amino group from another amino acid. The general process of synthesis of some (but not all) dispensable amino acids begins with transamination or amidation reactions. An amino group is transferred from an existing amino acid to an alpha-keto acid arising from metabolic pathways within the body to produce a new amino acid.

There is no long-term storage of free amino acids in the body. Rather, individual amino acids in excess of the requirement for **protein synthesis** or use for the formation of non-protein metabolites are catabolized.

The carbon skeleton of the glucogenic amino acids (alanine, arginine, **aspartic acid**, **cysteine**, glutamic acid, glycine, histidine, methionine, **proline**, serine, threonine and valine) provides precursors for the production of **glucose** via the **citric acid** cycle (*see* Gluconeogenesis). In many species, both the liver and kidneys are involved in the production of glucose from amino acids and from three-carbon intermediates (**pyruvate** and

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lactate) from glucose **catabolism**. The ketogenic amino acids (leucine and lysine) provide (acetyl-CoA) that is the precursor of **ketone** bodies or give rise to them directly (acetoacetate). Depending on the metabolic pathways used, some amino acids can give rise to either type of intermediate and are thus both glucogenic and ketogenic (isoleucine, phenylalanine, tryptophan and tyrosine).

The nitrogen from amino acid catabolism in mammals is excreted in urine as **urea** (CN_2H_4O) and ammonium ion (NH_{4+}). The production of urea occurs primarily in the liver and involves five enzymes, two of which are in the mitochondrial matrix. This subcellular division in the site of urea production requires transporters (ornithine/citrulline, **malate**, aspartate, **glutamate**) located in the membrane of the mitochondrion and gives rise to the potential for transporter control of urea synthesis. Other nitrogen-containing compounds found in urine (e.g. **creatinine**) are not part of a dedicated nitrogen excretion pathway. Birds lack carbamoyl-phosphate synthetase I and other enzymes, and therefore lack a functional **urea cycle**. In birds, the main end-product of nitrogen excretion is uric acid ($C_5H_4N_4O_3$). Production of uric acid requires the transfer of two single-carbon units via **tetrahydrofolate** and thus competes with other systems requiring one-carbon units as part of their **metabolism**. Fish primarily excrete ammonia, but under certain conditions may excrete some nitrogenous waste as urea.

The main site of catabolism of most amino acids is the liver but the catabolism of the transaminated **branched-chain amino acid**s may involve both muscle and liver. On a whole-body basis,

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the capacity for **transamination** with subsequent production of the branched-chain alpha-ketoacids is higher in muscle while the capacity to catabolize the branched-chain alpha-ketoacids via a branched-chain alpha-ketoacid **dehydrogenase** is greater in the liver. Another example of inter-organ cooperation is seen in the transport of nitrogen from amino acid catabolism in muscle to the liver via the 'alanine cycle'. Nitrogen from the branched-chain amino acids and other sources is combined with pyruvate to produce alanine, which is transported to the liver; the nitrogen can then be incorporated into aspartate and glutamate and then into urea.

A number of amino acids are precursors of such essential products as haem, **purine**, **pyrimidine**, hormones and **neurotransmitter**s. Arginine reacts with glycine and, following a reaction involving *S*-adenosyl methionine, gives rise to **creatine**, which is involved in **adenosine triphosphate** recycling. Lysine in proteins can be methylated by ***S*-adenosylmethionine** in a reaction catalysed by specific methyltransferases to **trimethyllysine** which, after the protein is broken down, becomes part of **carnitine**, which is involved in transport of **long-chain fatty acid**s into the mitochondrion and other functions. Histidine gives rise to **histamine**, which plays a role in local immune responses and neurotransmission. Histidine bound in certain proteins (e.g. **actin** and **myosin**) is methylated by *S*-adenosylmethionine to form 3-**methylhistidine** which, upon **protein degradation**, is released but cannot be reused for protein synthesis. Because it is quantitatively excreted in the rat

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and human, it has been used to estimate muscle protein catabolism. Histidine, with β-alanine, forms the dipeptide **carnosine**, which has **antioxidant** and other functions. The dipeptide anserine (a potential neuroprotectant) contains β-alanine and 1-methylhistidine, and is formed by the **methylation** of carnosine. Phenylalanine is a precursor of tyrosine, which provides the basic structure for L-3,4-dihydroxyphenylalanine (DOPA), the precursor for the neurotransmitters **dopamine**, **epinephrine** and **norepinephrine**. Tryptophan is converted into the vitamin **niacin** in many species; after conversion to 5-hydroxytryptophan, it can be metabolized to the neurotransmitter **serotonin**. Methionine, via its conversion to *S*-adenosylmethionine, is a source of methyl carbons for numerous **methylation**s. Additionally, via conversion to *S*-adenosylmethionine, methionine provides **sulphur** for the biosynthesis of cysteine (the carbon comes from serine), and the $-(CH_2)_3\text{-}NH_3^+$ group for the biosynthesis of spermidine and spermine. (DRK)

See also: Protein metabolism

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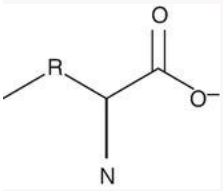
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Amino nitrogen

The amine nitrogen (-NH_2) attached to the α-carbon and, in some cases, the terminal carbon of an **amino acid**. The reaction of ninhydrin with α-amino nitrogen of free amino acids was an early basis for quantifying amino acids. (NJB)



Amino sugarsMonosaccharides (simple sugars) in which a single hydroxyl group (-OH) is replaced by an amino group (-NH_2). Glucosamine, **galactosamine** and mannosamine are examples. Glucosamine is a component of heparin, while the *N*-acetyl derivative is found in hyaluronic acid. Galactosamine, as the *N*-acetyl derivative, is a component of chondroitin. Mannosamine, as the *N*-acetyl derivative, is a component of sialic acid. (NJB)

Amino-oligopeptidase:

see Aminopeptidase

Aminobutyric acid

Can be found in two forms. α-Aminobutyric acid ($HOOC{\cdot}CH_2{\cdot}CHNH_2{\cdot}COOH$) is produced by **transamination** of

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α-ketobutyric acid produced in the **catabolism** of threonine and **methionine**. γ-Aminobutyrate ($H_2NCH_2{\cdot}CH_2{\cdot}CH_2{\cdot}COO^-$) is a **neurotransmitter** formed by the **decarboxylation** of **glutamate**. (NJB)

Aminopeptidase
A **peptidase** that cleaves **peptide** bonds from the N-terminal of peptides, e.g. **leucine** amino peptidase (EC 3.4.11.1), which is attached to epithelial cells of the **small intestine**. (SB)
See also: Protein digestion

Aminotransferases
Enzymes that are involved in transfer of an α-**amino nitrogen** from one **amino acid** to the ketoacid precursor of another amino acid. Aminotransferases can be found in many tissues and in the cytosolic as well as mitochondrial fractions of cells. The accepted vitamin co-factors for **transamination** reactions are **pyridoxine** 5′-phosphate (removal of $-NH_2$) and pyridoxamine 5′-phosphate (addition of $-NH_2$). (NJB)

Ammonia
Ammonia (NH_3) is a gas at normal ambient temperatures. It is produced industrially and used as a fertilizer for crops by injection into the soil. It is toxic, even fatally, and is an irritant to membranes exposed to it. It reacts with water to become ammonium hydroxide (NH_4OH). In **amino acid metabolism** it can be released as ammonium (NH_4^+) from the amino acid **glutamine** by the enzyme glutaminase or from the amino acid **glutamate** by the

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enzyme **glutamate dehydrogenase**. Because ammonium can be incorporated into glutamate by the enzyme glutamate dehydrogenase or into glutamine by glutamine synthetase, ammonium nitrogen (NH_4^+) in the form of ammonium citrate ($C_6H_{14}N_2O_7$) can be used as a source of nitrogen for the biosynthesis of dispensable amino acids in non-ruminants. In the rumen, bacteria convert **urea**-N into ammonium-N which is then incorporated into microbial amino acids and protein, which are later digested and become available to the host in the form of absorbed amino acids. (NJB)

Ammonia treatment of straws

The requirement for supplemental **ruminally available nitrogen** (RAN) and the observation that alkalis other than sodium hydroxide also improved **digestibility**, led to the development of systems using either gaseous (NH_3) or aqueous (NH_4OH) ammonia to treat low-quality **roughages** such as barley, oat and wheat straws. **Urea**, or even **urine**, can be used as the ammonia source, as these release ammonia when acted on by **urease** enzymes present in bacteria in the straw. Urease levels have been enhanced by the addition of **jackbean**s to the straw prior to treatment.

Ammonia treatment, at a rate of about 4% of the straw dry matter, increases **organic matter digestibility** (by about 10% units, from about 45%), nitrogen content (from 0.8 to 1.4% of dry matter) and intake (by about 30%). An added advantage is that ammonia treatment inhibits spoilage organisms, especially moulds,

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thereby increasing the storage properties of damp straw.

Ammonia, either as anhydrous ammonia (NH_3) gas or as an ammonium hydroxide (NH_4OH) solution, is injected into straw stacks or large bales sealed with plastic sheeting or film. Under temperate summer temperatures the process is generally complete in 4–6 weeks. In tropical conditions, treatment of straw (rice, barley, maize or sorghum) is achieved in 2–3 weeks. For ammonia retention to be effective, the treated straw must contain at least 10% moisture, and retention increases as the straw moisture content increases. For this reason it is recommended that treatment should occur as soon as possible after the grain harvest, before the straw has lost too much moisture. Forty to 60% of the added ammonia-N is lost when the treated stack is opened and aired. This loss can be reduced by treating the ammoniated straw with sulphur dioxide gas, although this has to be done carefully to avoid possible H_2S toxicity.

Treatment with gas can also be undertaken in 'ovens'. Oven treatment takes only 24 h and enables straw to be treated during periods of cold weather or under winter conditions.

Toxicity symptoms may arise if high quality forages (e.g. grass or **lucerne** hay) are ammoniated and offered to ruminants. This takes the form of a hyper-excitability, commonly referred to as 'crazy **cow** syndrome', which is totally unconnected with **bovine spongiform encephalopathy** (BSE). **Roughages** with a high carbohydrate content prior to ammoniation are particularly implicated, with the compound generally associated with this effect, 4-methylimidazole, being formed by the interaction of

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sugars with ammonia in the rumen. (EO, FLM, GMcLD)

See also: Alkali treatment

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Ammoniated feeds:

see Ammonia treatment

Ammonium:

see Ammonia

Amylase

An enzyme (α-amylase; 1,4-α-D-glucan-glucanohydrolase; EC 3.2.1.1) secreted in the saliva of omnivorous animals and from the **pancreas**. The enzyme hydrolyses **starch** and **glycogen** and produces the disaccharides **maltose** and **isomaltose**, and also **maltotriose** and α-limit dextrins. Preparations of α-amylase (EC 3.2.1.2) have been isolated from various sources, such as bacteria, barley malt and **sweet potato**, and are used for structural investigations of **polysaccharide**s. (SB)

Amyloglucosidase

An enzyme (EC 3.2.1.3) that acts on terminal units of α(1→4)-linked **glucans** from the non-reducing end, releasing **glucose**. (SB)

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Amylopectin
A branched polymer of **glucose** which has a role as a storage form of carbohydrate. **Starch** (from plants) and **glycogen** (from animals) consist of **amylose**, with linear chains of α(1→4) glycosidic bonds, together with amylopectin, in which linear chains of glucose are interspersed with branches due to α(1→6) glycosidic bonds. (NJB)

Amylose
A linear polymer of **glucose** which has a role as a storage form of carbohydrate (energy reserve) found in both plants and animals. Found in **starch** (from plants) and **glycogen** (from animals), amylose consists of linear chains of glucose units with α(1→4) glycosidic bonds. (NJB)

Anabolic steroids
Steroid **hormone**s (often synthetic) that stimulate anabolic processes, in particular **protein synthesis** from **amino acid**s, whilst inhibiting **catabolism** and in this respect act antagonistically to **glucocorticoids**. These agents promote retention of nitrogen, potassium and phosphate. The effect is to promote weight gain, provided that nutritional status is adequate. May act by influencing the transfer of amino acids from tRNA to ribosomes. Often derived from testosterone esters or 17α-methyl dihydro-testosterone, although oestradiol and its derivatives may also be effective. Typical examples used to promote growth in farm animals, particularly in beef cattle, are stilboestrol, trenbolone **acetate**, boldenone, nor-ethandrolone and ethylestrenol. The use

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of these agents in food-producing animals is banned throughout the European Union, and enforcement and monitoring are achieved by routine testing for residues and **metabolite**s in meat and in animal tissue, faeces and **body fluid** samples. However, they are still widely used in other parts of the world. (MMit)
See also: Glucocorticoids; Growth; Muscle

Anaemia
A deficiency in quality or reduction in the number of circulating functional red blood cells (erythrocytes) or in the **haemoglobin** content of circulating red blood cells. Anaemia is classified as regenerative (usually caused by haemorrhage or haemolysis) or non-regenerative (caused by decreased erythropoietin or an abnormality in the bone marrow). Symptoms include pale mucous membranes, increased heart and respiratory rate, poor growth rates and exercise intolerance. It is potentially fatal. Causes include:

Chronic or acute haemorrhage, either external or internal, due to trauma, vascular damage, endo- or ectoparasites, warfarin **poisoning**, platelet deficiency (e.g. in thrombocytopaenic pupura in piglets) etc.

Excess erythrocyte destruction (haemolytic anaemia), initiated for example by infections such as babesiosis (red-water), *Clostridium oedematiens* (bacillary haemoglobinurea), or copper poisoning.

Insufficient synthesis of either haemoglobin or red blood cells, caused by dietary deficiencies, e.g. iron in piglets, copper, vitamin B_{12} or **cobalt**, or by conditions affecting bone marrow, e.g. chronic

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bracken poisoning, radiation, certain drugs, leucoses.

Poisoning, or dietary excesses, e.g. **molybdenum**, excess feeding of kale and other brassicas, chronic lead poisoning.

Vaccination is available against some of the infectious diseases that cause anaemia. Treatment may be specifically for the primary cause or symptomatic therapy. For acute anaemia, blood transfusion may be appropriate. Correction or **supplementation** of the diet is essential. (EM; DB)

See also: Blood; Haemoglobin; Iron deficiency anaemia

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Anaerobic digestion:

see Fermentation; Rumen digestion

Analogues of amino acids

Carbon skeletons that are immediate precursors of **amino acid**s. To function nutritionally, analogues must be converted to the amino acid at rates consistent with need. Hydroxymethionine is a synthetic source of **methionine** used extensively in the poultry industry. It supports growth roughly equivalent to that obtained with methionine. Most D-amino acids may be considered analogues of the physiological L-amino acids since all but **lysine** and threonine can be converted to the L-amino acid. The **keto acids** of all amino acids except lysine and threonine may be considered analogues since when used singly they can support growth

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approaching that with the amino acid. (NJB)

Analytical methods:
see Chromatography; Gas–liquid chromatography; Mass spectrometry; Near infrared spectroscopy; Neutron activation analysis; Nuclear magnetic resonance; Proximate analysis of foods; Weende analysis; *see also* individual constituents

Anchovy
A small, schooling, pelagic fish found mainly inshore in bays and estuaries, but not in the open ocean. More than 130 species of anchovies are distributed in many parts of the world. They are important human food and animal feedstuffs (fish meal and oil). Anchovies swim through the water with their large mouths open and strain out small organisms (plankton) with fine, sieve-like structures called gill rakers. The main nutrients in dried anchovies are protein (59.4%) and lipid (16.0%), with plenty of minerals and vitamins. (SPL; QS)

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Angora goats
Goats named after the Turkish province, now known as Ankara, in which they originated. Like other breeds of domesticated goat (*Capra hircus*) they are thought to be descended from the bezoar

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or wild goat (*Capra aegagrus*). The distribution of Angora goats was, for many centuries, restricted to Turkey. In the mid-19th century they spread, firstly, to South Africa and shortly afterwards to the USA. Today they are found principally in the Middle East, southern Africa and Texas, with smaller numbers in other US states and in Argentina. In recent decades Angora goat populations have been established in a number of European states and in Australasia.



Angora goats, kept predominantly for wool production. Photo courtesy of Christine McIntosh. Licensed under CC BY-ND 2.0.

Mature female Angora goats (does) weigh about 40–45 kg and males (bucks) around 60–65 kg. They are farmed for their fibre, mohair (not to be confused with angora fibre, which comes from rabbits). Unlike all other goat breeds, which have coats comprising

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a mixture of coarse and fine fibres, Angora goats are single-coated: the mohair fleece is composed of only one fibre type and contains, or ideally should contain, no coarse hairs. In practice most mohair fleeces contain a small proportion of coarse hairy fibres known as kemps. These have a different morphology from the true mohair fibres and are regarded as a fault, because they cause problems in the manufacture of mohair garments and fabrics. Most Angora goats are white but some breeders specialize in the production of black or brown mohair. The typical mohair fleece is white, long and lustrous with wavy locks or staples. Mohair grows rapidly, at a rate of 2–2.5 cm per month, and the animals are generally shorn every 6 months to provide a fibre that meets the requirements of the processors (staple length up to 15 cm) and to prevent excessive soiling caused by the fleece trailing on the ground.

The average annual mohair production of adult does is between 2.5 and 6 kg of greasy fibre. The yield (i.e. the weight of the clean fleece, after scouring, as a percentage of the greasy weight) is typically around 75%, though this varies between different strains within the breed. Mohair fibre diameter increases with age, from less than 25 microns (μm) at the first shearing at 6 months of age to 35 μm or more at about 4 years old. It is now known that both fleece weight and fibre quality (fineness) are influenced by nutrition. High levels of feeding, particularly of high-protein diets, lead to the production of heavier fleeces with coarser (thicker) fibres, i.e. there is an inverse relationship between quantity and quality.

Like other domesticated breeds, Angora goats are seasonally

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polyoestrous. Does come into heat at 21-day intervals during the breeding season which, in the northern hemisphere, extends from about August to February, and in the southern hemisphere during autumn (March to May). Gestation length averages about 150 days.

The principal mohair-producing countries have dry climates and in these conditions the goats can be kept outdoors throughout the year. In other countries Angora goats are housed during winter or in the **wet season**. Their main nutritional requirements are met outdoors from grazing and indoors from conserved **forage**. Some supplementary concentrates are generally supplied during late pregnancy and in early **lactation**. (AJFR)

Animal fat

The **lipids** isolated from animal fat depots contain many fractions, most importantly **triacylglycerol**s, but also **phospholipid**s, **cholesterol**s, cholesterol esters and **free fatty acid**s. Fat rendered commercially from carcasses of cattle (*Bos taurus*) and sheep (*Ovis aries*) is commonly called tallow. Fat produced from pigs (*Sus scrofa*) is termed **lard** and rendered pork fat. Fat obtained from the tissues in the commercial processes of **rendering** or extracting during the slaughter of poultry, mainly chickens (*Gallus gallus*), is known as poultry fat. The major fat depots of mammalian animals are subcutaneous, intermuscular, abdominal and intramuscular. The distribution of the fat varies with animal species, breed, gender, age at slaughter and nutritional background. Suet is a term used for the raw fat of beef or mutton located around the loins and kidneys. Animals may also store fats in other sites or locations in the body such as the tail in sheep and

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hump in camels (*Camelus dromedarius*) and cattle (*Bos indicus)*. Tail fat in sheep comes from specific breeds, and it weighs up to 30% of carcass weight. The hump of camels contains a white fat, which is used as storage energy (food) for survival during **drought** or long trekking in deserts. Tallow and suet are hard and solid at room temperature (24°C). Lard and poultry fat are softer than tallow and are semi-solid at room temperature.

The expression of **fatty acid** (FA) concentrations in foods is vital because in recent years nutrient-based guidelines have been introduced by government authorities around the world, which include guidance on fatty acid intakes. These guidelines also aim to maintain the daily intake of energy, protein and other nutrients of each person to avoid **metabolic disorder**s associated with an imbalance of dietary intake or overconsumption. Previous research has reported the fatty acid composition in animal-based foods in two main ways. One is providing the fatty acid concentration in animal-based foods (e.g. meat) in mg FA per 100 g of fat (or lipid) within the food itself. The other is providing the fatty acid concentration in foods in mg FA per 100 g of the food itself or mg FA per meal portion. The latter way has been followed by many health professionals, nutritionists, dieticians, researchers and food regulatory bodies. The fatty acid composition of animal fat is determined by many factors, including nutritional background, feeding systems, animal species, breed, gender and age at slaughter. In general, ruminant fats are more saturated (e.g. with increased **stearic acid**) than non-ruminant fats. Ruminant fats have a very diverse fatty acid composition, due to the active

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microbial community in the rumen. As a percentage of total fatty acids, tallow typically contains 2–5% myristic, 20–26% palmitic, 7–17% stearic, 30–45% oleic, 0.5–2% linoleic and 2–4% ***trans*-fatty acid**s. Mutton tallow contains 5–10% more stearic acid than beef tallow, due to greater bio-hydrogenation in the rumen of sheep. Fat collected from fat-tail sheep contains 10% more **unsaturated fatty acid**s than visceral fat. Camel hump fat contains 10% myristic, 34% palmitic, 10% stearic and 28.2% **oleic acid**s, respectively. The fatty acid composition of lipid or fat from **monogastric** species (e.g. pigs, poultry) reflects the dietary lipids. Thus lard and poultry fat have a greater content of unsaturated fatty acids as compared with tallow. Lard typically contains 23–28% palmitic, 12–24% stearic, 30–45% oleic, 8–13% linoleic and 1–1.5% *trans* fatty acids. Chicken fat contains 50% more **linoleic acid** and 50% less stearic acid than lard.

Animal fat is largely used in the production of butter, cheese, yoghurt, shortening and compound fat. Industrial and non-food uses of animal fats include the production of soaps, pharmaceuticals, lubricants and feedstuffs. Since the occurrence of **bovine spongiform encephalopathy** (BSE, commonly known as mad **cow** disease), tallow from ruminant species has not been used in the formulation of animal feeds, but has been replaced by alternative vegetable fats with similar physical properties (e.g. palm oil). Inedible animal fat is suitable for the production of biodiesel and pharmaceuticals.

The quantity and fatty acid composition of animal fat are significantly influenced by animal nutrition. Feeding a concentrate-

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based diet increases carcass fatness, comprising mainly oleic and linoleic acid concentrations, while pasture and forage feeding increases the **polyunsaturated fatty acid**s, such as omega-3 and conjugated linoleic acids (CLAs) in animal fat. The inclusion of vegetable oils (e.g. flaxseed oil, canola oil) has been an effective nutritional strategy in modifying the fatty acid composition of fat in favour of a healthier fatty acid composition; for example, long-chain omega-3 fatty acids. Animal fat with increased levels of polyunsaturated fatty acids is vulnerable to **oxidation** of the double bonds, **lipolysis** by contaminating microbes, and formation of off-flavours or odours (e.g. greasy or rancid flavour). Tallow and lard respond well to the addition of **antioxidant**s (e.g. **vitamin E**). Appropriate applications of antioxidants (natural or artificial) and **polyphenol** compounds in feeds have been used to alleviate the development of abnormal flavours from lipid oxidation in animal fat or foods containing animal fat. (AK, ENP)

Further reading

Richards, M.P., Olson, J.M. and Haas, M.J. (2021) Animal fats. In: Shahidi, F. (ed.) *Bailey's Industrial Oil and Fat Products* No. 5. Wiley Online Library, pp. 1–49. doi:10.1002/047167849X.bio028.pub2

Toldrá-Reig, F., Mora, L. and Toldrá, F. (2020) Trends in biodiesel production from animal fat waste. *Applied Sciences* 10(10), 3644. doi:10.3390/app10103644

Animal plasma:

see Spray-dried animal plasma

Animal production level (APL)

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The amount of **metabolizable energy** (ME) (the **net energy** remaining after faecal and urinary energy loss) required to support the productive state of the animal, relative to its requirement for **maintenance**. For ruminants it is the ratio between the total net energy needed and that used for maintenance: APL = (total ME requirement)/(ME for maintenance). (JMW; DB)
See also: Plane of nutrition

Animal protein
Protein from animal sources. The term includes products derived from milk, eggs, meat and fish and derived proteins e.g., **casein**, **whey protein**, gelatine, egg proteins, and fibroin (in silk). As dietary protein made from varied type of amino acids, these products are distinguished from plant protein by generally containing complete nutrients. In general, animal **protein source**s have higher concentrations of essential amino acids, especially **lysine** and the **sulphur** amino acids, than most plant protein sources, but the plants can synthesize all of the 20 different amino acids. In excessive amounts, animal proteins are considered detrimental for human health and for developing non-communicable diseases. (MFF; DB)

Anions
Anions can be inorganic or organic. They carry a negative charge. The major anions in **blood plasma** are **bicarbonate** (HCO_3^-), **chloride** (Cl^-), phosphate (PO_4^{2-}), **sulphate** (SO_4^{2-}) and **organic acid**s ($R{\cdot}COO^-$). To maintain anion/cation balance, the

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anions are balanced by an equivalent charge in the form of cations (positive ions) such as **potassium** (K^+) and **sodium** (Na^+). (NJB)
See also: Acid–base equilibrium

Anoestrus
A period of infertility, ovarian inactivity or sexual quiescence which may be seasonal (in sheep, goats, horses etc.) or induced by nutritional imbalances, stresses (such as heat, cold, confinement, poor management), disease, **lactation** or old age. Nutritional causes of anoestrus include inadequate intake of energy, **micronutrient** imbalances and toxicoses. Xenobiotics that contribute to infertility include **oestrogen**-like compounds, phyto-oestrogens from some clovers, zearalenone from *Fusarium* moulds, ergot **alkaloid**s, locoweeds (swainsonine), ***Leucaena*** (**mimosine**), **mustard** family (**glucosinolate**s) and **selenium** deficiencies or toxicoses. (KEP)

Anorexia
General lack of appetite, markedly low **voluntary food intake** or complete abstinence from food. There are numerous causes, including infectious or non-infectious disease, unavailability of acceptable, nutritious feed and certain mental disorders. Severe stress can induce anorexia, as in the case of sheep travelling long distances by ship. Removal of affected sheep from overcrowded pens and placing them in individual pens with a variety of feeds can restore the appetite of affected sheep. Seasonal **inappetence** seen in winter in many species should not be regarded as anorexia.

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True anorexia is rare in non-human animals as there is natural selection against it. Humans suffering from anorexia voluntarily restrict their food intake, resulting in chronic **starvation**, **malnutrition**, a severe loss of body weight, and, if untreated, even death. This **eating disorder** is a serious mental illness and usually develops during **puberty** and young adulthood, primarily in females. In Western countries, up to 4% females and 0.3% males are anorexic. Affected individuals have an intense fear of body weight gain or abnormal body shape and a strong desire to be thin. The causes of anorexia in people are unknown but may include genetic, environmental, psychological and social factors. (JMF; CJCP; GW)

Reference

van Eeden, A.E., van Hoeken, D., and Hoek, H.W. (2021) Incidence, prevalence and mortality of anorexia nervosa and bulimia nervosa. *Current Opinion in Psychiatry* 34, 515–524.

Anorexia, pathogen-induced

A voluntary reduction in the food intake of animals and humans, which occurs during infection with pathogens. It is observed across mammalian and avian species, infected with either macro-parasites, such as worms, or micro-parasites, such as bacteria and viruses. Very frequently, it is the only, early symptom seen during such infections and its extent can vary from a small reduction in food intake (10–20%) to complete cessation of eating for a period of time. Therefore, it is considered largely responsible for the consequences of infection on growth, reproduction and the overall biological fitness of an organism.

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Currently, there are hypotheses to account for both the functional (i.e. why it happens) and causal (i.e. how it happens) basis of anorexia. Kyriazakis *et al*. (1998) suggested that anorexia developed to allow animal and human hosts to cope with infection, since its persistence appears to confer advantages to the affected hosts. Infected hosts that show anorexia appear to suffer to a lesser degree from the consequences of infection and recover at a faster rate. The causal basis is linked to the host immune response to infection, as anorexia is seen mainly in hosts that have not yet developed **immunity** to a pathogen, or in hosts whose immunity breaks down due to stressful events in their life cycle, such as pregnancy.

By definition, the occurrence and characteristics of anorexia (its duration, extent, and the rate of recovery from it) depend on the characteristics of the pathogen and the ability of the host to eventually overcome the consequences of the infection. Anorexia may last for several weeks in infections with parasitic worms in sheep and cattle, or for a few days in bacterial infections of pigs. Nevertheless, anorexia constitutes a paradox, because it occurs at life stages when the **nutrient requirement**s of the infected host are increased, due to the nutritional demands of the pathogen on the host, including the need to repair the damage caused to the host's body by the pathogens or the need to develop an immune response to overcome the pathogen. Currently it is unclear whether diet composition plays a role in the occurrence and characteristics of anorexia, although it is known that infected animals on poor-quality diets seem to show anorexia for a longer period of time and

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recover more slowly from it. This is consistent with the view that links anorexia with the development of the immunity to a pathogen. The interaction between diet composition, anorexia and response to infection is an area of research that merits greater attention. Understanding how host nutrition affects pathogen-induced anorexia will shed light on how infected animals, and even humans, should be fed during the critical stages of an infection. (IK)

Reference

Kyriazakis, I., Tolkamp, B.J. and Hutchings, M.R. (1998) Towards a functional explanation for the occurrence of anorexia during parasitic infections. *Animal Behaviour* 56, 265–274.

Antagonism

A negative interaction between a nutrient and other nutrients, or between nutrients and non-nutrients. The interaction may be related to uptake or to use. An example is **branched-chain amino acid** antagonism in which three- to fourfold increases in dietary **leucine** in a low-protein diet result in decreases in food intake and weight gain and in the blood and tissue concentrations of the other branched-chain amino acids, **valine** and **isoleucine**, and their **keto acid**s. Another amino acid example is the **lysine–arginine** antagonism in which two- to threefold increases in dietary lysine result in an increase in the need for arginine. Antagonisms can be found in mineral interactions in which one mineral affects the rate and extent of uptake of another mineral such that more of the other mineral is required in the diet. Examples are zinc–copper, zinc–iron, calcium–zinc, calcium–iron,

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calcium–phosphorus, iron–copper and many more. (NJB)

Key reference

Shinneck, F.L. and Harper, A.E. (1977) Effects of branched-chain amino acid antagonism in the rat on tissue amino acid and keto acid concentrations. *Journal of Nutrition* 107, 887–895.

Antagonist

A compound that blocks the physiological action of another compound. For example, **acetylcholine** released by parasympathetic nerves binds intestinal muscarinic receptors to stimulate **motility**. Atropine also binds these receptors but does not increase motility. Thus, atropine can act as an antagonist by outcompeting acetylcholine for these receptors, effectively blocking acetylcholine actions. (JPG)

Anthocyanins

These plant pigments are **glycoside**s containing a nucleus (aglycone) called an anthocyanidin. Anthocyanidins are flavonoids, or water-soluble phenolic derivatives. They are generally red, crimson, blue, purple or yellow. They tend to be metabolically inert in animals but some have **antioxidant** activity. They form dimers (procyanidin) which can polymerize to form condensed **tannins** (proanthocyanidins). (PC)

Antibiotics in animal feed

Antimicrobial pharmaceuticals, usually of plant or fungal origin. Antibiotics have been included as a **growth promoter** in the feed of chickens, pigs and cattle since the industries intensified in the 1950s. The industrialized animal production systems are

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susceptible to pathogen growth and antibiotic inclusion in feed was seen as a means to prevent the spread of disease organisms. Antibiotics may be routinely administered to livestock at increased risk of disease. Low-level, routine antibiotic inclusion also improves the **efficiency of feed conversion** (FCE) by controlling microorganism growth in the **gastrointestinal tract**. Thus, although the primary use of antibiotics was originally in the treatment of infections, certain antibiotics came to be used as **feed additives** in order to improve growth and feed conversion efficiency. The modes of action of antibiotics used as growth promoters include reduction in sub-clinical disease, thinning of the wall of the intestine and, in ruminants, a change in the microflora and fauna in the rumen. For example, in chickens the popular antibiotic Flavomycin stops microorganisms from reproducing by preventing the synthesis of murein, an essential component of cell walls. This causes cell lysis in ***Escherichia coli*** and salmonella, but lactobacilli and bifidobacteria are not affected; indeed they competitively inhibit pathogenic bacteria. In addition, **villi** and crypts are shorter when antibiotics are fed, reducing the mass of the intestines.

In 2006, antibiotics previously licensed in the European Union for use as growth promoters were banned because of fears that their use might encourage the development of antibiotic resistance and prejudice the treatment of human disease.

Flavophospholipol is used for promotion of growth and improvement of feed efficiency in pigs, domestic fowl, turkeys, rabbits, calves, growing and fattening cattle and fur animals. It is a

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phosphoglycolipid, and is not absorbed from the digestive tract, so is not metabolized by the animal. It changes the pattern of **rumen microorganism**s by inhibiting some Gram-positive bacteria and by reducing the formation of **peptidoglycan**. Another antibiotic, avilomycin, has been used in pigs, broiler chickens and turkeys. Salinomycin is an **ionophore** available for use in pigs and also used to prevent **coccidiosis** in broiler chickens.

Monensin is still used for growth promotion in non-lactating cattle. It has had fatal effects when fed to horses, and when fed to cattle within 7 days before or after being treated with tiamulin. Monensin is an ionophore, and is poorly absorbed from the digestive tract, about two-thirds being lost unaltered in faeces. Ionophores facilitate the movement of ions across membranes by forming hydrophobic complexes with ions such as potassium and sodium, and in so doing disrupt bacterial cell walls, and possibly the cell walls of **protozoa**. They thereby change the pattern of rumen microorganisms, reducing the production of **acetate**, **butyrate** and **methane**, and increasing the proportion of **propionate**. Since methane is a waste product, the efficiency of rumen activity is improved. Ionophores also reduce the total mass of bacteria and thereby decrease the amount of dietary protein degraded.

Inclusion of antibiotics in the feed of farm animals confers resistance in pathogenic bacteria, which have a survival advantage. These may transmit from meat products or the environment of the meat-producing farms and factories to humans, who are then susceptible to the resistant pathogenic bacteria. In 2021, the EU

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banned the use of monensin sodium, salinomycin sodium, avilamycin and flavophospholipol as growth promoters in animal feed.

Consumer resistance to inclusion of antibiotics in animal feed is strong, and alternatives, mainly in the form of **probiotic**s, prebiotics, synbiotics, vaccines, **organic acid**s, enzymes and medicinal plants (or phytobiotics), such as garlic and ginger, are starting to replace the antibiotics in animal feed. Replacements are more useful for growth promotion and improving **feed conversion** efficiency than for treatment of disease or prophylactic use. In this respect, pro- and prebiotics both improve gut health, whereas vaccines have to be administered well before any potential infection, and bacteriophages and antimicrobial peptides have to be administered at the time of initial infection.

All antibiotics must be used with care and the current data sheet should be consulted for dosage, contraindications and other precautions. Some are incorporated into **feed block**s or used as top-dressing of feeds such as **silage**. (WRW; CJCP)

See also: Additive, feed; Growth promoters

Reference

PEW (2017) *Alternatives to Antibiotics in Animal Agriculture*. PEW Charitable Trusts, Philadelphia, Pennsylvania. Available at : https://www.pewtrusts.org/-/media/assets/2017/07/alternatives_to_antibiotics_in_animal_agricu (accessed 17 August, 2022).

Antibodies

Long-chain **globulin** proteins produced by plasma cells in

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response to the presence of an **antigen** (foreign protein) as part of the body's defence system. Antibodies are made of two light and two heavy **peptide** chains. Constant regions are common to all antibodies; variable regions are specific to the antigen that stimulated their production, and can form a site that binds with that specific antigen to form an antigen–antibody complex. This aids the elimination or destruction of that antigen.

Antibodies are produced in five different classes, depending on the structure of the constant regions, and this determines the site in the body at which they have their action (*see* Immunoglobulin). Antigens that stimulate the production of antibodies can be from the environment, food, infection or vaccination.

Plasma cells in the **mammary gland** produce antibodies (IgA) shortly before parturition, which are concentrated in the colostrum and are also present in declining amounts in early **lactation**. Circulating antibodies (IgG) are also transported and concentrated in the colostrum. They provide the potential source of passive **immunity** to most of the domestic species. The relative importance of IgG and IgA varies with species. The greater the number of antigens the dam has been exposed to, the more antibodies there are likely to be in the colostrum, assuming adequate health and nutrition. (EM)

See also: Antigen; Colostrum; Immunity

Antigen

Any substance that stimulates an immune response. Many different substances can act as antigens, but most are proteins of more than 20 **amino acid**s. **Microorganism**s act as antigens but their

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complex structure provides many antigenic sites or epitopes. Large protein molecules may also have many epitopes. (EM)
See also: Antibodies; Immunity

Anti-infective agents
Anti-infective agents in feedstuffs include natural phytochemicals and **feed additives** (e.g. antibiotics). Phytochemicals with anti-infective activity, especially against **protozoa**, include **phenolic compound**s and **saponin**s. They cause lysis of protozoal cell membranes. Anti-infective phytochemicals in herbal products may become more important if use of antibiotics as feed additives is restricted. (PC)

Antimicrobial activity
The ability to kill or impair the growth of bacteria or **protozoa**. Many natural toxins have antimicrobial action and most antimicrobial pharmaceuticals used today are of plant or fungal origin. Although many antimicrobials are used to treat infections, others impair the digestion of feed, especially in ruminants. Plants such as broom snakeweed (*Gutierrezia* spp.), pine needles and sage brush (*Artemesia* spp.) contain toxins that inhibit rumen fermentation and reduce animal production. (BLS)

Antinutritional factors (ANFs)
Feed components that have negative effects on the intake or utilization of feeds, or that may be inherently toxic when ingested. Many common feeds, such as **legume** seeds, contain ANFs; many **rangeland** plants contain phytochemicals or toxins. The most

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important ANFs are **alkaloid**s, **haemagglutinin**s (**lectins**), phenolics, **phytates**, phytooestrogens, **saponin**s, **tannins** and **trypsin inhibitor**s.

Alkaloids are cyclic **organic compound**s containing nitrogen. When ingested they may cause feed refusal, **abortion**, birth defects, wasting diseases, agalactia and death. There are marked animal species differences in reactions to alkaloids, which may be due to differences in rumen microbial metabolism or in the **absorption**, metabolism or excretion of alkaloids, or may be directly related to alkaloid affinity to target tissues such as binding at receptor sites. Alkaloids constitute the largest class of **plant secondary compound**s, occurring in 20–30% of perennial herbaceous species in North America. Major categories of toxic alkaloids include pyrrolizidine (e.g. *Senecio*), quinolizidine (e.g. *Lupinus*), indolizidine (e.g. *Astragalus*), diterpenoid (e.g. *Delphinium*), piperidine (e.g. *Conium*), pyridine (e.g. *Nicotiana*) and steroidal (*Veratrum*-type) alkaloids. Management schemes to prevent losses are usually based on recognizing the particular toxic plant, knowing the mechanism of toxicity, and understanding the temporal dynamics of plant alkaloid concentration and consumption by livestock. Once these are understood, losses may be reduced by maintaining optimal forage conditions, adjusting grazing pressure and the timing of grazing, strategic **supplementation**, changing livestock species and herbicidal control.

Phenolic compounds are produced by a wide range of plants. Low molecular-weight (MW) plant phenolics are often converted to

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tannins when plants mature. When ingested, phenolics reduce feed intake and weight gain. After ingestion, phenolics are absorbed, producing negative effects on physiological functions. Conversely, hydrolysable tannins may be converted to low-MW phenolics in the **gastrointestinal tract** of ruminants and may be toxic (*see* Tannins).

Phytates are divalent mineral ions complexed with organic phosphorus in seeds. Phytate phosphorus is poorly available to non-ruminant livestock. Most (50–70%) of the phosphorus in cereal grains is in the form of phytic acid. Phytates may be soluble (e.g. sodium or potassium) or insoluble (e.g. calcium). Phytates readily complex with phytic acid and **inositol** in cereal grains, and these **chelate**s then bind much of the phosphorus and zinc in grains, while complexing to a lesser extent with copper, cobalt, magnesium and calcium. Phosphorus deficiency is characterized by distorted appetite, reduced weight gain and impaired reproduction. Zinc deficiency is manifested by reduced weight gain and skin lesions. Through microbial fermentation in the rumen, ruminants are capable of cleaving **phosphorus** from phytates, making it available to the animal. Phytates are particularly high in maize and in wheat by-products, and are also present in most other cereal grains. Adding the industrial enzyme **phytase** to pig and poultry rations may be economically feasible, because phosphorus is relatively expensive to supplement; it also reduces phosphorus elimination in faeces.

Phyto-oestrogens are **plant oestrogen**s that affect reproduction. Phyto-oestrogens inhibit release of reproductive hormones and

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compete with oestrogen at cellular receptors. Hence, livestock consuming forages containing phyto-oestrogens exhibit reductions in fertility, including abnormal **oestrous cycle**s and ovulation, and defective development of reproductive organs and genitalia. Forages that typically contain phyto-oestrogens include **lucerne** and clover (*Trifolium* spp.). Cattle are much less sensitive to phyto-oestrogens than are sheep, which appear to activate phyto-oestrogens in the rumen to more potent compounds and may also have more sensitive oestrogen receptors. Poultry may also be affected by phyto-oestrogens; there is some evidence that quail are adversely affected by phyto-oestrogens in range plants.

Saponins are steroidal or triterpenoid **glycoside**s that have considerable biological activity. Saponins have a bitter taste, reducing the palatability of feeds. They may also reduce the digestion and absorption of nutrients, including minerals. These effects occur primarily in non-ruminant livestock. Nevertheless, saponins in some range plants from the Caryophyllaceae (pink) family (e.g. *Drymaria*, *Agrostemma*, *Saponaria*) or in snakeweed (*Gutierrezia* spp.) can have toxic effects in ruminants, including loss of appetite, weight loss, diarrhoea, abortion and photosensitization. The primary livestock feed with significant amounts of saponins is lucerne (*Medicago sativa*), which causes frothy **bloat**. The concentration of saponins in lucerne changes seasonally, with the highest amounts in midsummer.
Tannins are high-MW phenolic compounds that bind strongly with proteins and other macromolecules such as starch, cellulose or minerals. Two major classes of tannins are hydrolysable and

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proanthocyanidins (condensed tannins). Tannins reduce feed intake because of astringency (i.e. reduced acceptability) and reduce digestibility by the formation of largely indigestible complexes in the digestive tract. Deleterious effects vary depending on the type of tannin and the tolerance of the animal, but concentrations above 10–20% may be toxic to ruminants. Clinically affected ruminants may show signs of kidney failure and elevated serum **urea** nitrogen. Non-ruminant animals may have reduced growth rates with low (< 5%) concentrations; higher concentrations may be fatal. Tannins are common in plants, occurring in both gymnosperms and angiosperms. Woody species and broadleaf plants are more likely to contain tannins than are **Gramineae**. Compounds such as polyethylene glycol (PEG) may be added to feed and water to bind and inactivate tannins, allowing high-tannin feeds to be used for grazing or pen-fed livestock. For ruminants, tannins may have some positive effects through complexing with high-quality protein (allowing it to bypass rumen degradation) or through increased **nitrogen recycling** to the rumen.

Trypsin inhibitors are plant proteins that inhibit the pancreatic enzyme trypsin, which is partly responsible for **protein digestion**. Trypsin (and other protease) inhibitors bind tightly to trypsin and **chymotrypsin**, inhibiting their proteolytic activity. Trypsin inhibitors occur primarily in legume seeds, particularly soybeans, but are also found in low concentrations in cereal grains such as wheat, oats, buckwheat, barley and maize. There are two classes of trypsin inhibitors: the low-MW Bowman–Birk inhibitor

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and the larger Kunitz inhibitor. The anti-tryptic activity is destroyed by moderate heat, which may be applied during the processing of plant materials. The Bowman–Birk inhibitors are more heat-stable than the Kunitz type. Excessive heating may reduce **protein quality** through non-enzymatic **browning** reactions. Ruminant livestock are less affected than non-ruminants, because most trypsin inhibitors are degraded slowly in the rumen, though some may escape the rumen and enter the **small intestine**. In poultry, trypsin inhibitors cause pancreatic enlargement and reduce feed efficiency and growth rates; in pigs and calves, growth rates are depressed from reduced protein digestibility without accompanying pancreatic enlargement. Trypsin inhibitors from soybeans may be added to bovine colostrum, resulting in increased immunoglobulin **absorption** in calves. (JAP)

See also: Alkaloids; Haemagglutinins; Lectins

Antioxidant

Natural or synthetic compounds in origin that delay or inhibit the **oxidation** of molecules in cells or tissue compartments of biological systems. Oxidative processes in biological systems are essential to produce energy to drive the metabolic events that take place in organisms. The utilization of oxygen by the cellular systems provides animals with the benefit of metabolizing fats, proteins and carbohydrates for energy. The oxidation process also serves as a medium for the production of reactive oxygen species (ROS) and cellular defence action for the maintenance of life, for example improving immune function. However, ROS also have

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negative consequences in organelles when produced at high levels. The production of ROS in the cell at a high level can cause damage to DNA and proteins and induce membrane damage through **lipid peroxidation**. Antioxidants present in biological systems reduce the formation and actual number of **free radical**s by directly scavenging ROS such as **hydrogen peroxide** (H_2O_2) or **chelate** the metal ions serving as an oxidative base such as Fe^{2+}. Both actions, in turn, minimize the overproduction of free radicals in biological systems.

Synthetic antioxidants include butylated hydroxyanisole (BHA), butylated hydroxytoluene (BHT), propyl gallate (PG) and tertiary-butyl hydroquinone (TBHQ). Natural antioxidants mostly derive from plant materials, such as fruit, vegetables, **yams**, herbs and spices. The antioxidants that are available to the cells either originate from ingested foods or can be synthesized endogenously, and they are classified as enzymatic and non-enzymatic. The non-enzymatic antioxidants include vitamins (A, C and E), minerals (**selenium**, **zinc**, **manganese**), **carotenoid**s (β-carotene, **lycopene**, **lutein**, zeaxanthin), organo-sulphur components (lipoic acid, alliums, allyl sulphide, **indole**s), **polyphenol**s, **glutathione** and uric acid. The enzymatic antioxidants, synthesized endogenously, are **superoxide** dismutase (SOD), catalase (CAT), **glutathione peroxidase** (GPx) and glutathione reductase. Alternatively, antioxidants can be grouped as membrane antioxidants, soluble antioxidants and antioxidant enzymes. Membrane antioxidants are lipophilic; mostly **tocopherol**s, but also ubiquinones and carotenoids. Soluble antioxidants are

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NADPH, NADH, **ascorbic acid**, reduced glutathione and other thiols, uric acid, thioredoxin, bilirubin, polyphenols, and several metal-binding proteins (**copper**: ceruloplasmin, **metallothionein** and **albumin**; **iron**: **transferrin**, **ferritin** and myoglobin). SOD is a **metalloenzyme** present in the mitochondria (contains manganese) and in the cytosol (contains both copper and zinc). GPx has four isoforms, containing selenium (Se). GPx regenerates the reduced glutathione (GSH) from its oxidized glutathione form (GSSG). Thioredoxin reductase is also a selenoprotein. Catalase has iron and its distribution is almost exclusively limited to the peroxisomes/lysosomes. All endogenously synthesized (e.g. antioxidant enzymes, GSH) and exogenously supplied (**vitamin E**, carotenoids, etc.) antioxidants work cooperatively to maintain optimal redox (reduction/oxidation) balance in the cell or body. For example, in the cellular systems, SOD enzyme converts two superoxide radicals to one oxygen molecule and one hydrogen peroxide and then CAT and GPx further decompose the hydrogen **peroxide** molecules to water.

Free radicals are produced in cells by normal aerobic cellular metabolism and also in response to environmental radiation and pollutants. Oxygen is a highly reactive atom that is capable of becoming incorporated into potentially damaging free radical molecules. The main free radicals are ROS and reactive nitrogen species (RNS), derived from oxygen and nitrogen, respectively. The production of ROS in cells is linked to the use of oxygen as a primary electron acceptor for generating energy through the

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respiratory chain. The ROS compounds includes superoxide anion ($O_2^{-\bullet}$), H_2O_2, hydroxyl radical ($^{\bullet}OH$), alkoxyl radical ($RO^{\bullet}$) and peroxyl radical ($ROO^{\bullet}$). The RNS compounds are **nitric oxide** ($NO^{\bullet}$), peroxy **nitrite** ($ONOO^-$), peroxynitrous acid (ONOOH) and nitrogen dioxide (NO_2). Although free radicals at low to moderate concentrations play key roles in immune function and essential metabolic functions, as signalling molecules, their overproduction in biological systems can damage cells. This can trigger the oxidation of lipids, DNA and proteins and produce adverse modifications. For example, the peroxyl radical ($ROO^{\bullet}$), which is produced from the long-chain **unsaturated fatty acid**s (PUFA) of cellular membranes, initiates a chain reaction that can lead to compromised cell membranes, loss of membrane permeability and tissue integrity, and eventually cell/tissue death.

The main function of antioxidants in biological systems is to protect animal and plant tissues against damage due to free radicals. In the antioxidant defence system, natural antioxidants of exogenous origin, such as vitamin E, scavenges radicals within the membrane, where it blocks initiation and interrupts the propagation of lipid peroxidation. Enzymes produced endogenously, such as SOD, GPx, and CAT, also collectively block the initiation of peroxidation from within the soluble phase of the cell. The processes are the conversion of $O_2^{-\bullet}$ to H_2O_2 by SOD; further reduction of H_2O_2 to H_2O by catalase and GPx. The aggregate effect of this enzymatic system is to clear $O_2^{-\bullet}$ by reducing it fully to H_2O, thus preventing the generation of highly

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active ROS [e.g., $^{\bullet}OH$, and singlet oxygen ($^1O_2$)]. GPx can also reduce fatty acyl hydroperoxides to the corresponding fatty alcohols, thus serving to interrupt the propagation of lipid peroxidation in the cellular compartments of biological systems. Lipid hydroperoxides are naturally found in all food containing fats and oils. Removal of hydrogen and lipid peroxides from biological tissues of living organisms is critical to prevent oxidative damage and ultimately the preservation of their products, in particular milk and meat.

Vitamin E is the commonly used antioxidant in animal feed and human food formulations. Vitamin E consists of four tocopherols (α-, β-, γ- and δ-) and four **tocotrienol**s (α-, β-, γ- and δ-), which are all naturally occurring lipophilic compounds. Vitamin E can therefore be seen as a generic name for all tocopherols and tocotrienol derivatives that exhibit the activity of α-tocopherol (trimethylated tocopherol). The chemical antioxidant activity of natural α-tocopherol is about 200-fold that of the commonly used artificial food antioxidant BHT. The main sources of vitamin E are green plants, vegetable oils, seeds and cereal grains. Animal tissues tend to contain low amounts of α-tocopherol, the highest levels occurring in fatty tissues. In most non-adipose cells or tissues, vitamin E (mostly α-tocopherol) is localized almost exclusively in membranes. The average tocopherol concentration in membranes is one α-tocopherol molecule per 500–1000 **phospholipid** molecules. Vitamin E can scavenge lipid peroxyl radicals from the tissue systems. This is because vitamin E has a chromanol nucleus with a hydroxyl group at position C-6 (phenolic hydrogen) with the

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ability to accommodate an unpaired electron. The chromanol hydroxyl group gives α-tocopherol the ability to accept one or two electrons, thus converting it into α-tocopheroxyl radical and α-tocopheryl **quinone**s, respectively. The α-tocopheryl quinones are non-radical products. Therefore, vitamin E inhibits chain reactions initiated by peroxyl radicals when exposed to PUFA.

A by-product of lipid peroxidation is malondialdehyde (MDA), which can be determined by the thiobarbituric acid reactive substances (TBARS) assay. The accumulation of MDA in biological systems is used as an indicator of oxidative damage to membrane lipids. The chain reaction producing MDA is terminated when a peroxyl radical ($ROO^{\bullet}$) reacts with α-tocopherol to produce an α-tocopherol radical intermediate (α-tocopheroxyl radical) that reacts with another peroxyl radical to produce a non-radical product (α-tocopheryl quinones). Because α-tocopherol can compete for peroxyl radicals much faster than PUFAs, small amounts of the vitamin E present in biological membranes are adequate to neutralize large amounts of peroxyl radicals in the system; the relative molar ratio of vitamin E to PUFA in biological membranes is very low (1:850). To be effective, the tissue vitamin E concentration must be above a critical threshold. When the tissue vitamin E concentration is below the threshold, peroxyl radicals can propagate extensively and deplete α-tocopherol, but when the vitamin E concentration is above the threshold, the activity of peroxyl radicals is suppressed by the adequate α-tocopherol reserve. Fortunately, in biological systems, most vitamin E is recycled by the reduction of α-tocopheroxyl radical back to α-

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tocopherol.

Vitamin C (L-**ascorbic acid**) contributes to the prevention of oxidative damage to lipids, proteins and DNA in cells. Vitamin C is the major water-soluble antioxidant in plasma and soluble phases of cells. As a strong reducing agent, ascorbic acid is oxidized to dehydroascorbic acid in two successive losses of single electrons. The first monovalent oxidation results in the formation of the ascorbyl free radical (monodehydroascorbic acid). The partially reduced form can establish a reversible electrochemical couple with ascorbate, or it can be further oxidized to dehydroascorbic acid. Vitamin C reduces the superoxide radical ($O_2^{-\bullet}$) to H_2O_2. Ascorbate peroxidase enzyme reduces H_2O_2 to water by using vitamin C as an electron donor. Ascorbate undergoes oxidation by reaction with tocopheroxyl radical and regenerates the metabolically active form of vitamin E. The antioxidant efficiency of vitamin C is significant at physiological concentrations of 20–90 μM.

Reduced **glutathione** (GSH) is another water-soluble antioxidant. The GSH is made in the liver, kidneys and intestine from three amino acids (glutamyl-cysteinyl-glycine). The SH in GSH refers to the **cysteine** portion of the molecule, which is involved in oxidation/reduction reactions. In its role as an antioxidant, two molecules of GSH (2GSH) are oxidized into glutathione disulphide (GSSG) coupling with reduction of the α-tocopherol radical into α-tocopherol. The enzyme glutathione reductase is involved in the interconversion of GSSG to GSH (i.e.

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GSSG → 2GSH). The reducing equivalents required to convert GSSG into GSH come from glucose-6-phosphate via the production of NADPH. When GSSG is reduced to 2GSH an equivalent of NADPH is oxidized to $NADP^+$. The direct use of glutathione in protection against ROS depends on GPx. GPx is a cystolic **enzyme** that catalyses the reduction of H_2O_2 and lipid peroxides (ROOH). In the presence of GPx, 2GSH reacts with H_2O_2 and produces $2H_2O$ and GSSG. When H_2O_2 is not catabolized by GPx, it can produce the hydroxyl radical ($^{\bullet}OH$), in the presence of ferrous iron (Fe^{2+}), which is the most powerful ROS involved in tissue damage (such as the production of MDA from PUFA).

Lipoic acid (1,2-dithiolane-3-pentanoic acid), known as **thioctic acid**, acts as an antioxidant. It is synthesized in the mitochondria from PUFA and cysteine. Lipoic acid contains two vicinal sulphur atoms that are subject to oxidation/reduction; the reduced form of lipoic acid (dihydrolipoic acid) has two thiols. Lipoic acid functions as an amphipathic antioxidant capable of quenching free radicals, regenerating other cellular antioxidants. Lipoic acid is involved in cellular antioxidant protection through both direct and indirect functions. Dihydrolipoic acid is able to reduce oxidized forms of other cellular antioxidants, including glutathione, α-tocopherol and ascorbic acid, as well as quenching ROS and RNS. Several studies have reported that dietary supplementation of lipoic acid enhances antioxidant capability and shelf life of ruminant and poultry meat and meat products.

Carotenoids, well known as pigments, are effective fat-soluble antioxidants protecting cells against oxidative damage. Carotenoids

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most efficiently react with peroxyl radicals ($ROO^{\bullet}$). β-Carotene, α-carotene, lycopene and lutein are the main carotenoids with antioxidant activity. Lycopene is the most potent carotenoid antioxidant, being twice as effective as β-carotene in quenching singlet **oxygen** ($^1O_2$) and ten times as effective as α-tocopherol. It is found in significant amounts in red-coloured foods such as tomatoes, watermelon, pink grapefruit and guava. Lutein and zeaxanthin found in corn represent major sources of pigmentation for poultry diets. The **xanthophyll**, **astaxanthin**, is the source of the pink colouration of salmon.

Polyphenol compounds in plants, a subclass of phytochemicals, have antioxidant properties. They have a large diversity of structures, from simple molecules to complex polyphenols, grouped as phenolic acids (e.g. rosmarinic acids, caffeic acids and gallic acid), phenolic diterpenes (e.g. carnosol and carnosic acid), flavonoids (e.g. quercetin and catechin) and essential volatile oils (e.g. carvacrol, thymol, eugenol and menthol). Tannins and flavonoids can scavenge free radicals, rendering them inactive; they are widely found in agricultural by-products. For example, grape pomace, olive pomace and pomegranate fruit are rich sources of polyphenol compounds. Although antioxidant activity for some flavonoids (e.g. quercetin, catechin, anthocyanins, gallic and ellagic acid) has been shown *in vitro,* not many studies have been conducted *in vivo* to validate their antioxidant functions in biological systems, and this area has the potential for future research.

By maintaining and/or increasing the intake of natural

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antioxidants or antioxidant enzymes as feeds (foods) and supplements, the development of free radicals in the animal body can be minimized. This in turn will reduce animal health issues (e.g. by alleviation of oxidative stress), improve livestock performance on-farm and ultimately product quality, through its effects on the preservation of meat and milk. For example, supplementation of animal diets with high levels of vitamin E inhibits the development of off-flavours in meat and meat products by lipid peroxidation (oxidative **rancidity** of lipids) and colour deterioration (**haemoglobin** oxidation). A vitamin E concentration of 3.0–3.5 mg kg^{-1} of **meat** is sufficient to maintain the retail colour stability of beef and sheep meat under simulated commercial retail conditions. Similarly, polyphenols improve oxidative stability, retard the development of off-flavours, and improve the colour stability of meat. Phytochemical supplementation in the diets of farm animals has shown enhanced antioxidant activity in milk and dairy products. (ENP, AK)

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Antiparasitic agents

Parasites may colonize either the internal or external medium of animals, or occasionally both, but are present in greatest numbers outside their host animal vector. Currently treatment of infected animals is usually based on anthelmintic agents but resistance is increasing, particularly in nematode worms. Attention is turning to prophylactic measures, such as the provision of uninfected pasture, and biological control, in particular by treatment of the parasite with fungi in its native pasture environment. (CJCP)

Antiprotozoal agents

Protozoa are single-celled organisms that are often present in soil and may be transmitted to farm animals when feeding or by insect vectors. Many infect the digestive tract; others penetrate vital organs. A variety of drugs are available to treat protozoal diseases but they can be difficult to eradicate. Some antibacterial and anti-fungal agents have a limited effectiveness in treating protozoal infections. Chemoresistance is also emerging and new drugs must be targeted for effective chemotherapy. (CJCP)

Apo-enzyme

An enzyme form that requires a co-factor in order to function. The intact enzyme protein without the enzyme cofactor bound to it is called the apo-enzyme. When the enzyme co-factor is bound to the enzyme protein this combination is called the holo-enzyme. An example is the red blood cell enzyme transketolase. The vitamin co-factor **thiamine** diphosphate binds to the enzyme and aids in

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the reaction but is not permanently changed by the reaction. This relationship is different from that of other vitamin-dependent co-substrates such as NAD or NADP, which are changed to NADH and NADPH, respectively, as a result of the **enzyme** reaction. (NJB)

Apolipoproteins

Proteins that are essential components of the lipid transport system in the body, which involves **chylomicron**s and the **lipoprotein**s HDL, LDL, IDL and VLDL (high-density, low-density, intermediate-density and **very low-density lipoprotein**s). Two general types of lipoproteins are identified: those that are integral (e.g. apo B-100), which cannot be removed and are critical to structure and function; and those that can be exchanged (e.g. apo A, apo C etc.). Apolipoproteins also act as enzyme co-factors and as ligands for lipoprotein receptors on cell surfaces. (NJB)

Apparent digestibility

Digestibility determined simply from the difference between the amount of a nutrient consumed (I) and the amount excreted in the faeces (F), expressed as a proportion of the intake. Thus, apparent digestibility = (I – F)/I. It is also determined at the terminal **ileum** by measuring the loss of the nutrient in ileal **digesta** (D); thus apparent digestibility at the terminal ileum = (I – D)/I. Unlike **true digestibility** or **real digestibility**, apparent digestibility ignores losses of endogenous origin which increase faecal excretion and give a lower digestibility value. (SB)

See also: Digestibility

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Appetite

An instinctive desire for food or drink, or any other instinctive desire necessary to maintain life. Regarding feeding, appetite is an object or objective, such as obtaining a food or foodstuff. For example, during a meal, the appetitive phase is the goal-directed behaviour focusing on acquiring food, while the consummatory phase is the act of ingestion. During the consummatory phase, mechanisms are initiated that help to terminate the meal. The degree of disposition towards obtaining food may vary greatly, so that the appetite may be a subtle or overwhelming compulsion.

Hunger is often used synonymously with appetite, but differs in several aspects. Hunger may be viewed as the 'stimulus to eat' that arises from internal cues which provide information about energy or essential nutrient status. Hunger may be considered the motive to eat, in the same way that thirst is considered to be the motive to drink. Appetite may arise from the same internal cues that are responsible for hunger, as well as from the sight or smell of food, or from psychological desires or cravings. Appetite often implies a greater selectivity towards the food(s) consumed than hunger.
In contrast to food intake, which can be quantified in terms of the amount of food consumed per unit time, appetite is difficult to quantify and so the mechanisms controlling appetite are not differentiated from the mechanisms that control food intake. Food intake is controlled, both on a long-term, day-to-day and within-meal basis. On a long-term basis, adult animals will adjust their food intake to maintain a relatively stable body weight. On a day-to-day basis, animals will eat a relatively constant amount of energy

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each day and will correct for daily perturbations in **energy intake**. Circadian, diurnal or specific daily feeding patterns also contribute to how and when food is consumed within a day – these patterns can vary greatly between species. Within a meal, there are mechanisms that initiate the meal, sustain the meal and terminate the meal. Stimuli arising from within the body (internal) as well as from environmental (external) stimuli may be involved in initiating a meal. Very little is known about the internal stimuli that initiate a meal. Nonetheless, these stimuli are probably **energy metabolite**s in nature, and signal information regarding energy or essential nutrient (e.g. **glucose**) stores. The internal stimulus responsible for initiating the meal probably gives rise to the feeling of appetite or hunger. External stimuli that may be involved in initiating a meal can include social eating habits, the sight or smell of food, or other environmental factors. Signals from long-term energy stores such as **adipose tissue** also influence feeding, as low levels of **insulin** or **leptin** enhance feeding.

The appetite for food is controlled by the central nervous system (CNS), but is also responsive to metabolic, humoral and vagal signals originating from the periphery. Metabolic modulators include small transient drops in blood glucose that precede a meal, as well as hepatic glucose and fatty acid metabolism. Hormonal signals include factors such as amylin, **apolipoprotein** AIV, enterostatin, **oestrogen**, leptin, **glucagon**, **glucocorticoids**, insulin and somatostatin. The vagus nerve transmits information to the brain regarding gastric or rumen distension and the release of gastrointestinal peptides during a meal.

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While it is generally thought that animals eat to meet their energy demands, there are numerous circumstances when this is not true. Highly palatable diets often cause animals to overeat and become obese, while extremely unpalatable diets will cause animals to undereat. A diet extremely deficient in an essential nutrient will cause **anorexia** if it is the only diet available. At the same time, animals fed mildly protein-deficient diets may overconsume the diet in an attempt to obtain more protein. Appetite is also suppressed during infection and cancer. **Cytokines** such as tumour necrosis factor-α, interleukin-1 and interleukin-6 appear to be the primary cytokines responsible for infection- and cancer-induced anorexia.

Neurotransmitters such as **norepinephrine**, **serotonin**, **dopamine**, **histamine** and GABA have all been shown to be involved in the control of feeding. Neuropeptides or peripheral peptides that act at CNS sites to affect food intake include agouti-related protein, amylin, α-melanocyte-stimulating hormone, bombesin, cocaine and amphetamine-related transcript (CART), corticotropin-releasing factor, enterostatin, galanin, glucagon, glucagon-like **peptide**, insulin, melanin-concentrating hormone, opioids, orexin (hypocretin), neuropeptide Y, somatostatin, thyrotropin-releasing hormone and urocortin. Differences in the role and importance of these neurotransmitters and neuropeptides vary with species.

Numerous brain areas are involved in the control of appetite. The **hypothalamus** plays a critical role, particularly the arcuate nucleus, paraventricular nucleus, lateral hypothalamus,

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ventromedial hypothalamic nucleus and the dorsomedial nucleus. The caudal brainstem also plays an important role in feeding, as it contains the motor neurones that function as the central pattern generator for the rhythmic and stereotyped movements of ingestion (e.g. **mastication**, licking, lapping). The caudal brainstem also receives afferent fibres from the mouth, stomach and small intestine. Higher cortical brain areas are involved in multiple aspects of food intake, including making food associations, such as learned preferences and learned aversions, controlling motor movements necessary for finding or catching food, or making appropriate food choices.

Specific appetites arise from the animal's attempts to maintain an adequate intake or prevent a deficiency of dietary essential nutrients such as protein, vitamins and minerals. For example, animals maintain a level of protein intake above their requirement when allowed to select between different foods – this is often considered a specific appetite for protein. Animals deficient in a specific essential nutrient will select foodstuffs or diets containing the deficient nutrient over foodstuffs lacking the needed nutrient – this is also considered a specific appetite and serves to restore **homeostasis** in deficient animals. All specific appetites except sodium appetite appear to require post-absorptive feedback and learning before an animal will display a specific appetite for a given food. That is, the animal must first consume and absorb a specific food that contains adequate quantities of the needed nutrient. The brain then senses some event associated with the repletion of the limiting nutrient or the restoration of homeostasis. This 'positive

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post-absorptive event' is then associated with some aspect of the consumed food (usually taste) and will direct the animal toward obtaining and consuming this specific food during subsequent meals. In contrast, sodium appetite is innate and does not require post-absorptive feedback or learning. Animals deficient in sodium will immediately recognize foods containing this nutrient.

Perverted appetites or pica involve the intake of inedible or non-nutritive material such as earth, hair, bone, etc. The purpose of pica is unknown, but under some circumstances pica may occur during expression of a learned taste aversion or during states of **nutrient deficiency**. (NJB)

Appetite disorders

Appetite disorders may be secondary effects of diseases, most of which cause a reduction in food intake, or they may be diseases themselves, such as **anorexia**. Many diseases cause a fever, with elevated body temperature. A reduction in food intake occurs, which is presumed to derive from a direct effect of the elevated temperature on the brain. Diseases involving abdominal discomfort (e.g. ovarian cancer) also depress intake: the reduction in intake should alleviate the discomfort, particularly if the food was the source of the problem. Other diseases are metabolic, i.e. in the body as distinct from the digestive tract, and again a reduction in intake is an innate response to metabolic imbalance or discomfort. In a normal animal, this is most likely to be due to the food but, even if it is not, intake will still be reduced. On the other hand, there are certain metabolic abnormalities that lead to an increased intake; for example, insufficient **insulin** secretion, as in **diabetes**,

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does not allow normal cellular uptake of **glucose**, with the result that certain cells (liver, hind-brain) signal their shortage of energy to the intake-controlling circuits of the brain. Appetite disorders are not likely to be transmitted genetically as they cause infertility and premature death. (JMF)
See also: Anorexia

Appetite stimulant

A single compound or group of compounds that flavours a feed to increase the appetite. These include yeasts, mixtures of herbal extracts, distillery or brewing **by-product**s and simple **sugars**. Appetite refers to the desire of an animal or bird for food or water, but is generally used to refer to a long-term effect. A number of compounds have been reported to be effective in the diets of young pigs but the literature is somewhat conflicting. Poultry have < 1% of the taste buds found in humans or other farm animals and these stimulants are ineffective (Chiy and Phillips, 1999). (SPR)
See also: Flavour compounds

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Apple

The juice of apples (*Malus* spp.) is extracted for apple juice or cider, leaving a residue of apple pomace that contains the remaining tissue, skins, pips and stalks. Pomace may be fed directly to livestock, dried, or sold moist. Some pomace has absorbents (e.g. wood shavings) added to aid juice extraction, which increase the

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fibre content and reduce the nutrient concentrations. Apple pomace is palatable and suitable for feeding to adult ruminants but it is low in protein (*c.* 5%) and in minerals. It is also low in **dry matter** (DM) and has only the moderate energy level of ~10 MJ ME kg^{-1} DM for cattle. Moist apple pomace can be stored for up to 6 months covered in clamps and its **bulk density** when moist is < 150 kg m^{-3} and when dried < 350 kg m^{-3}. The pectin and **pentosan** contents make it unsuitable for young ruminants, piglets and poultry. Maximum DM inclusion rates as a percentage of diet are 20% for dairy and beef cattle, 10% for lambs and 5% for ewes, sows and finishers. (JKM)

Aquaculture

The cultivation of **aquatic organisms** (fish, crustaceans, molluscs, unicellular algae, macroalgae and higher plants), using extensive or intensive methods in order to increase the production or yield per unit area or unit volume to a level above that obtained naturally in a particular **aquatic environment** (Hall and Holby, 1986). The term does not apply to the impoundment of aquatic organisms for direct sales in markets; nor does it include the culture of essentially terrestrial organisms (e.g. terrestrial plants grown hydroponically).

Aquaculture includes ponds, raceways, cages, pens, rafts, paddy fields, intertidal zone and greenhouse culture. Marine (as opposed to freshwater) aquaculture has been termed 'mariculture'. Aquaculture encompasses the culture of aquatic organisms for stock enhancement, ocean ranching and ornamental purposes. The

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objectives of aquaculture are to increase production above levels occurring in natural ecosystems and to provide a more stable temporal supply of food organisms of consistently higher food quality under greater human control than can be supplied through the natural fisheries. These objectives are realized through selection of species or strains with higher feed conversion efficiencies, higher growth rates, later maturity and greater resistance to disease.

Commercial aquaculture is an ancient practice, though large-scale farming is relatively recent. The earliest known treatise on aquaculture is the *Classic of Fish Culture* in 500 BC by Fan Lɛi, a Chinese politician turned fish culturist who attributed his accumulation of wealth to pond production of carp. However, in reality the first practical aquaculture probably was the integrated fish farming in paddy rice fields in Hemudu Site in Qiantang River, China, in approximately 5000 BC, as evidenced by the discovery of large quantities of carbonized rice and fish together at that site. Oyster culture is known to have been practised in Japan and Greece *c.* 2000 years ago. **Seaweed** culture is much more recent, the earliest known text being published in 1952 in Japan. Fish farming in Europe was first carried out by the Etruscans, in approximately 500 BC.

World aquaculture production attained a record high of 114.5 million tonnes in liveweight in 2018, with a total farmgate sale value of US$ 263.6 billion. This comprised 82.1 million tonnes of aquatic animals, 32.4 million tonnes of aquatic algae and 26,000 t of ornamental seashells and pearls. The farming of aquatic animals

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in 2018 was dominated by finfish (54.3 million tonnes). Fed aquaculture production (57 million tonnes) has outpaced that of the non-fed subsector in world aquaculture. World aquaculture production of farmed aquatic animals grew on average at 5.3% per year in the period 2001–2018, although it slowed towards the end, 4% in 2017 and 3.2% in 2018. The recent low growth rate was caused by a slowdown in China, the largest producer (FAO, 2020)

In 2018, inland aquaculture produced 51.3 million tonnes of aquatic animals, accounting for 62.5% of the world's farmed food fish production, an increase from 57.9% in 2000. Mariculture and coastal aquaculture collectively produced 30.8 million tonnes of aquatic animals in 2018. Major aquatic organisms currently under culture include several species of carp, catfish, tilapia, oyster, scallop, clam, mussel, prawn, marine shrimp, salmon, trout, grouper, sea bass and sea bream. Despite technological developments in marine finfish aquaculture, marine and coastal aquaculture produce many more molluscs than finfish and crustaceans (FAO, 2020).



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Coastal net pens off the coast of Maine. Photograph courtesy of NOAA National Centers for Coastal Ocean Science

World aquaculture production of farmed aquatic animals has been dominated by Asia, with an 89% share in the past two decades or so. Among major producing countries, PR China, Egypt, Chile, India, Indonesia, Vietnam, Bangladesh and Norway have consolidated their share of world production over the past two decades (FAO, 2020).

The contribution of world aquaculture to global fish production reached 46.0% in 2018, up from 25.7% in 2000. At a regional level, aquaculture accounted for 17.9% of total fish production in Africa, 17.0% in Europe, 15.7% in the Americas and 12.7% in Oceania. The share of aquaculture in Asian fish production outside of China reached 42.0% in 2018, up from 19.3% in 2000. Inland aquaculture produced most farmed fish (51.3 million tonnes, or 62.5% of the world total), mainly in fresh water, compared with 57.7% in 2000. The share of finfish production decreased gradually from 97.2% in 2000 to 91.5% (47 million tonnes) in 2018, while production of other species groups increased, particularly through freshwater crustacean farming in Asia, including that of shrimps, crayfish and crabs (FAO, 2020). (RHP; QS)

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Aquatic environment

Aquatic environments encompass both freshwater (lakes, rivers, wetlands) and saline (oceans, estuaries, salt lakes and sloughs) conditions. They display a wide range of thermal regimes, pH, salinity and other chemical characters, clarity, and degree of movement, all of which determine the type of organisms that occupy them. A stagnant pond, for example, is a very different aquatic environment from a fast-flowing river or exposed ocean coast. Although aquatic habitat is usually judged to be physically more stable than the aerial or terrestrial environment, it is nonetheless subject to periodic changes. In temperate latitudes, seasonal thermal changes may be considerable, from freezing to 30°C or more. Water levels rise and fall seasonally, or more frequently in the case of tides, periodically exposing some inhabitants to air. Estuarine habitats may experience large fluctuations in salinity within hours. The organisms that live in these environments influence the physical properties to some extent, as in trapping or producing sediment, obscuring clarity of

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the water, or changing the content of oxygen and other chemical constituents. (CB)

Aquatic organisms

Organisms living in fresh, brackish and **sea water** are generally divided into plankton, nekton, benthos and neuston (invertebrates, fish, mammals, etc.). Most fish and aquatic invertebrates are poikilotherms (body temperature conforms to external environment) with their **metabolic rate** increasing as the **water temperature** increases. Marine invertebrates are osmoconformers; **marine fish**, however, maintain their plasma hypotonic to that of the seawater medium by drinking, reducing urinary water loss and excreting salt through the gills. **Freshwater fish** osmoregulate by pumping out water while retaining the salts. External respiratory surfaces (gills) must be kept moist for gas exchange.

In the **marine environment**, many small free-floating eggs are often released and externally fertilized. The larvae are widely dispersed and feed on plankton, thus reducing the need for a large **yolk sac** within the egg. High mortality rates are associated with these planktonic larvae. In a freshwater environment, generally eggs are either retained by the parent or associated with the bottom and contain a large yolk sac, which produces more highly developed larvae or juveniles at hatch. Aquatic animals usually excrete nitrogenous wastes in the form of **ammonia**, a soluble toxic substance requiring large amounts of water for its removal. (DN)

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Aquatic plants

Vegetation that has adapted to living in saltwater or freshwater **aquatic environment**s. It is normally associated in nature with standing water, either permanently or at least for prolonged periods during the year. The plants may be wholly submerged, or with photosynthetically active parts entirely or partly submerged. In the broad sense of the term 'plants', they are represented by flowering plants, ferns, bryophytes, algae and fungi. As **marine plant**s are generally categorized separately, the term 'aquatic' is often applied to only the freshwater species. The distinction between true aquatic plants and those that inhabit wet soils is unclear and ultimately relies on whether the plant requires some degree of submersion or merely tolerates it. Some intrinsically terrestrial plants can be relegated to aquatic habitats by poor competitive ability on drier soils, for example *Taxodium* (bald cypress). Herbaceous vascular plants dominate the aquatics, spanning a large number of families and ranging in size and habit from minute floating species, for example *Lemna* and *Wolffia* (duckweeds), to tall emergent forms such as *Oryza* (rice) and *Typha* (cattails). Freshwater algae comprise at least 15,000 species but are mostly microscopic and inconspicuous. Fungi are small filamentous species.

Aquatic plants are important in stabilizing shorelines and purifying water. They exhibit capacity to remove **arsenic** (As) from the water and soil sediments. Ironically, where water movement is minimal, they often contribute to the destruction of their aquatic habitat by accruing sediment, towards hydrarch

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succession to terrestrial conditions. Aggressively growing and invasive macrophytes can be nuisances, clogging waterways, altering food webs, reducing dissolved oxygen concentrations and producing anoxic conditions after death. The large biomass of such plants means that it may be used as a supplement to silage and other livestock feed; for example, *Eichhornia crassipes* (water hyacinth), one of the well-known aquatic invaders, has sometimes been used for this purpose.

As a result of human activities some aquatic plants are expected to undergo radical changes because of increased **bicarbonate** concentrations in lakes due to acidification, deforestation and use of nitrogen fertilizers. (CB; DB)

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Arabinogalactans

Branched heteropolysaccharides with molecular weight 16,000–100,000, having varying proportions of D- or L-**arabinose**, and D-**galactose**; arabinose may be present in the **furanose** or **pyranose** ring form, galactose in the pyranose form. The backbone frequently consists of galactose residues. Arabinogalactans are usually water soluble and they may be covalently linked with protein. They may contain small amounts of **rhamnose** and **uronic acid**s. They are the major **hemicellulose**s in plants. (JAM)

See also: Arabinose; Dietary fibre; Galactose; Hemicelluloses

Arabinose

A five-carbon **sugar**, $C_5H_{10}O_5$, molecular weight 150, in L- or D-form and as a **pyranose** or **furanose** ring. Does not occur free in nature. A major component of plant **polysaccharide**s. Absorbed in the **small intestine** by passive **diffusion**. (JAM)

Arabinoxylans

Branched heteropolysaccharides with molecular weight 6000–30,000, having varying proportions of **arabinose** (usually in L-form and as the **furanose** ring) and **xylose** (in D-form and as the

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pyranose ring). Arabinoxylans frequently contain linear chains of xylose residues and may include small amounts of **uronic acid**s. They are water soluble and are the major constituents of plant cell walls, particularly in cereals and grasses. (JAM)
See also: Arabinose; Carbohydrates; Dietary fibre; Hemicelluloses; Structural polysaccharides; Xylose

Arachidic acid
Eicosanoic acid, a saturated **long-chain fatty acid**, $CH_3{\cdot}(CH_2)_{18}{\cdot}COOH$, shorthand designation 20:0. It is found in **groundnut** oil, **rape** oil, butter and **lard**. (NJB)

Arachidonic acid
5,8,11,14-Eicosatetraenoic acid, molecular structure $CH_3{\cdot}(CH_2)_4(CH{=}CH{\cdot}CH_2)_4{\cdot}(CH_2)_2{\cdot}COOH$, a long-chain **unsaturated fatty acid**, shorthand designation 20:4, found in fish and groundnut **oils**. It is an **essential fatty acid** for the cat family, but can be produced from **linoleic acid** in many animals. This makes linoleic acid an essential fatty acid and without it a deficiency of arachidonic acid is expected. Arachidonic acid is found in high concentration in membranes as part of the **phospholipid** fraction. Metabolically it is a precursor of the **prostaglandin**s, thromboxanes and **leukotriene**s. (NJB)

Arctic char (*Salvelinus alpinus* (L.))
The most northerly adapted of the **salmonid** fish, with a circumpolar natural range. There are both anadromous and strictly freshwater forms. Eggs should be incubated at less than 8°C, and

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the optimum temperature range for growth is 10–13°C. Iceland is the major producer of cultured Arctic char. A major problem for culture to date has been highly variable growth rates. (RHP)

Arginase

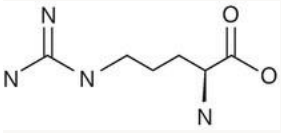
This enzyme catalyses the **hydrolysis** of L-**arginine** into **urea** and L-**ornithine**. There are two isoforms of arginase in animals. Type-I arginase is present in the cytosol of hepatocytes and many other cell types, whereas type-II arginase occurs in the mitochondria of extrahepatic tissues and cells. Arginase is also found in some tissues (e.g. the kidneys) of birds, which excrete **nitrogen** mainly as uric acid. Arginase activity in avian cells is much less than that in most mammalian tissues. In ureotelic animals, the highest activity of arginase is found in the liver but this protein is also expressed in other tissues such as the kidney, small intestine, brain, mammary gland, macrophages and red blood cells. Arginase plays important roles in **ammonia detoxification** in all mammals, as well as in the synthesis of **proline** and **polyamine**s in all animals. (GW; NJB)

Arginine

An **amino acid** ($NH_2{\cdot}NH{\cdot}C{\cdot}NH{\cdot}(CH_2)_3{\cdot}CH{\cdot}NH_2{\cdot}COOH$, molecular weight 174.2) found in protein and physiological fluids. Arginine is synthesized from **citrulline**, which is generated from **glutamine**, **glutamate** and **proline** in the **enterocyte**s of most mammals, including humans, pigs, cattle, sheep and rats. Although arginine is formed via the **urea cycle** in mammalian hepatocytes, there is no net synthesis of this amino acid by the liver due to an

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exceedingly high activity of **arginase**. In neonatal mammals, the **small intestine** is the primary site for arginine synthesis from glutamine, glutamate and proline. In post-weaning mammals, the kidneys become the major site for the conversion of the small intestine-derived citrulline into arginine. Most of young mammals (e.g. humans, pigs, rats, cattle, sheep and dogs) can synthesize sufficient arginine to achieve growth rates that are about 50% of maximal and, therefore, require this amino acid for maximum growth and optimum health. Most adult mammals do not require arginine in the diet for maintaining **nitrogen balance**, but they do need dietary arginine to meet physiological needs such as **nitric oxide** synthesis, **blood flow**, spermatogenesis, embryonic survival, wound healing and maximum **lactation**. Feline species, however, have a limited ability to synthesize arginine and therefore require arginine in their diets. (GW; DHB)



See also: Citrulline; Urea cycle

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Arsanilic acid

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Formerly used as a feed additive, as a coccidiostat in broilers and as a **growth promoter** in pigs and broilers, which makes use of its antibacterial properties. Feed efficiency is increased but residues of **arsenic** occur in meat and offal. (JMF)

Arsenic

A mineral element (As) with an atomic mass of 74.92. It is found naturally in small amounts in **sea water** and rocks. Soils contain from 1 to 40 mg kg^{-1} but can accumulate more where **arsenical pesticide**s and herbicides are used. Vegetables and grains contain < 0.5 mg kg^{-1}; **freshwater fish** contain an average of 0.75 mg kg^{-1} and seawater **shellfish** may contain much higher concentrations. Arsenic compounds can leach into ground water and contaminate well water. This has prompted some regulatory agencies to suggest a limit of 10 μg As l^{-1} drinking water for human consumption.

Arsenic as arsenate or arsenite is readily absorbed from the intestine and some of the As is converted to the methylated form in the liver before being excreted in the **urine**. There is no known metabolic function for As and it is generally considered to be a toxic substance. However, some investigators have found evidence, though weak, that As might have limited nutritional benefit in certain animal species, especially ruminants. The phenyl-arsenic compounds are the least toxic and are used as feed additives in the diets of pigs and poultry as a growth stimulant, whereas the water-soluble inorganic compounds are the most toxic, resulting in their use as **pesticide**s. Although the element is also considered a

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carcinogen, its trioxide form has been used to induce remission of acute promyelocytic leukaemia in humans. Low concentrations of **selenium** and As have been shown to induce hypomethylation of DNA in isolated intestinal cell models. This mechanism is thought to give selenium its anti-carcinogenic properties. Whether As has similar properties is not known. Natural **antagonist**s to **intestinal absorption** and organ accumulation of As are other dietary minerals such as **selenium**.

Although the inorganic forms of As are more toxic than the organic forms, it has been reported that cattle and sheep can tolerate various inorganic As compounds in dietary concentrations up to 280 mg kg^{-1} for 60 days or more without ill effects. Pigs also tolerate rather high amounts of dietary arsenic, but they have reduced food intake at concentrations > 500 mg kg^{-1}. (PGR, CJCP)

See also: Selenium

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Arsenicals

Arsenic-based compounds used as **pesticide**s in crops and livestock, especially for tick control. Arsenical pesticides present

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significant hazards to animal health, causing gastroenteritis and a rapid drop in blood pressure. (CJCP)

Artemisia

Artemisia annua, from the Compositae family, is widespread and diverse.



Artemesia tridentata ssp. *Wyomingensis* (Wyoming big sagebrush), with seed stalks. This plant is of value in the nutrition of livestock and wildlfe. Photo courtesy of USFWS Mountain Prairie. Licensed under CC BY 2.0.

A. annua is an annual plant with relatively bitter and aromatic leaves due to the presence of the high content of terpenoids and lactone-**terpene**. It is abundantly found in temperate regions. Its main effective ingredient is artemisinin, which is distributed throughout the plant (Al-Khayri *et al*., 2022). The WHO believes

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that this plant has valuable nutritional and medicinal properties (WHO, 2006). With the support of the United Nations, the *A. annua* plant has been used in the treatment of malaria (Soni *et al*., 2022). Artemisinin in *A. annua* can be effective against various cancer cells, such as leukaemia and **colon** cancer (Baldi and Dixit, 2008), and in the treatment of AIDS, hepatitis and corona virus. A hydroalcoholic extract of *A. annua* causes the destruction of the cyst stage of *Giardia lamblia* parasite (Bahman *et al*., 2012). Ethanolic and chloroform extracts of this plant can prevent the growth of ***Escherichia coli***. Artemisinin can strengthen the host's immune system, and, as an immune stimulant, it can be considered as an alternative to in-feed antibiotics. Also, due to the antiparasitic effects of the compounds of artemisinin and the high **antioxidant** capacity of crude extracts of this plant, its use as a dietary supplement for humans and domestic animals (ruminants and poultry) is expanding. In animals (sheep and goats), *Artemisia* spp. have antiparasitic activity, for example against *Fasciola*, *Eimeria*, *Trichostrongylus* and *Haemonchus*. It also has positive effects on the performance and health of broiler chickens and laying hens (improvement of atherogenic index, antioxidant status and the reduction of **coccidiosis**) (Cherian *et al*., 2013; Baghban-Kanani *et al*., 2019). (AS, BH-G, CJCP)

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Artificial drying

Artificial drying of crops (‘parching’ over fire) dates back to biblical times. Green crop drying is normally associated with artificially drying with hot air. This method allows green crops to be preserved independent of weather conditions, at high nutritive quality with low conservation losses (as low as 3% of the dry matter). While dried grass accounted for 200,000 t in 1972 in the UK, this process

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declined in popularity during the 1980s due to the high cost of fossil fuels. Almost 300 l of oil is required to dry 1 t of dried grass from a crop of 80% moisture content. Composition of leafy dried grass can be dry matter (DM) 90%, **crude protein** 18.7% DM, **metabolizable energy** 10.6 MJ kg^{-1} DM. Barn drying provides a method of blowing cold air through a stack of cured hay bales to ensure that the moisture content of the dried hay is < 12%. Hay preservatives and drying agents allow for increased flexibility in haymaking systems. Under certain conditions, they can greatly increase the efficiency of nutrient preservation. The most common preservatives are **organic acid**-based formulations. Drying agents available are usually carbonate-based products, which may also contain **fatty acid** esters. (RJ)

Artificial rearing of mammals

The process of substituting intensive technology for the normal care and nutrition provided by the dam in neonatal life. The most extreme need applies when offspring have been removed directly from the womb by hysterectomy to establish minimal-disease flocks or herds. It also has a function for neonates deprived of maternal care by an accident, a breakdown in maternal health or because of failure of the dam to lactate. The boundary between artificial rearing and very **early weaning** is not exact. Very early weaning following a very short **lactation** may facilitate the breaking of the disease chain from parent to offspring, particularly if this is accompanied by intensive medication of the offspring. Some success is claimed for reducing the incidence of some pig diseases such as porcine respiratory and reproductive syndrome

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and enzootic pneumonias.

For successful artificial rearing, the complex physiological needs must be met. The environment must be controlled so that the nutritional, social and physical environment provided by the dam can be simulated in the essential aspects. The immune system of the neonate at birth is naive. Rearing is greatly facilitated if the neonate can receive passive **immunity** via colostrum or by an equivalent dose of relevant **immunoglobulins** extracted from blood. At birth the gut is permeable to proteins and the globulins can be absorbed directly into the bloodstream. The benefits may be sustained well towards adult life. Offspring that are totally deprived of colostrum need 'hospital quality' care. This should include protection from air- and food-borne pathogens, a stable temperature and isolation from other livestock. The process of normalization of the environment needs to be very gradual and in step with the development of active immunity.

Nutrition during artificial rearing is critical to its success. The closer the artificial diet is to the composition of the natural milk of the species, the better the outlook. Growth rates tend to be more normal if the artificial diet is offered in a liquid rather than a solid form. Liquid feeding requires particularly diligent hygiene. In ruminants, **liquid diet**s carry an additional benefit because they stimulate the reflex closure of the oesophageal groove and allow the food to bypass a non-functioning rumen. The reflex is assisted by a husbandry routine that raises the expectation of being fed. The **protein source** in the artificial diet is critical. The **casein** in milk has clotting properties in the presence of the stomach enzyme

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rennin, and this attribute aids **digestion**. Proteins other than those of milk are often less suitable partly because they do not clot and are usually less soluble. Those of vegetable origin tend to be difficult to digest, because the molecules are larger than those of the milk proteins and they may provoke an immune reaction. Milk fats are easily digested, particularly if emulsified, but in dry diets **lipids** rich in **medium-chain fatty acid**s tend to be the most readily digested. **Lactose** not only supplies energy but is also readily fermented in the gut, encouraging the development of a friendly, lactobacillus-based flora. (VRF)

Artificial rumen

A vessel in which rumen contents can be incubated under conditions resembling those of the rumen *in vivo*. It may be a closed or open system operating batchwise or a continuous-flow stirred tank reactor (CFSTR) or chemostat that will achieve a steady state. Such systems allow study of the products of rumen fermentation, the population dynamics of rumen microflora or studies of the degradation kinetics of components of forage and feeds, **methanogenesis** etc. The most complex of these continuous fermenters involve dialysis of the products to mimic **absorption** and gaseous exchange. Temperature, pH and redox potential may be monitored or controlled. The system may be used to study isolated pure cultures or mixed microbial and **protozoa**n ecosystems. Artificial rumen systems allow study of the time course of change of **substrates**, gases and organisms. They are usually kept anaerobic using hydrogen and reducing agents. Simple batch systems are more easily managed. The semi-continuous rumen

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simulation technique (RUSITEC) designed by Czerkawski and Breckenridge (1977) is a widely used artificial rumen system.

Artificial rumens do not exactly parallel conditions in the rumen and give typically different results, for example lower total **volatile fatty acid** and **acetate** concentrations, reduced or absent **protozoa**l populations, and lower **organic matter** and neutral detergent fibre digestibilities (Hristov *et al*., 2012). When comparing results from different laboratories, it is important to understand the effects that differing sources of rumen liquor, **feed particle size**s and flow rate are likely to have on the results (Hristov *et al*., 2012). (IM, GMcLD)

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Artificial sweeteners:

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see Attractants; Flavour compounds

Ascites (or hydroperitoneum)
A non-inflammatory peritoneal effusion, seen as an accumulation of serous fluid in the abdominal cavity. Though ascites can be part of generalized vascular oedema (vascular **hypertension** or hypoproteinaemia), more typically it results from chronic passive congestion of the portal venous system of the liver, often as a sequel to hepatic diseases such as **cirrhosis** or veno-occlusive disease. Other traumatic, neoplastic or vascular diseases that obstruct venous or lymphatic draining can also cause ascites but are relatively rare. Ascites must be differentiated from other accumulation of fluid in the peritoneal space, including exudates from inflammatory diseases or urine from a damaged urinary system.

There are nutritional, infectious, immunological and toxic diseases that result in **liver disease** and ultimately cirrhosis. As cirrhosis is a non-specific change, definitively identifying the inciting cause is often a diagnostic challenge. Toxins that are commonly associated with liver disease in livestock include copper (sheep are most susceptible), **gossypol**, pitch (clay pigeons), cocklebur, lantana, sacahuista, lechugilla, some vetches, blue-green **algae**, **aflatoxin**s and pyrrolizidine-containing plants (*Senecio*, *Crotolaria*, *Amsinkia*, *Cynoglossum*, *Echium*, *Symphytum* and *Heliotropium* spp.). One of the common lesions of pyrrolizidine **alkaloid** intoxication is fibrosis and obliteration of the hepatic central vein (veno-occlusive disease).

Avian ascites or broiler pulmonary hypertension syndrome is a

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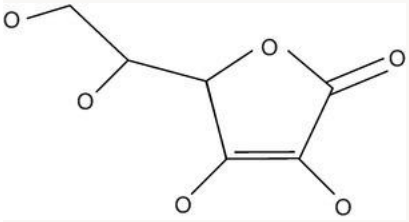
disease of rapidly growing broilers. Birds 3–4 weeks old are the most commonly affected and flock mortality can be nearly 20%. Ascites syndrome worldwide costs about US$1 billion, with an average incidence of 4.7% in broiler flocks. Affected birds are stunted and lethargic, with abdominal enlargement and lack of appetite. Post-mortem changes include marked right ventricular dilation and hypertrophy, arterial hypertrophy, ascites (serous fluid distension of the abdomen), pulmonary congestion and oedema. Although the aetiology of ascites syndrome is not completely known, it is closely associated with right congestive heart failure. Other proposed contributing factors include chronic oxygen deficits (housing at elevations of 3000 m), poor ventilation, high-energy diets and salt, monensin or furazolidone **supplement**s. Of all these aetiologies, those that contribute to rapid growth appear to be most closely linked to broiler ascites. A likely pathogenesis is that rapid growth and increased oxygen requirements lead to cellular oxygen deficits, pulmonary arterial **hypertension**, right heart failure, passive congestion of the abdominal organs and ascites. A comparable syndrome with similar nutritional and genetic contributing factors is seen in turkeys (round heart disease). Other toxins have also been shown to cause ascites in birds. Severe ascites and oedema were reported in the 1960s when thousands of birds were poisoned with polychlorinated dibenzo-*p*-dioxin 'chick oedema factor'. Poisoned birds developed extensive hepatic necrosis and cholangiolar hyperplasia and portal hypertension. Heart failure is common in ascites produced in birds poisoned with high-salt diets or furazolidone. Ducklings and

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turkeys appear to be most susceptible to furazolidone toxicosis. (BLS)

Ascorbic acid

L-Ascorbic acid is **vitamin C**, $C_6H_8O_6$. It is required in the diet of primates, guinea pigs and some bats and birds. In humans a dietary deficiency results in the classical symptoms of scurvy in which wound healing is impaired and subcutaneous haemorrhages are seen as well as muscle weakness, swollen gums and loose teeth. L-Ascorbic acid is a major water-soluble **antioxidant** involved in **oxidation**/reduction reactions in the body (ascorbic acid ⇌ dehydroascorbic acid + 2H). It participates in many processes, including **collagen** synthesis, in **epinephrine** synthesis from **tyrosine** and absorption of iron. (NJB)



Ash

The mineral elements in a feed, or in biological tissue, measured by burning off ('ashing') the **organic matter** and weighing the residue (the ash). During ashing the organic matter in the material under test is oxidized and minerals present in organic combination are changed to inorganic form. The measurement does not provide any information on the specific elements present and ash may include carbon from organic matter as carbonate when base-forming minerals are present in excess. As with the measurement

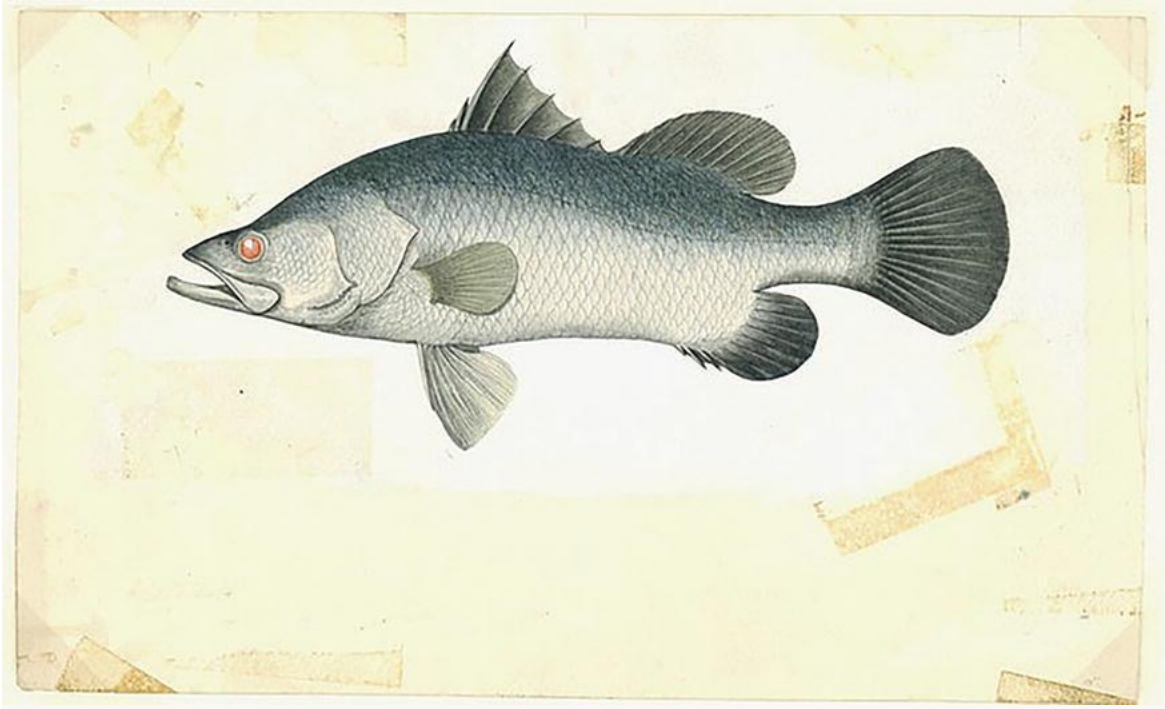
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of any feed component, it is important that a representative **sample** of the feed be used. The sample should be ground so that it will all pass through a sieve with 1 mm diameter openings; the sample should then be thoroughly mixed. A portion (2–3 g) is then dried to constant weight at 103°C and the moisture content determined. A portion (approximately 2 g) of the dried feed is weighed into a crucible (nickel or porcelain) and placed in a muffle furnace. The temperature is raised, stepwise, to 600°C. Ashing is allowed to proceed overnight (18 h), after which the crucible is transferred directly to a dessicator, cooled and weighed and the ash content of the sample determined as the weight remaining. (CBC)

Asian sea bass (*Lates calcarifer*)

A commercially important fish species farmed in several Asian countries and northern Australia. It belongs to the family Centropomidae and is commonly known as barramundi, bhetki or giant sea perch. Asian sea bass are widely distributed in tropical and subtropical areas of the Indo-Pacific region inhabiting a wide variety of freshwater, brackish and marine habitats, including streams, lakes, estuaries and coastal waters, but **spawning** only in inshore marine waters. These predatory fish feed initially on small crustaceans and later switch to fish. Juvenile sea bass may be cannibalistic. (RMG)

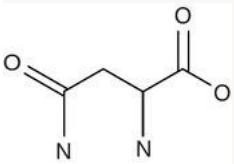
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Giant Perch, otherwise known as Palmer or Barramundi, Photo courtesy of Queensland State Archives. Licensed under Public Domain Mark 1.0.

Asparagine

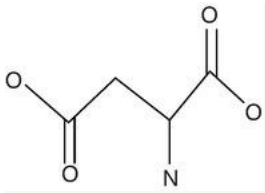
An **amino acid** ($NH_2 \cdot CO \cdot CH_2 \cdot CH \cdot NH_2 \cdot COOH$, molecular weight 132.1) found in protein. It contains both an amino and an **amide** group. It can be synthesized in the body from **aspartic acid**. (DHB)



Aspartic acid

A dicarboxylic **amino acid** ($COOH \cdot CH_2 \cdot CH \cdot NH_2 \cdot COOH$, molecular weight 133.1) found in protein. It can be synthesized in the body from **oxaloacetate** and an amino group donor. (DHB)

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Aspergillosis

A fungal infection (mycosis) caused by a number of *Aspergillus* spp. It is primarily a respiratory infection, especially in birds, but can affect the digestive and reproductive tracts. Clinical findings include dyspnoea, gasping and polypnoea, with microscopic evidence of fungal growth in affected tissues. Mastitis and **abortion** may occur in ruminants. (PC)

Associative effects of foods

The effect of one food on the utilization of another given with it; for example, the change in **digestibility** of feed A attributable to the presence of food B. Thus, a diet of equal parts of dry matter (DM) from coarse **forage** (DM digestibility 0.45) and a concentrate mix (DM digestibility 0.75) will not necessarily have a DM digestibility of 0.6. This means that the **metabolizable energy** value attributed to an individual feed is not necessarily its value when used as a dietary component.

Although associative effects occur in all species, they are most important in ruminants given concentrates and **roughages** together. Ruminants, through their **rumen microorganisms**, have a unique capacity to digest plant cell wall constituents (especially **cellulose** and **hemicellulose**), which allows them to utilize poor-quality forages, such as crop residues. However, to meet production targets for milk and meat, the poorer the quality

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of the forage the more necessary will be supplementary starch-rich and/or protein-rich feeds. **Starch** is rapidly fermented in the rumen, causing a fall in the pH of the rumen liquor which, in turn, inhibits the cellulose-fermenting enzymes. This depresses the breakdown of the cellulose contained in the forage component of the diet. The effects will be greater when large amounts of concentrate are added and the forage component includes mature grasses or crop residues. Feeding concentrates that supply **ruminally available nitrogen** may enhance the activity of rumen microorganisms and thus improve cell wall **digestion**.

Adding concentrates to an all-roughage diet can either reduce or increase roughage intake, thus giving a 'substitution' or 'replacement rate', defined as the change in roughage DM intake per unit change in supplement DM intake.

True associative effects of foods are not easy to estimate, especially when mature forage or crop residues are a major dietary component. Such feeds are also generally deficient in protein, thereby restricting the growth of cellulolytic bacteria and limiting the rate and extent of fibre digestion. To maximize rumen efficiency from widely divergent foods, a combination of rapid and slowly degradable proteins is needed. The overall effect of combining forages and concentrates depends on the amount of each in the diet and on the quality of the forage (which is influenced by species composition and season) (Galyean and Goetsch, 1993; Stockdale 2000).

Many feeds are subjected to some form of physical processing. For grains, this is usually either rolling or hammer-milling.

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Breaking the grain exposes the starch-rich **endosperm**, which allows the rumen microbes easier contact with the grain contents, potentially resulting in an increase in the extent and rate of digestion. With roughage, **milling** reduces the **particle size** and allows for more complete mixing with other feed ingredients. This reduces the ability of the animal to select the more nutritious plant components. It can also make the feeds more dusty and, therefore, less palatable.

Positive associative effects of foods can also be described as synergy, when the effect of the combination in the diet is greater than when either food is fed alone. Benefits can be measured either as increased intake or as digestibility, or a combination of both. (TS; GMcLD)

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Astaxanthin

Many plants and animals contain a variety of natural pigments that impart yellow, orange and red colours to the flesh, skin and eggs of **fish**. One of the most important groups of natural pigments in the plant and animal kingdom is the **carotenoid**s. In salmonids, two

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oxycarotenoids, **astaxanthin** (3,3′-dihydroxy-4,4′-diketo-β-carotene) and canthaxanthin (4-4′-diketo-β-carotene) are responsible for the red to orange colouring of the flesh, skin and fins. Astaxanthin is the main carotenoid pigment of wild salmonids and is derived mainly from **zooplankton**. Astaxanthin is the principal pigment for **rainbow trout** (Storebakken and No, 1992), **Atlantic salmon** (Christiansen *et al*., 1995), Atlantic charr (Olsen and Mortensen, 1997), Australian snapper (Doolan *et al*., 2009) and tiger shrimp (Okada *et al*., 1994).

Carotenoids have been shown to have several physiological functions, including: (i) accessory pigment in photosynthesis; (ii) protective pigment against photosensitization; (iii) provitamin A source; and (iv) communication in aquatic animals. Responses to physiological or pharmacological administration of carotenoids are normally classified as actions. Potential mechanisms associated with carotenoid actions include **antioxidant** and singlet **oxygen** quenching, provitamin A activity, upregulating of DNA expression, co-oxidation, and enhancement of immune functions associated with increased tumour **immunity** and modulation of macrophage and lymphocyte activation (Bendich, 1993).

It was found that supplementing diets with astaxanthin can increase growth of Atlantic salmon (Torrissen, 1984; Christiansen *et al*., 1994). Similar results were found for Nile **tilapia** (Boonyaratpalin and Unprasert, 1989) and Kuruma **shrimp** (Chien and Jeng, 1992). Consequently, astaxanthin can be considered a vitamin for fish and shrimp (Torrissen and Christiansen, 1995). Astaxanthin **supplementation** has improved egg quality and

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larval production in Atlantic cod (Sawanboonchun *et al*., 2008) and **spawning** and fecundity in tiger shrimp broodstock (Pangantihon-Kühlmann *et al*., 1998; Huang *et al*., 2008). Antioxidation capacity and survival after thermal and osmotic stress can be enhanced in tiger shrimp by including astaxanthin in their diet (Chien *et al*., 2003). Astaxanthin incorporation in feed (Kumar et al., 2009) or by injection (Angeles *et al*., 2009) improves immune responses and disease resistance of giant river prawn (NRC, 2011).

However, not all researchers have obtained such positive results: Christiansen and Torrissen (1997) reported that astaxanthin is not essential for fertilization and egg survival in Atlantic salmon. Choubert *et al*. (1998) found that frequency of maturing females or the date of maturation in rainbow trout was not improved by supplementing astaxanthin in the diet. More information is needed on the essentiality of astaxanthin in diets for fish and shrimp, not only qualitatively but also quantitatively (i.e. dose–response relationship). Evidence of deficiency symptoms associated with absence of the compound is also needed (NRC, 2011). (QS)

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Astragalus

A member of the Leguminosae family with more than 3000

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species, usually existing in montane environments (Maassoumi, 1989; Li *et al*., 2014). Astragalus is believed to strengthen the immune system of humans and domestic animals, due to the presence of bioactive compounds. It has **polysaccharide**s that modulate the immune system, increasing the activity of macrophages, natural killer cells, dendritic cells, T lymphocytes, B lymphocytes and microglia and causing gene expression of various **cytokines** and chemokines. The immunomodulatory effects of the astragalus polysaccharide suggests that its use for the treatment of some diseases, including cancer, infections, type 1 **diabetes**, asthma and autoimmune diseases, may be successful (Zheng *et al*., 2020; Li *et al*., 2022). Poultry research reveals that the astragalus extract can enhance the effectiveness of vaccines and can potentially be an alternative to in-feed antibiotics (Farag and Alagawany, 2019; Shan *et al*., 2019). In addition to astragalus polysaccharides, the presence of more than 200 bioactive compounds, such as **flavonoid** and **saponin**s, may be beneficial for improving the health of animals (Shan *et al*., 2019; Zheng *et al*., 2020; Li *et al*., 2022). (AS, BH-G, CJCP)

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Ataxia

A **gait disorder** in which the movement of the animal is uncoordinated, typified by a swaying gait. It occurs in young lambs and goat kids suffering from swayback, which is caused by **copper** deficiency. (WRW)

Atherosclerosis

A condition in which atheromas, consisting of fatty material, occur in the wall of arteries. It is not normally a problem in farm animals. (WRW)

Atlantic salmon (*Salmo salar* (L.))

A typically anadromous **salmonid** fish of the North Atlantic, ranging from the Arctic circle to Portugal in the eastern Atlantic and from Iceland and Greenland to Connecticut in the western Atlantic. Eggs are spawned in late autumn in freshwater streams. The fry hatch the next spring and migrate to sea as smolts after 1–8 years, depending upon latitude. Landlocked forms, living the full

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life cycle in **fresh water**, also occur. Over 98% of Atlantic salmon production worldwide is cultured.

In cultivated salmon systems, feed provision has to provide adequate nutrients, minimize water pollution and maximize **welfare**. Competition between fish at feeding time can lead to unequal distribution of feed and divergent weights (Santurtun *et al*., 2018).

Efficient feeding systems have not only to meet the salmons' **nutrient requirement**s and minimize water pollution but also need to result in good salmon welfare. Factors such as **appetite**, number and size distribution of fish and feed distribution influence pellet concentration in a sea cage and hence discarded pellets. Agonistic behaviour at feeding times not only adversely affects fish welfare but also increases **feed intake** by dominant individuals and hence causes size divergence within the group, making a uniform product at a single point in time unattainable. Such an effect could lead to a positive feedback situation in which agonistic behaviour causes size disparity and this further increases agonistic behaviour. This is complicated by the fact that at least at low stocking densities Atlantic salmon show territorial behaviour and are able to defend an area within their tank or enclosure, preventing others from accessing pellets that arrive there. Atlantic salmon are often fed with a pelleted diet through **automatic feeding** services which can deposit pellets either at a pre-determined rate or at a rate that increases or decreases according to fish activity ('on demand'). They are normally fed in sea cages using a pneumatic conveying system with a rotor spreader.

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On-**demand feeding** systems have been developed to replace imposed regime systems in order that agonistic behaviour and competition are reduced and growth is more uniform within the group of salmon. In salmon parr, the on-demand system reduces dorsal fin injuries, competition and overfed fish, leading to more efficient food conversion. Offering a single daily meal increases conspecific aggression, even though the fish are fed to satiation.

Pneumatic conveying systems have raised some concerns, as pellets colliding with the pipe wall may break and not be uniformly distributed or go outside the cage and cause water pollution. Therefore aspects such as the revolutions per minute of the air blower, **particle size** and spreader arrangements should be considered in the development of an efficient feeding system. Spatial distribution of pellets within an enclosure can influence food intake and water pollution with **ammonia**, with the type and intensity of the water current playing important roles. Circular water tanks with current at the edge produce a more uniform feed distribution over the entire water body, compared with water tanks without such currents. Hence the latter are not used in salmon production, as they lead to aggression, lower growth rates and more individual and group food intake variability.

Modifying **fish feeding behaviour** represents a useful tool to determine feeding regime efficiency, with information on swimming patterns and spatial distribution of the fish contributing to improved feeding systems, providing that they can be accurately measured. Salmon show fast swimming in a vertical orientation towards pellets during high intensity feeds, disrupting their natural

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schooling behaviour. Depth transmitters have revealed that fish approach the surface zone during feeding (1–2 m) and later swim to deeper areas (8–9 m).

Salmon feed in a synchronized manner and feeding rhythms have to be considered when implementing feeding systems, as they can influence appetite, consumption, uniformity of growth, feed wastage and water pollution. Natural feeding rhythms are primarily circadian and seasonal, but tidal and lunar rhythms are also reported. Salmon are preferentially diurnal feeders but at certain stages in their life cycle they can seasonally change to nocturnal feeding under natural feeding conditions. Thus season has to be considered when attempting to feed the fish at their most active time of day. Salmon parr also have natural feeding rhythms that vary with season, including a morning peak in late summer and a midday feeding during spring. Attempts to maintain their natural behaviour, and hence welfare, should take this into account. The daily ration is also affected by seasonal and environmental factors, correlated with temperature variations and day length in on-demand feeding systems. Highest intake is at about 14°C and lowest at about both 18°C and 6°C in Atlantic salmon smolts.

The predictability of the feeding time can influence feed intake and stress levels in the fish. There is increased frequency and severity of dorsal fin damage when there is unpredictable feeding of 1+ salmon parr. However, aggression and attacks can also occur with predictable feeding, probably because of food anticipatory activity. When food is distributed consistently at the same time and

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place, dominant fish eat first at the surface and the subordinate ones later, with the latter using different strategies such as eating in the middle or bottom of the sea cage. Some fish may receive no food at all. In other farmed animals, feeding systems that seriously disadvantage subordinate animals are either not recommended or not permitted. Feeding systems that result in **starvation** (a severe deficiency in the intake of nutrients necessary for the maintenance of life) and severely damaged fins for a significant number of salmon would clearly be unacceptable to most consumers. As the fish that consume most have less variation in day-to-day intake, unpredictable feeding times make intake more even across fish. However, this might lead to more fin damage. With an unpredictable feeding time, initiators of aggressive interactions are heavier and longer and have less fin damage in comparison with receivers. The solution would seem to be to find better feeding systems. The range of size in fish groups is normally recommended to be kept to a minimum but some scientists suggest the use of older fish (1+ parr) within a younger group (0+ parr) to reduce agonistic behaviours. The older fish should not be of a size where they might eat the younger fish, as this might be difficult to manage. (RHP; CJCP)

See also: Salmon culture

Further reading

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Attractants

Animals have innate preferences and aversions that can be used to

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make feeds attractive or repellent. Sweet flavours are commonly added to foods for young animals, especially weaned piglets and calves, as most animals have an innate preference for sweetness. This flavour normally indicates the presence of sugars which are readily available sources of energy. Even in the absence of such sugars, sweet flavours can induce animals to prefer foods containing them, as long as they do not also have **antinutritional factor**s such as high fibre, toxins, or nutritional imbalances. There is a belief (or hope) that the inclusion of **palatability** agents in a food will increase **feed intake** but this has rarely been demonstrated to last for more than a few days. However, improving the attractiveness of one food when it is offered as a choice with one or more other foods may increase the short- and long-term preference for the flavoured food, depending on the relative nutritional value of all the foods on offer. (JMF)

Atwater factors

These factors describe the **metabolizable energy** per gram of protein, fat and carbohydrate (4, 9 and 4 kcal, respectively). They are used in relation to human diets but are not commonly used in animal nutrition. (JAMcL)

Automatic feeding

Mechanical methods of providing feed to animals without human intervention. For poultry, the most common form is the chain feeder, in which **compound feed**, as **mash** or crumbled pellets, is conveyed round the house in an open-topped metal duct. The feeder is controlled by a time clock so that animals can be fed at

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fixed times, even when the stockman is not available. This system allows equal access to feed by all the birds and is normally used for breeding birds in lay and for layers during rearing. Spin feeders distribute pellets over the floor of the house. These are only suitable for birds on restricted intake, such as **broiler breeder**s during rearing, to ensure maximum distribution in the minimum time. With pan feeders a central auger conveys feed into a number of suspended feeding dishes known as pans. These can be adjusted to hold a given quantity of feed to ensure that all the pans receive the same amount of feed. As the last pan empties, it triggers the drive mechanism to refill the pans. Pans are the preferred system for *ad libitum* feeding, as in broiler houses.

For pigs, the most usual system for *ad libitum* feeding is similar to pan feeders, having an overhead conveyor that replenishes self-feeders, which are hoppers in which the feed flows by gravity into a trough to which the pigs have continuous access. For restricted feeding, predetermined amounts of meal or pellets are released into troughs, or on to the floor of the pen. Liquid feeding systems are also easily automated for both *ad libitum* and restricted feeding. Electronic systems can be used to control the intake of loose-housed animals such as dry **sows**: each animal has an electronic tag which identifies it and triggers the release of a predetermined amount of food when the animal enters the feeding station, but also denies it access if it has already eaten all its allotted food.

A similar system is commonly used for dairy cows, which are fed a predetermined ration when they enter the milking stall.

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Calves may be automatically fed reconstituted milk powder in single or group pens. Fully automatic systems are less common for other farm animals, though self-feeding and controlled grazing are widely used for cattle and sheep, and many systems of feeding are mechanized. (KF; CJCP)

Availability

'Availability' and '**bioavailability**' are terms used to describe the percentage of a nutrient in a feed ingredient that is digested, absorbed and metabolically utilized so that it is available for growth, maintenance, reproduction or production (milk, eggs, work). 'Relative bioavailability' refers to how well a nutrient in a feed ingredient is used relative to a known standard. For example, a growth assay might be used to compare the utilization of threonine in **soybean** meal to that of threonine fed as pure L-threonine, which is completely available. This is commonly a slope ratio assay, which involves feeding at least three doses of L-threonine in the linear area of the growth response curve (usually between 40% and 70% of the requirement). A criterion of response such as weight gain or protein accretion is then related to supplemental threonine intake to generate a standard slope. Graded doses of soybean supplying similar amounts of threonine are also fed and again the response is related to threonine intake. The slope for soybean meal threonine is divided by the slope for standard L-threonine to provide an estimate of relative bioavailability. A similar procedure can be used with a single level of soybean meal. In this assay, the resulting weight gain is inserted into the regression for free threonine to give the bioavailable

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threonine intake. This value is then divided by the actual measured threonine intake to arrive at an estimate of relative bioavailability.

With **amino acid**s, relative availability determined by growth assay should be similar to **true digestibility** measured directly. However, growth assays do not work well for many nutrients, such as phosphorus, iron, manganese and **vitamin A**. For such nutrients, response criteria are needed that respond linearly to graded doses of the nutrient in question, such as bone ash, **haemoglobin**, bone manganese concentration and liver accumulation of vitamin A, respectively.

The term 'available' is used in a more restricted sense in connection with **lysine**, to describe the percentage of lysine in a feed ingredient that is not chemically conjugated in ways that make it unusable in **metabolism**. 'Available lysine' used in this sense does not include any measure of its **digestibility**. (DHB)
See also: Nutrient bioavailability

Avidin
A natural glycoprotein found in egg white. It tightly binds **biotin** and has been shown to induce biotin deficiency in chicks and rats when fed raw. There are also anecdotal reports of avidin-induced biotin deficiency in other livestock. As avidin is easily denatured by heat, cooking or biotin, **supplementation** is recommended when animals are fed raw egg whites. (BLS)

Ayu (*Plecoglossus altivelis*)
Also known as 'sweet fish' or 'pond smelt', a member of the salmon family, native to East Asia. This anadromous **fish** spawns in **fresh**

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water and after a year it returns to the sea, where it feeds on benthic organisms such as diatoms and blue-green **algae**. Ayu are cultured in either freshwater or seawater ponds and their optimum **water temperature** range is 15–25°C. Larvae hatched in captivity require acclimation to **sea water** before being fed live food organisms such as **rotifers** and artemia. The average market size is 50–150 g. (SPL)

B-complex vitamins

The B-vitamin complex is a group of eight **water-soluble vitamins** which, like all vitamins, must be provided in sufficient amounts in the **diet**. They are **thiamine**, **riboflavin**, **niacin**, **pyridoxine**, **folate**, **biotin**, **pantothenic acid** and vitamin B_{12}. Each of these is intimately involved as a **coenzyme** or co-substrate in one or more reactions in cellular **metabolism**. For example, thiamine is converted to thiamindiphosphate and pantothenic acid to coenzyme A. Co-factors such as these are not changed as a result of the chemical reaction in which they participate. These enzyme co-factors play critical roles in metabolism. Because of their

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participation in cellular metabolism, they are widely distributed in nature. (NJB)

Backfat
The layer of subcutaneous fat lateral to the spine. The thickness of this layer is a good predictor of the total **body fat** content of the **carcass** and this measure is often used in grading the carcasses of pigs, for which a common point of measurement is the P_2 position, 6.5 cm lateral to the spine at the level of the last rib. (SAE)

Bacteria:
see Gastrointestinal microflora

Bagasse
The fibrous residue remaining after **sugarcane** has been milled and the juice extracted. It is normally used as a fuel in sugar mills, in the manufacture of fibreboard or paper, as animal bedding and as a ruminant feed. Untreated bagasse has a very low **digestibility** but this can be improved by treatment with high-pressure steam or alkali (sodium hydroxide). (EO)

Bakery products
Wastes from bread, cake, biscuit and pasta making. Typically these are high in starch and oil (see table) but composition varies and each product should be analysed before it is used in animal diets. These products can be fed to ruminants and non-ruminants but their high levels of oil can reduce rumen fibre degradation rates. They are an excellent source of energy but the quality of the protein and starch can be reduced by heat processing. Fresh

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products are very palatable but should be used before they become mouldy or rancid. **Palatability** may be reduced when the products are dried and ground. The main factors limiting the use of bakery products are the high oil content and risk of contamination from packaging. Their high oil concentrations can reduce the **vitamin E** level of the diet. (JKM)

Composition of bakery products.

	Nutrient composition (g kg^{-1} DM)					**Energy** (MJ kg^{-1} DM)	
	Dry matter (g kg^{-1})	**Crude protein**	**Oil**	**Starch**	**Sugar**	**MER**	**MEP**
Bread	650–680	120–125	30	260–280	75–80	14	16
Bakery waste	500–890	10–150	10–250	200–600	50–250	9–19	18.5
Confectionery	800–900	5–200	10–250	0–100	150–250	12–18	–

DM, dry matter; MEP, metabolizable energy for poultry; MER, metabolizable energy for ruminants.

Bale

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A large bundle of material bound with twine or wire. There are four basic types of bale: (i) the traditional small rectangular hay bale 0.35 m × 0.45 m × 0.9 m weighing 20–30 kg; a small round bale 0.45 m × 0.60 m; (iii) a large square bale 1.5 m × 1.5 m × 2.4 m weighing 400–700 kg; and (iv) a large round bale 1.2 m × 1.2 m weighing 400–700 kg. For ensilage, bales are either wrapped in polythene film or placed into polythene bags and sealed, to ensure anaerobic conditions. (DD)



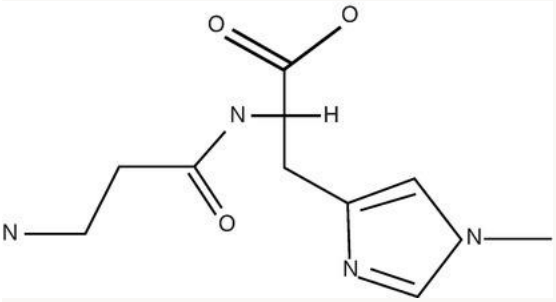
Round bales of straw that can be used for livestock feeding or bedding. Photo courtesy of Andrew Bowden. Licensed under CC BY-SA 2.0.

Balenine

β-Alanyl 3-**methylhistidine**, the **dipeptide** formed of 3-methylhistidine with β-**alanine**. It has also been called ophidine. Protein-bound **histidine** in muscle is methylated in the 3 position and is released as free 3-methylhistidine when **actin** and **myosin** are broken down in normal **protein turnover**. Other compounds of similar structure are **carnosine** (β-alanylhistidine) and

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anserine (β-alanyl 1-methylhistidine). Balenine is found in the blood and tissues of some animals, such as whales and pigs. (NJB)



Bamboo

Plant of the family **Gramineae** (**grasses**), with seven species used as animal feed. Bamboos are the largest grasses, sometimes reaching 30 m in height. The stalks are round with evergreen or deciduous leaves. Uses include wood for construction, paper production and fuel. The sprouts are eaten as food. Bamboo may be fed to ruminants either fresh or as **silage** of boiled bamboo-shoot shell. Bamboo has a high potential nutritional value and rumen degradability. The addition of **wheat bran** increases the rumen degradability of dry matter and protein. In bamboo seed, the carbohydrate and **vitamin C** contents are highest in *Bambusa arundinacea* and the protein content is highest in *Dencrocalamus strictus*. The **nutritive value** of bamboo leaves is shown in the table. (JKM; GMcLD)

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A bamboo forest. These forests bind soil, prevent water runoff and their extensive rooting system allows them to recover quickly after fires. Photo courtesy of CLF. Licensed under CC BY-NC-ND 2.0

Nutritive value for ruminants of bamboo leaves (data from Heuzé and Tran, 2015)

	Chusquea baculifera	***Bambusa bambos***	***Bambusa vulgaris***
Location	Brazil	India, Southern Asia	Pacific Islands
NDF (% DM)		79.6	61.9
Crude fibre (% DM)	34.4	24.1	28.8
Protein (% DM)	8.8	15.7	16.9

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	Chusquea baculifera	*Bambusa bambos*	*Bambusa vulgaris*
Location	Brazil	India, Southern Asia	Pacific Islands
Protein degradability (%)		52	
ME (MJ kg^{-1} DM)		10.1	9.7
Phosphorus (% DM)		0.09	

References

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Banana (*Musa*× *paradisiaca* L.)

Bananas and plantains (cooking banana) are grown in the tropics as staples for human consumption and for export. **By-product**s fed to livestock are surplus and reject fruit, peels, leaves and pseudostems.

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Banana tree. Photo courtesy of Przemyslaw Idzkiewicz. Licensed under CC BY-SA 2.0

Banana (and **plantain**) fruit are mainly **starch** (*c.* 70% in dry matter), some of which is converted to **sugars** with ripening. As protein (< 4% in dry matter), minerals (especially Na) and fibre contents are low, **supplementation** is necessary when feeding. Normal usage is for pigs; supplementation with a **protein source** of appropriate amino acid spectrum is important. Ripe bananas promote higher growth than green ones, probably because of 'active' **tannins** in unripe bananas. Cooking slightly improves green bananas for pigs. Chopped green bananas are highly palatable for cattle, but less so for sheep and goats. For ruminants, **urea** is a suitable (and less expensive) source of much of the supplemental nitrogen. Banana-based diets require fibre

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supplementation to ensure normal rumen function. Bananas can be ensiled. Peels can be fed when ripe, but not green. Leaves are fed to ruminants during scarcities, but low protein and high tannin make for low **digestibility** and low intake. The pseudostem of banana comprises fleshy leaf sheaths that surround the stem. It is high in moisture (> 90%) and is fed, freshly chopped, to ruminants and pigs. The dry matter is low in protein (< 4%) and mostly **nitrogen-free extract**s (*c.* 60%). Ensiling is also possible. (EO)

Key references

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Bar biting

This is common in caged animals whose diet is restricted in one or more nutrients. **Sows** in stalls may spend several hours per day in this behaviour, and it is also common in individually stabled cattle. It is primarily a behaviour signalling the desire to escape. It may also function to increase salivation, with the salivary buffers neutralizing acids in the **gastrointestinal tract**, produced in large quantities when the animals are fed large amounts of concentrated feed. It is commonly seen in caged rodents and rabbits, when it is also known as wire gnawing. (CJCP)

Barley (*Hordeum sativum*; syn. *Hordeum vulgare*)

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A member of the **Gramineae** (**grass**) family. It is cultivated primarily for its grain, which is used for human and animal food, and as a **cereal forage**. The **grain** (kernel) comprises the seed and **pericarp** (seed coat) and is surrounded by a hull (or husk) representing 0.1–0.15% of the grain weight. The hull is composed of two structures, the palea and lemma, collectively referred to as glumes, and these fuse with the outer coat of the developing grain to produce a covered kernel. The **chemical composition** and **nutritive value** of barley grain (see table) are influenced by the presence of the hull.

Chemical composition and nutritive value of barley grain and barley by-products (as g kg^{-1} dry matter unless specified). (After MAFF, 1990; Heuzé *et al*., 2015.)

				Energy value (MJ kg^{-1} DM)				
Feed type	**DM** (g kg^{-1})	**CP**	**Starch**	**NDF**	**GE** (MJ kg^{-1} DM)	**Ruminants** [a]	**Pigs** [b]	**Poultry** [c]
Barley grains								
All seasons	864	129	562	201	18.5	13.3	15.4	–

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				Energy value (MJ kg^{-1} DM)				
Feed type	**DM** (g kg^{-1})	**CP**	**Starch**	**NDF**	**GE** (MJ kg^{-1} DM)	**Ruminants** [a]	**Pigs** [b]	**Poultry** [c]
Winter	857	130	585	178	18.5	13.5	15.4	14.3
Spring	869	128	572	207	18.5	13.2	15.5	–
Barley by-products								
Fresh brewers' grains	250	218	38	619	21.3	11.5	–	–
Draff	248	211	18	673	21.5	10.2	–	–

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Feed type	DM (g kg^{-1})	CP	Starch	Energy value (MJ kg^{-1} DM)				
				NDF	GE (MJ kg^{-1} DM)	Ruminants [a]	Pigs [b]	Poultry [c]
Distillers' dark grains	907	275	26	420	21.3	12.2	–	–
Malt culms	906	290	57	556	18.9	11.1	–	–
Potale syrup	483	374	–	6	20.0	15.4	–	–
Forages								
Straw (all seasons)	867	41.5	10.9	811	18.4	6.4	–	–

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Feed type	DM (g kg^{-1})	CP	Starch	Energy value (MJ kg^{-1} DM)				
				NDF	GE (MJ kg^{-1} DM)	Ruminants [a]	Pigs [b]	Poultry [c]
Straw (spring)	862	42.6	17.8	811	18.5	6.6	–	–
Straw (winter)	874	37.6	2.2	809	18.3	6.2	–	–
Whole-crop silage	363	102	156	476	17.7	8.7	–	–
Fresh forage	250	110	80	576	17.3	9.2		

[a] As metabolizable energy;

[b] as digestible energy;

[c] apparent metabolizable energy (corrected to zero). CP, crude protein; DM, dry matter; GE, gross energy; NDF, neutral-detergent fibre.

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Livestock feeding represents the single most important market for the world's barley production (~50% of the total), the remainder being used for human food consumption and for **malting** purposes. When fed to animals, barley is usually first processed by rolling or hammer-milling. These processes break the seed coat and expose the **endosperm** to **digestion** by rumen and/or intestinal enzymes.

The main use in human food is for baking. Barley contains little of the **gluten** protein whose elastic properties are important in bread making. Barley **flour** is therefore used to make unleavened or flat bread, and porridge in North Africa and parts of Asia, where it is a staple food grain.

By-products of barley arise mainly from the brewing, distilling and pearl barley industries. Brewing gives rise to two main by-products: malt culms (or malt sprouts) and brewers' grains. Malt culms comprise the dried rootlets and sprouts of germinated barley grains produced in the malting process. Brewers' grains are the spent grains from the mashing and filtration and are widely used to replace both **forage** and concentrates in the diets of ruminants. The production of malt whisky from the distillation of barley malt alone or a mixture of cereals (grain distillation) produces a number of wet and dry by-products for use in the animal feed industry. These include distillers' wet spent malt (malt draff) or grains (grain draff) and light grains (dried draff), pot ale syrup, malt distillers' dried solubles, 'super draff' and distillers' (malt or grain) dark grains. Also produced are malt culms (dried rootlets and shoots) and malt residual pellets, consisting of pelleted malt culms, thin

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and broken grains (after dressing) with barley hulls and dust. Barley feed is the by-product arising from the preparation of pearl barley for human consumption. This comprises three grades of dust produced during processing and contains approximately 140 g and 100 g kg^{-1} dry matter (DM) of protein and fibre, respectively. Dried brewers' grains and distillers' dark grains can be fed at a level of 20% diet DM in growing cattle and dairy cows and 10% diet DM for calves and sheep. Their high **unsaturated fatty acid** contents may cause a reduction in fibre degradation in the rumen and a depression in **feed intake**. Copper toxicity may arise from feeding distillers' grains to sheep. For pigs, the use of distillers' grains is generally restricted to feeding to **sows**, due to the high fibre content.



Barley is grown primarily for animal feeding and brewing; by-products of brewing are also used for animal feeding. Photo courtesy of Richard Alloway. Licensed under CC BY 2.0.

In addition to the use of barley and barley by-products in livestock diets, barley may also be grown as a **forage crop** and grazed, made into hay, or ensiled as a whole-crop forage. Barley

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forage, **silage** and hay are useful ruminant feeds, although the fibrous awns in mature forage can irritate animals' mouths. Forage barley can accumulate **nitrate**, leading to nitrate toxicity in the grazing animal. Barley straw is also produced following harvesting of the grain and can be utilized for feed purposes; the straw responds well to **ammonia treatment**. (ED; GMcLD)

See also: Brewery by-products

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Basal metabolism

The irreducible **energy cost** of maintaining the processes required to keep cells alive and functioning, synthesizing substances to replace catabolized tissue, and maintaining muscle tone, blood circulation, respiration, etc. Measurements are taken of the basal **metabolic rate** (BMR) (the rate of energy use for the animal's basal functions) of the body during complete rest. It was originally intended to provide a standard condition of measurement for

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human subjects, which would make possible comparisons between individuals, ages, sexes, races, social groups, etc. The conditions for measuring the BMR in humans are that the subject must be in a thermoneutral environment, have not eaten for 12 h and be lying down but not asleep; usually it is measured soon after the subject has awoken from a night's sleep. Compliance with these conditions demands a cooperative subject and is virtually impossible with animals. Nevertheless, the concept of basal metabolism still provides a useful starting point, not only for interbreed and interspecies comparisons, but also for consideration of the additional energy needed for food ingestion, **digestion**, **lactation**, pregnancy, exercise and environmental discomfort, all of which increase metabolic rate above the basal level.

BMR as measured in animals is called the standard metabolic rate (SMR) or the fasting metabolic rate. The SMR is measured under 'standard' conditions, when the animal is post-absorptive (i.e. is not eating or digesting feed), at rest but not asleep and moving as little as possible, in a thermoneutral state (i.e. not using energy to maintain its core body temperature at about 37°C), and in good health and nutritional condition. 'Post-absorptive' for ruminants means when the animal's **methane** production has declined to 500 or 2000 ml per day for sheep or cattle. Alternatively, the animal's **respiratory quotient** (RQ) can be used. When the RQ is less than 1.0, this indicates that **carbohydrate** (i.e. feed) is not being oxidized as an **energy source**. In studies of wildlife and companion animals, where there is no practical need to distinguish between the BMR and the

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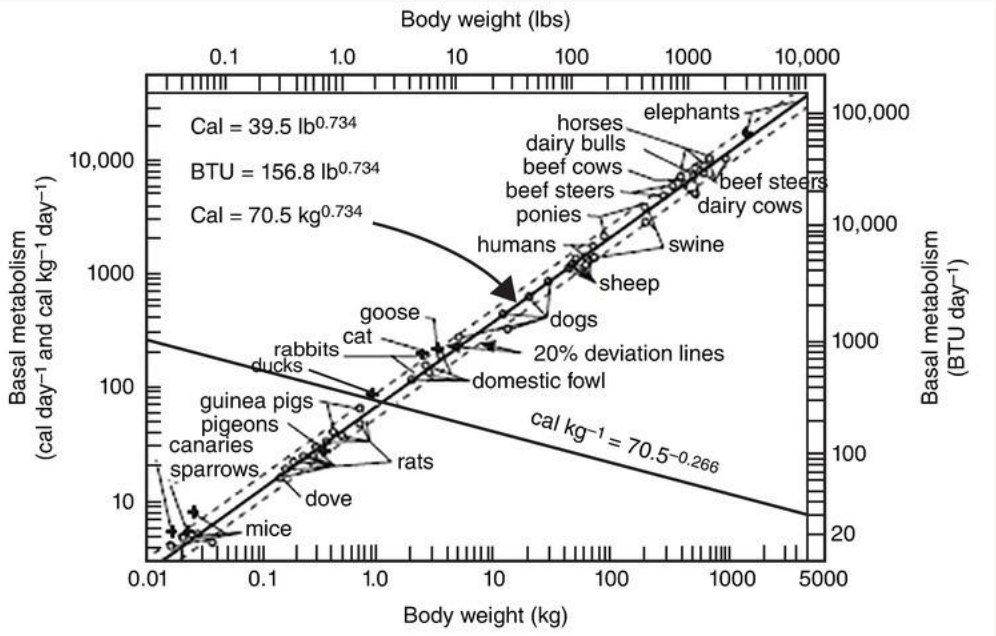
animal's total energy use, a concept known as the field metabolic rate can be used.

The BMR measured as described above is not the minimum level of energy use; the rate drops, for example, during sleep and in **starvation**. Metabolic rate is higher in growing animals and productive adults than in those fed **maintenance** rations, and although it is obviously greater in large than in small animals, the latter have a much greater BMR per unit weight. Brody's (1945) classic graph, reproduced here, shows that when body weights and 'basal' metabolic rates are plotted on a double logarithmic grid, the results from mature animals of different species ranging from mice to elephants fall close to a straight line. Brody's regression equation, converted into SI units, may be written as:

$$\text{BMR} = 3.41 \times (\text{weight in kg})^{0.734} \text{ Watts}$$

or

$$\text{BMR} = 295 \times (\text{weight in kg})^{0.734} \text{ kJ/24h}$$



Brody's (1945) graph relating basal metabolism of mature species to body

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weight.

It is emphasized that the 'basal' metabolic rates considered by Brody do not fulfil the conditions as originally defined for humans. They probably most nearly represent either **fasting metabolism** of animals that are free to stand or lie at will but not recently fed, or resting metabolism of normally fed animals lying down. The interspecies comparison may not be so exact as it at first appears from Brody's graph; the dashed lines on either side represent 25% divergences of BMR from the predicted values. More recent measurements suggest that for some species BMR tends to be consistently different from the values predicted by the Brody relationship (approximately 20% higher in cattle and 20% lower in sheep). Brody's regression does, however, demonstrate that tissue of small animals is metabolically more active than that of large ones; BMR per unit of body weight of mice is 25 times as great as that for elephants.

The BMR is related to the animal's metabolic size. This is the **liveweight** raised to a power – often 0.73 or 0.75, or some other value determined from the analysis of a specific set of data. The exponent 0.734 found by Brody is frequently rounded to 0.75. Although a commonly used definition of metabolic size is $W^{0.75}$ (following a decision made at the 1964 EAAP conference in Scotland), there is no universally accepted exponent. (JAMcL; GMcLD)

Further reading

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Beak

The beak (also known as bill or rostrum) in birds includes the upper and lower projecting mandibles, which are covered by horny layers of keratinous tissues and grow continuously. When food is ingested via the beak, it is mixed with **saliva** containing digestive enzymes secreted from glands around the mouth. The functions of the beak, in addition to gathering and ingesting food, include communication, grooming feathers, defence, and attacking rivals. The shape of the beak varies according to the main source of food, i.e. seeds, fruit, insects and other soil arthropods, nectar, fish, or small mammals. (RB)



Great Blue Heron using its beak to ingest a Ballyhoo. Photo courtesy of Kthypryn. Licensed under CC BY 2.0

Bean

Beans include the *Vicia* species – field bean (*Vicia faba*, L.), horse bean (*V. faba* var. *equina* Pers) and broad bean (*V. faba* var.

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minuta (Alef) Mansf.) – as well as kidney (common) beans (*Phaseolus vulgaris*) and other species (*see* Castor bean; Cocoa bean; Jackbean; Locust bean; Soybean). Beans are **legumes** mainly grown for human consumption but some varieties are grown for animal **feed**. There are winter and spring varieties which have contrasting agronomic characteristics suitable for different sites, but yield and harvest date differences are small. Beans are a good source of protein and energy, with high levels of **lysine**, but they are low in **methionine** and **cysteine**. Spring varieties are higher in protein than winter varieties. Beans are rich in **thiamine** and **phosphorus** and are often used to replace peas in animal diets. They contain **tannins** and **trypsin inhibitor**s, which may reduce **protein digestibility**, though new low-tannin varieties are grown. **Urease**, **phytates**, **haemagglutinin**s and **glucosides** are regularly present in raw beans. These **antinutritional factors** limit dietary inclusion rates, particularly in diets for non-ruminants, but they can be inactivated by heat processing. Field beans can be included in dairy, beef and ewe diets at 20% of total diet, in finisher pig and sow diets at 10%, in grower pig diets at 7.5%, and in lamb, calf and breeder and layer chicken diets at 5%. A blend of extruded beans and full-fat rapeseed (50:50) known as 'Extrupro' is used as a high-energy and high-protein **supplement** for all ruminants. The dry matter (DM) content of spring beans is 840–880 g kg^{-1} and the typical nutrient composition (g kg^{-1} DM) is **crude protein** 210–290, **crude fibre** 70–90, **ether extract** 10–25, **ash** 25–41, neutral detergent fibre 100–211, **starch** 300–400 and **sugars** 15–55, with MER 10.5–14.0 and MEP 13.5 MJ kg^{-}

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[1]. (JKM)



Variety of dried beans, including red kidney, pinto and cannellini. Photo courtesy of Scott. Licensed under CC BY 2.0.

Beckmann process

This technique, named after the German chemist Ernst Beckmann, uses alkali to hydrolyse the **ester** bonds between **lignin** and cell wall **polysaccharide**s to improve the degradability of cereal straws. Cereal straw is soaked for up to 2 days in a dilute (1.5%) solution of sodium hydroxide and then washed to remove excess alkali, prior to feeding. (FLM)

See also: Alkali treatment

Beef

Meat from cattle, mostly from specialized beef breeds.

Beef, effects of nutrition

Beef carcass and physiochemical characteristics

Beef is a rich dietary source of essential **amino acid**s (e.g. **lysine** and **phenylalanine**), vitamins (e.g. vitamin B_{12}) and minerals (e.g. iron), and **essential fatty acid**s (e.g. **docosahexaenoic acid** and **eicosapentaenoic acid**) necessary for human health.

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The carcass and physiochemical features of beef will depend on the nutrition provided to the cattle during rearing and finishing (*see* Beef cattle production systems). The breed and stage of **maturity** of cattle and the management of cattle diets will impact the **dressing percentage**, fat:lean tissue ratios and, ultimately, the type of meat produced. For example, compared with **rangeland** and **grazing** systems, cattle raised on grain or concentrate-mixed rations usually have higher **energy intake**s (Daley *et al*., 2010). Excess dietary energy can be stored within the muscle tissue as **glycogen** or in specific fat deposits as triglycerides. The prevalence and concentration of these deposits will impact on carcass features and value, such as the ratio of **fat** to lean tissue. It is possible to combine extensive and intensive production systems and supplement grazing cattle with energy-rich feed types to enhance the quality of their diet (semi-intensive). These **supplement**s may be cereal grains and meals, **by-product**s of biofuel production, distillers' grains, **molasses** and other suitable feeds.

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Beef meat showing extensive marbling. Photo courtesy of United States Department of Agriculture. Licensed under Public Domain Mark 1.0.

Sufficient levels of energy in the diet are important for the metabolic function of cattle. The modification of a diet's energy content is not the only way to manage beef carcass features and **meat quality**, with the protein content of a diet also important to consider. **Protein** can be categorized as ruminally degradable or non-degradable, depending on its passage through the rumen and its susceptibility to the proteolytic actions of ruminal microbes. Good sources of ruminally degradable protein for cattle include quality pasture, **silage** and **grazing** forages. Sources of ruminally available N (e.g. non-protein N, or degradable feed protein) can be provided as a supplement to cattle raised on poor quality pasture, and include cereal **grain**s and solvent-extracted **oilseed** meals. **Urea** can also be used to improve the ruminally available N content of poor-quality rations, and therefore the supply of rumen **microbial protein**. However, its inclusion in cattle diets must be

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strictly managed to avoid toxicity, growth suppression and reduced muscle deposition. That said, it is important to match the protein content of a diet to the animal's requirement for **maintenance**, **growth** and muscle protein accretion. The level of protein in the diet will contribute to the growth rate of cattle and ultimately, their carcass weight and **dressing percentage**. Higher growth rates have been shown to be associated with increased muscle **protein turnover**, promote a favourable ratio of **connective tissue** and proteolytic potential (**enzymes**) to lean muscle mass, and therefore enhance beef tenderness. It should be noted that if dietary protein is excessive, the protein will be lost through excretion; and if dietary protein is insufficient, the protein and energy ratio will be affected, as will cattle growth rates and muscle deposition.

The lean yield of a beef carcass will determine its value and quality, the latter because fatter carcasses insulate against rapid post-mortem carcass temperature fall and pH reduction that underpin many quality traits. For instance, beef tenderness, **water-holding capacity** and colour stability attributes are compromised if the rate of carcass temperature decline does not provide sufficient time for muscle **acidification**. This is particularly relevant in cattle as unsatisfactory carcasses are often identified using grade classifications and discounted by industry. Larger carcasses have greater resilience to cold-shortening and are therefore more likely than smaller carcasses to achieve appropriate temperature and pH declines. Excessive fat coverage will insulate the carcass but may also require additional inputs (feed, carcass

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trimming and dressing) to ultimately deliver a lower yield of lean tissue. The concentration of **glycogen** in the muscles of cattle immediately prior to slaughter will determine the likelihood of dark cutting and associated impact on beef retail potential. Dark cutting refers to defective beef that is dark, firm and dry (DFD) due to the suboptimal post-mortem acidification of the muscles. The provision of high-energy feed types in the lead-up to slaughter increases muscle glycogen reserves and therefore, potentially, reduces the incidence of dark cutting (Ponnampalam *et al*., 2017). This outcome is subject to the severity of other factors that contribute to dark cutting, such as pre-slaughter stressors and carcass handling systems.

Chemical composition and eating quality

High-energy diets will also produce cattle with heavier carcass weights, higher levels of intramuscular fat (IMF) and increased subcutaneous fat coverage than equivalent cattle fed low-energy diets. These characteristics may attract a premium for some **meat product**s (e.g. Wagyu) and drive improvements in eating quality; for example, the juiciness, **palatability** and flavour profiles of beef are enhanced with increased IMF. However, in other instances, excessive fat deposition contributes to low **dressing percentage**s, an increased need for carcass processing and trimming, and poor returns. For these reasons, it is advisable to consider the end market for cattle when formulating the energy content of their diet.

Beyond nutritional **enrichment**, dietary modification of beef **fatty acid** profiles will affect its oxidative stability and acceptance

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by the consumer. Beef flavour (aroma and taste) is derived from the thermal reaction of non-volatile fatty acids upon cooking, with the type and concentration of volatiles released being dependent on the initial fatty acid profile. This principle can be illustrated by cattle fed fish **oil** producing beef with an unacceptable 'fishy' aroma and taste, and by grass-fed cattle producing beef with a characteristic 'grassy' odour. **Polyunsaturated fatty acid**s are also highly susceptible to **oxidation**, which in sufficient concentrations and inducive storage conditions can contribute to the generation of volatiles associated with **rancidity** and malodourous beef (Wood *et al*., 2008). Furthermore, the **free radical**s and secondary **metabolite**s associated with and generated from **lipid** oxidation are also associated with beef colour deterioration when displayed under retail conditions. Consequently, beef with high concentrations of polyunsaturated fatty acids may be at increased risk of consumer rejection and reduced retail potential. Nonetheless, it is possible to mitigate these outcomes with the appropriate inclusion of **antioxidant**s in the diet of cattle where the management system makes it feasible to feed these.

Fatty acids

The energy content of a cattle diet can be enhanced with the provision of fats and oils, from plants and marine products in the form of **oilseed**s and **fat**. **Fish oils** (but not fish meals which are banned in some jurisdictions because of rules aimed to prevent the occurrence of **bovine spongiform encephalopathy** or 'mad cow disease') can also be used. Dietary fats can be categorized as

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protected or unprotected, depending on their susceptibility to biohydrogenation in the rumen. **Protected fats** are those that are conditioned to limit their degradation in the rumen. **Conditioning** methods include the use of whole oilseeds, fat emulsification or encapsulation within proteins, chemical interventions to form **calcium** soaps, and **amide**s to confer protection against rumen degradation. Unprotected **polyunsaturated fatty acid**s are hydrogenated in the rumen into saturated and **free fatty acid**s as a result of the **lipase** activity of ruminal microbes. Biohydrogenation is not comprehensive, with a portion of unprotected fats bypassing degradation in the rumen and available for **absorption** and deposition in the muscle (Prado *et al*., 2019). The proportion of unprotected fats that bypass degradation in the rumen is increased as dietary levels increase; however, excessive dietary fat levels (> 6%) can compromise plant fibre **digestion** in the rumen, dry matter intake and cattle productivity. Irrespective, the provision of dietary fat of either category will have implications for beef quality, nutritional value and sensorial attributes (Scollan *et al*., 2006).

Through dietary modifications, the concentration of specific health claimable and marketable fatty acids in beef can be increased. The inclusion of **algae**, fish oil, flaxseed or canola meal into cattle rations may increase the concentration of EPA, DPA, DHA and total omega-3 fatty acids in the beef (Scollan *et al*., 2017). These fatty acids contribute to the health and welfare of consumers, as well as contributing to a more balanced ratio of omega-6 to omega-3 fatty acids, as this is somewhat skewed in the

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typical modern diet. **Branched-chain fatty acids** may offer health benefits to consumers and research has demonstrated that cattle fed flaxseed produce beef with higher concentrations of these fatty acids (specifically iso-17:0 and anteiso-17:0) when compared with cattle fed **cottonseed** within the same mixed ration (Vahmani *et al.*, 2020). Changes to fatty acid profiles are achievable not only by the provision of supplements, but also with the selection of an animal's basal diet. For example, cattle grazing pastures and fed **silage** produce beef with higher concentrations of omega-3 fatty acids when compared with cattle fed concentrate-mixed rations, rich in cereal grains, that produce beef with higher concentrations of omega-6 fatty acids (Nuernberg *et al.*, 2005). This demonstrates the value of understanding nutritional effects on beef quality, as, in some incidences, further **supplementation** may not be necessary.

The oxidative stability of beef is improved when cattle are provided with dietary antioxidants, **vitamin E** (α-**tocopherol**) being a major contributor. Specifically, vitamin E acts in the muscle as a **free radical** scavenger, reducing the capacity for lipid **oxidation** and, in doing so, preserving fatty acids and proteins against oxidative deterioration. It is this function of vitamin E that helps to stabilize the nutritional value, retail colour and flavour properties of beef. **Rangeland** and **grazing** production systems offer substantial basal concentrations of vitamin E (α-tocopherol), although the stage of plant **maturity** will impact on its concentration. This outcome is the result of more mature plants (pasture senescence) containing less lipid and associated fat-

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soluble vitamins, such as vitamin E, than less mature plants (green pasture or **fodder**). **Cereal** grains have little vitamin E and cattle fed rations containing high proportions of these feeds must instead source vitamin E from supplementation to achieve the recommended daily intake of 15-40 mg kg^{-1} DM. Natural and synthetic forms of vitamin E can be supplemented to cattle, but free tocopherol is more effective in terms of transitioning from the diet into muscular systems than tocopheryl **acetate**. Some sources of natural vitamin E are fresh pasture, **forage crop**s, **legumes** (e.g. **lucerne**), silage, **yeasts** and bioactive plants and herbs. A vitamin E concentration of 3.30 mg kg^{-1} of beef is sufficient under commercial conditions, although levels down to 0.90 mg kg^{-1} have also been reported as sufficient to support short-term chilled storage durations. Other antioxidants offer similar benefits to beef quality, and while they can be provided within cattle diets, their contributions are relatively minor in comparison with that of vitamin E. These include **vitamin C**, **carotenoid**s, flavonoids, **selenium** and **phenolic compound**s, all of which are often available at the same dietary sources as listed for vitamin E. They may, however, offer secondary benefits to beef quality; for example, dietary **tannins** have been shown to help minimize biohydrogenation in the rumen of **polyunsaturated fatty acid**s to increase their **availability** for **absorption**. (BWBH; ENP; GMcLD)

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Beef cattle

Cattle used to produce meat. Beef cattle are produced either for sale or for on-farm consumption throughout most of the inhabited world, except in areas of Africa infested with tsetse fly where trypanosomiasis prevents all but a few resistant breeds from being kept, and areas where the Hindu religion is practised (India) as cattle are considered to be sacred and are not eaten.

Five bovine species are used for beef production: (i) *Bos taurus*, which are indigenous to Europe, northern Asia and parts of Africa; (ii) and (iii) *Bos indicus* and *Bos javanicus*, which are mainly indigenous to the tropics; (iv) *Bos grunniens* (yaks), which originated in northern China; and (v) *Bos frontalis* (gayal or mithan) used as beef animals in north-eastern India and northern Myanmar. The *B. taurus* group includes European breeds such as Aberdeen-Angus, Hereford, Belgian Blue, Charolais, Limousin and Murray Grey; and the Hanwoo and Tswana cattle from northern Asia and Africa. *B. indicus* breeds include the Afrikander, Boran, Gir, Kenkatha and Nellore. Twelve yak breeds are recognized in China. All of these five species will interbreed, with the yak × *B. taurus* or *B. indicus* male offspring being infertile.

Animals used for beef production normally come from one of three sources: (i) specific beef-breed dams mated to beef-breed sires, e.g. the specialized single-purpose breeds listed above and dual-purpose beef–dairy types such as the Abondance, N'Dama, Nguni, Normande, Ongole and Shorthorn cattle; (ii) from dairy cow dams mated to beef breed sires; and (iii) animals that are 100% dairy or of multipurpose breeds that can also be used for beef

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production, although with poorer productivity.

Ideally beef cattle are large, well-muscled animals, with good conformation (i.e. muscling around the shoulders and especially the hindquarters), fast rates of growth and good **feed conversion ratios**. These attributes are found to varying degrees in most specialist beef cattle breeds. In western temperate regions the usual beef cattle breeds are either British or European. British breeds (e.g. Hereford, Aberdeen-Angus, Welsh Black) are early maturing; that is, they reach their mature size early and, if they continued to be fed on energy-rich feeds, will lay down **body fat**. European breeds (e.g. Charolais, Romagnola, Chianina) are often late maturing and can be grown out to heavier **liveweight**s before they begin to lay down excess fat.

European breeds have been exported worldwide, and whilst under ideal temperate conditions European breeds are better suited to the production of beef than many general-purpose indigenous tropical cattle, under tropical conditions and stresses European breeds are not as productive. Selection within imported European breeds for tolerance of local conditions (especially hot climates) and development of stabilized crosses with local breeds have created a number of breeds such as the Brahman, Droughtmaster, Braford, Brangus and Santa Gertrudis. Brahman were created by selecting and crossing productive tropical cattle, whilst the other four were developed by crossbreeding the Brahman with European breeds such as Shorthorn, Aberdeen-Angus and Hereford. These derived breeds are able to handle heat, low-quality and highly seasonal tropical pastures, and parasites

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such as cattle ticks (*Rhipicephalus microplus*). However, not all successful beef breeds are *B. taurus*. Good examples of *B. indicus* breeds and stabilized crosses are the Feng (Chinese Yellow) breed, which has an excellent feed conversion ratio and can survive on poor-quality feeds such as rice straw, which is plentiful in China, and the Madura, a highly valued Indonesian breed which is a *B. indicus* × *B. javanicus* hybrid. (MMal; GMcLD)

Beef cattle production systems

Beef cattle production ranges from extensive systems where the product is weaned calves or 'store' cattle ('store' cattle are animals that are well grown but not finished for slaughter), to intensive systems where the product is finished animals ready for slaughter. Extensive beef production (usually on large farms, also called ranches or stations) is found where land is cheap and pasture may be of low **nutritive value**, whereas **feedlot**s are found near grain-producing regions or sources of agri-industrial wastes. Smallholder production occurs where families fatten a small number of cows on whatever vegetation, wastes and residues are available.

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Hereford beef cattle in a feedlot. Photo courtesy of the Beef Cattle Institute at Kansas State University. Licensed under CC BY 2.0.

These types of production are managed in a variety of feeding systems: extensive grazing, intensive grazing, 'cut-and-carry', housed animals, and lot feeding. Used in the grazing systems are various types of grazing management: continuous, rotational, strip grazing and 'leaders and followers'. The choice of production system is determined by the **climate**, type of feed resources available, and the costs of feed and land. In turn, the environment influences the type of product that can be economically produced – weaners or store cattle to be sold for finishing, or finished cattle.

Extensive grazing systems are based on native grasslands with minimum inputs of improved pasture species, fertilizer, or pasture irrigation, and where pasture growth, quality and species composition vary substantially throughout the year in response to seasonal changes in day length, temperature and rainfall. Examples are the steppe pastures of Ukraine, Mongolia, Russia and northern

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China, the prairies of Canada and the USA, the South American pampas, and the **rangelands** of northern Australia. The nutritional environment of animals grazing these pastures can be enhanced by providing non-protein N and **mineral supplements**, or by providing access to **fodder** trees such as **leucaena** (*Leucaena leucocephala*).



Grazing is a central feature of many systems of beef cattle production, as here in the Sibellini Mountains. Photo courtesy of Roy Luck. Licensed under CC BY 2.0.

At the other extreme, pasture-based systems can utilize temperate-species pastures that are fertilized and sometimes irrigated, and may have annual species that are renewed each year. These pastures are of high nutritional value. Examples are the temperate grass pastures of western Europe, southern Australia and coastal New Zealand. Cattle may be fed supplementary **silage**, **hay**, or root crops, or small amounts of grain through self-feeders, when pasture growth is lower than that needed to sustain the

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required animal performance.

Smallholder systems are often used in tropical regions. These may use 'cut-and-carry' management for cattle that are confined in small yards, or tethered. In 'cut-and-carry', the owner has a plantation of fodder trees or paddock of grass, and each day cuts enough **forage** for the animals.

Lot feeding is a specialized technique in which cattle are confined in yards to reduce **energy expenditure** in movement and to facilitate the convenient delivery of feed and observation of animal **welfare**. They are fed diets based on cereal grain (e.g. in North America and Australia) or **molasses** and **roughage** (in Latin America). Grain-based feedlot diets are typically 70–80% grain, with added **protein concentrate**s, minerals and vitamins, and about 25% roughage (often straw or low-quality hay). In some cases, where they are cheaply available, ingredients such as bread waste and dried fruit pulp are used. Young animals that are intended for finishing in feedlots are often 'backgrounded' before being sold on to a feedlot. Backgrounding involves accustoming these animals to concentrate feeds, feeding from troughs in yards and being moved through handling facilities.

In regions where winters are severe, beef cattle may be housed – usually in winter but sometimes through the whole year.

Choice of breed

The environment plays a large role in the choice of beef cattle breed. Large-framed, late-maturing European breeds are best suited to high-quality nutritional environments because these breeds produce a large, relatively low-fat carcass. Early-maturing

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British breeds should not be finished to high liveweights, as this causes the carcass to become overfat. *Bos indicus* cattle have characteristically lower dry matter intakes (per unit of **metabolic weight**) than *Bos taurus* cattle, and while these breeds perform similarly on low-quality feeds, *B. indicus* cattle respond less well when given concentrate **supplement**s.

Phases of beef cattle production

There are three phases of beef cattle production. The first is rearing, where the calf suckles its dam or is separated from its dam and artificially fed a liquid feed. In both cases, the calf is also given a concentrate and a roughage supplement. The second phase is growing out, where the weaned animal is fed pasture, silage or hay, and possibly a concentrate supplement. In this phase the cattle are managed on pasture in regions where winters are mild or may be housed during winter. The final stage is finishing, where the animal is prepared for market; this is done from pasture where the pasture is of sufficient quality, or in housing where the climate requires this, or in a feedlot.

Cattle for beef production do not have to be fed high-quality diets, but the fast growth and rapid **turnover** that can be achieved when supplements of energy and protein are fed to grazing or housed roughage-fed animals may make this a more profitable system than low-input production, and lot feeding can be used as a strategy for finishing beef cattle during droughts or at other times of pasture shortage.

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Grazing is a central feature of many systems of cattle production. Photo courtesy of G.McL. Dryden. Licensed under CC BY 2.0.

Animals used for beef production

Weaned calves or store cattle are sourced from breeding herds. Breeding cows are usually kept on land that cannot be used for the production of high-value crops or pasture (e.g. hilly or arid regions). The nutritional demands of breeding cows can be met from medium-quality fodder (9 or 10 MJ ME kg^{-1} DM), which is all that can be grown in such regions. Note, though, that if pasture quality is too low, breeding cows may conceive only every 18 or 24 months.

Weaned calves produced on breeding farms may be finished there if the pasture is of sufficient quality. However, many weaners and yearlings bred on these farms are sold for **fattening** to farms where better-quality food can be grown. These 'store' cattle can be fed a variety of diets, but any change in diet should be introduced gradually. High-quality forages, especially **maize** silage, root crops (e.g. mangels, **turnip**s, **fodder beet**) and **cereal**s, are most likely to be included in the ration, but waste products from the vegetable industry, such as stock feed **potato**es, can be included and reduce

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the cost of the ration. The skill of the farmer in buying low-cost feeds (and cattle) undoubtedly plays a part in the profitability of the store-finishing enterprise.

In the UK, a medium-sized (550 kg liveweight) breeding cow has a **metabolizable energy requirement** of about 100 MJ per day during winter. This is provided by about 8 t of silage for an autumn-calving cow which is lactating during winter, whereas the requirements of a spring-calving cow are likely to only be about two-thirds of this amount. This means that more land must be reserved for forage conservation for autumn-calving cows – perhaps 60% of the grassland area for two cuts, compared with perhaps 40% for a spring-calving herd. In many hill farms, setting such a high proportion of land aside for conservation, when the grass-growing season is short anyway, is not possible, due to constraints of the terrain and the need for grazing. The introduction of machinery for making and handling silage in big bales has assisted many farms in moving from making hay, with all its difficulties in wet areas, to conserving fodder as silage. Local arable farmers may be contracted to produce whole-crop **barley** silage with some chopped hay or straw and rolled barley for the final **fattening** period.

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Supplements of hay or silage can be used when pasture growth is low in winter. Photo courtesy of GMcL Dryden. Licensed under CC BY 2.0.

Growing out and finishing housed cattle

Cattle can be finished indoors in winter, in which case they are usually fed good-quality forage and a limited amount of concentrates, perhaps 2–3 kg per head per day. Grass and maize silages are commonly used, or a mixture of the two, since the high protein concentration in grass will complement the high energy content of maize. Roots (e.g. mangels, fodderbeet) can be fed, but not usually at more than one-third of the diet. Weaned calves are usually reared on hay initially and transferred to a silage diet at 8–10 weeks. **Protein supplement**s can be kept at a constant level, so that as the cattle grow they consume more silage and the protein content of the ration is reduced. The system of feeding a predominantly cereal grain diet is common where the two main inputs, grain and calves, are inexpensive relative to the finished product. The main feeding-related disorders that occur on high-grain diets are rumen acidosis, **bloat**, liver abscesses and

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laminitis.

Sufficient concentrate must be fed to allow the cattle to finish indoors, if this is what was planned. If insufficient concentrate is fed on a daily basis early on in the winter, the farmer may actually end up providing more concentrates in total, because marketing of the cattle cannot start in the mid-winter period. The successful operator knows how fast the cattle are growing and feeds supplements accordingly, so that the cattle can be marketed at the right time and plans can be made for the next season's cattle. If cattle are reared over a longer period, such as a 24-month system that finishes the autumn-born cattle off pasture in their second summer, it must be ensured that not too much expensive food is fed during winter if the system is to be profitable.

Finishing cattle at pasture

In the UK, if the cattle are purchased in early or mid-winter, this will only be applicable to animals of late-maturing breeds. In this case they should not be fed a high-quality ration in the winter or the cost of finishing will be too great; silage alone or clean straw and a small amount of concentrates (*c.* 1.5 kg per head per day) would be appropriate. They may only grow at about 0.5 kg per day during winter but they will compensate for this when they are at pasture. The grazing cattle can be sold when they are finished or, in an emergency, when the grass availability is very low.

In Australia, cattle are sold for slaughter at the end of the pasture growing season – in late summer/early autumn in the northern **rangeland**s, and in late spring in southern Australia. Cattle grazing native grass pastures (e.g. *Heteropogon contortus* or

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Astrebla spp.) may respond to non-protein N in winter and **phosphorus** supplements in summer. It is economic to give these to animals that are to be sold at the end of the supplementation period. A grain supplement can be used where the nature of the farm allows, and grain is not too expensive to buy, transport and store. In southern Australia, where cattle graze native (e.g. *Rytidosperma* spp., *Austrostipa scabra*, *Cynodon dactylon*) and improved (e.g. *Chloris guyana*, *Paspalum* spp., *Lolium* spp., *Dactylis glomerata*) pasture, the pasture quality is sufficient to support adequate growth rates and animals can be finished on these. Again, supplements can be used. (MMal; CJCP; GMcLD)

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Beet, fodder:

see Fodder beet

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Beet, sugar:
see Sugarbeet

Behaviour, feeding:
see Feeding behaviour

Behenic acid
Docosanoic acid, a saturated **long-chain fatty acid**, $CH_3{\cdot}(CH_2)_{20}{\cdot}COOH$, shorthand designation 22:0. It is found in **oils** such as **groundnut** and rapeseed oils, some milk fats and marine animal oils. (NJB)

Belly nosing
This stereotyped abnormal behaviour in piglets reared in intensive husbandry conditions is believed to be a redirected **suckling** behaviour. It is particularly common in early-weaned piglets. Piglets that **suckle** the sow a lot pre-weaning are more likely to engage in this behaviour. Encouraging piglets to suck by other means reduces the behaviour. This can be achieved by attaching artificial nipples to a **feed trough**, by providing feed in a **mash**, rather than the dried form, and water in a bowl, from which it is imbibed with a **sucking** behaviour, rather than nipple drinkers. (CJCP)

Benzoic acid
$C_7H_6O_2$, an unsaturated six-carbon ring with a carboxyl carbon attached. It is found in berries and **gum** benzoin and is used as a food preservative. Benzoic acid is not apparently catabolized by animals but is conjugated with **glycine** in the liver to form

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hippuric acid, which is excreted in **urine**. Hippuric acid makes up a greater fraction of urinary **nitrogen** in grazing ruminants than in simple-stomached animals. (NJB)

Beriberi:
see History of Nutritional Sciences

Beta-agonists
Beta-agonists (β-adrenergic agonists) are substances that activate β-adrenergic receptors. They include both the naturally occurring **catecholamines** (i.e. **dopamine**, **norepinephrine** and **epinephrine**) and synthetic compounds that are structurally similar to them. Epinephrine appears to be the natural agonist for these receptors. Norepinephrine also activates them but only at high (pharmacological) concentrations. Norepinephrine is instead thought to act via α-adrenergic receptors (the other major class of catecholamine receptors). The β-adrenergic receptors are further broken down into three classes: β1, β2 and β3. There are both broad-based and selective pharmacological agonists for each type. The classic β-agonist is isoproterenol. Synthetic β-adrenergic agonists such as **clenbuterol**, **cimaterol** and ractopamine have major effects on the growth and **metabolism** of **skeletal muscle** and **adipose tissue** of food animals. (NJB)

β-**Alanylhistidine:***see* Carnosine

Beta-oxidation
The metabolic processes involved in **catabolism** of **free fatty acid**s. Even-chain fatty acids are cleaved into a common two-

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carbon intermediate, acetyl-CoA. **Odd-chain fatty acid**s produce mainly two carbon units (acetyl-CoA) but the terminal three-carbon unit is released as propionyl-CoA. Since this process occurs in the mitochondrion, all cells (with the exception of the mature mammalian erythrocyte) are thought to catabolize fatty acids in this way. (NJB)

Betaine

A water-soluble compound, $(CH_3)_3{\cdot}N^+{\cdot}CH_2{\cdot}COO^-$, widely distributed in plant and animal tissues. Biologically, betaine is involved in **methylation** reactions and **detoxification** of **homocysteine**. The pronunciation of the compound reflects its origin and first isolation from sugar 'beets' (*Beta vulgaris* subsp. *vulgaris*). In **metabolism**, betaine is derived from the **oxidation** of **choline** in a two-step process. One of the methyl groups of betaine can be used by the **liver** enzyme betaine homocysteine methyltransferase to methylate L-homocysteine to form L-**methionine**. The remaining two methyl groups of betaine are converted into one-carbon units of the **folate** system. (NJB; QS)

Bicarbonate

Formed in animals from CO_2 produced in the **catabolism** of **carbohydrates**, **fats** and **amino acid**s. The **carbon dioxide** produced is dissolved in water and, with the aid of the erythrocyte **enzyme** carbonic anhydrase, carbonic acid (H_2CO_3) is produced. Carbonic acid can dissociate into bicarbonate HCO_3^- and **hydrogen** H^+ ions. The carbonic acid–bicarbonate system (H_2CO_3

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$\rightarrow H^+ + HCO_3^-$) is one of the three major blood buffering systems. This system differs from the **haemoglobin** and **protein buffer** systems because the blood concentration of CO_2 is maintained and is continually replenished. It is controlled by respiratory rate and the plasma concentration of HCO_3^- is controlled by the kidney. Bicarbonate plays a major role in maintaining the pH of blood near 7.4. (NJB)

Bifidobacteria:
see Gastrointestinal microflora

Bighead carp
Bighead carp *Hypophthalmichthys nobilis* is widely distributed in South-east Asia and it is the fifth most intensively cultured fish species, producing 3.5 million tonnes globally, according to FAO (2018). The increasing introduction and stocking of bighead carp in most reservoirs in China has not only increased fish production, but it has also proved an effective bio-management strategy, as algal blooms have been prevented or eliminated (Guo *et al*., 2012). As a representative economically important **freshwater fish**, bighead carp provide the human **food chain** with abundant **unsaturated fatty acid**s and **protein** (Upadhyaya *et al*., 2019). n-3 **Polyunsaturated fatty acid**s, especially EPA and DHA, play an important role in the prevention of diseases, especially cardiovascular disease in humans (Hong *et al*., 2015). (QS)

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Bighead carp. Photo courtesy of Asian Carp Regional Coordinating Committee. Licensed under CC BY 2.0.

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Bile

Bile is made in the liver, stored in the gallbladder and secreted into the **small intestine** at the level of the **duodenum**. It contains **sodium** and **potassium** salts of the bile acids **cholic acid** and

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chenodeoxycholic acid. The salts of deoxycholic acid and lithocholic acid are also found in bile but these bile acids are the result of microbial **metabolism** of cholic acid and chenodeoxycholic acid, respectively, in the intestinal contents. The bile pigments, bilirubin and biliverdin, are products of **haemoglobin** degradation. Limited amounts of inorganic salts, **fat**, **lecithin**, **fatty acid**s and **cholesterol** are also found in bile. The bile acids are conjugated with one of two **amino acid**s: **glycine** or **taurine**. These conjugates are referred to as glycocholic and taurocholic acids. Bile acids can be reabsorbed from the intestinal tract at the level of the **ileum** and returned to the liver by the portal circulation, from which they can be secreted again in bile; this is called the enterohepatic circulation. Bile enhances **lipid digestion** due to the formation of fatty acid-containing micelles that can diffuse through the unstirred water layer on the mucosal surface where the fatty acids are subsequently taken up by the **enterocyte**s. (NJB)

Binding agents

Materials added to **compound feed** at relatively low rates of inclusion (0.05–2.5%) to increase the durability and hardness of the pellets. Improved durability allows further mechanical handling during transport, transfer into storage systems and feeding. Hardness is important to avoid pellet destruction due to pressure when stored in bulk bins. It is not always correlated with durability. Binding agents are also thought to increase press capacity and **pelleting** efficiency as some allow more fat and steam to be added to the meal during **conditioning**. The table

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gives common binding agents.

Common binding agents

Binding agent	E number
Citric acid	E330
Sodium, potassium and calcium stearates	E470
Silicic acid (precipitated and dried)	E551a
Colloidal silica	E551b
Kieselguhr (diatomaceous earth, purified)	E551c
Calcium silicate (synthetic)	E552
Sodium aluminosilicate (synthetic)	
Kaolin and kaolinitic clays (free from asbestos and containing at least 65% complex hydrated aluminium silicates whose main constituent is kaolinite)	E559
Natural mixtures of steatite and chlorite free of asbestos	E560
Vermiculite	
Lignosulphonates	E565

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Binders are particularly important in aquafeeds to prevent pellet decomposition in the water. They are essential in **shrimp** and crab feeds because the feed stays in the water for a long time as consumption is slow. Most used are Na and Ca bentonites, lignosulphates, **hemicellulose**, carboxymethylcellulose, alginate, **guar** gum and some inert polymeric binders. Gelatinized **starch** from **cereal grain**s is stable in water, and, along with **whey**, wheat **gluten** and **molasses**, act as both binders and nutrients. (MG; QS)

Binding proteins

Proteins that specifically interact with some other molecule (e.g. another protein) or atom (e.g. a mineral). Binding proteins are varied in their function. They can be involved in a variety of physiological functions. Interaction of a binding protein with its ligand can result in a conformational change in the binding protein that alters its function. **Enzymes** can be considered specific binding proteins for **substrates** and, when they bind them, co-factors.

Regulation of gene expression (DNA or RNA binding proteins)

Transcription factors can regulate the production of messenger RNA (mRNA) by turning on or off the expression of specific genes. RNA binding proteins can influence the production of mature mRNA by affecting RNA splicing, polyadenylation (addition of multiple adenosine residues to an mRNA precursor) or RNA transport. In addition, RNA binding proteins are critical in mRNA translation into protein. RNA binding proteins are critical for the function of the ribosome, for putting the proper amino acid on to a

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specific tRNA (aminoacyl tRNA synthetases) for binding to specific regions of mRNA.

Cell signalling

Protein–protein interactions are critical for transmission and decoding of **hormone** signals by cells. Examples include binding of hormones to their receptor (**insulin** binding to the insulin receptor) and for the interaction of the hormone receptors with other proteins that transmit the signal into specific cellular actions.

Transport of compounds

Binding proteins exist for certain vitamins (**vitamin D** binding protein) or minerals (transferrin) and are important in moving such compounds between organs and cells or, in some cases, within cells.

Cell structure

A variety of filament systems organize the cytoplasm of cells and can alter cell shape. An example is microtubules (MTs) made of the protein tubulin. MTs form hollow fibres that are used to transport proteins to different locations in the cell. MTs are also important in chromosome separation during cell division. A variety of MT binding proteins exist that can alter MT function. (RSE)

Binge eating:

see Comfort eating

Bioavailability

That proportion of a dietary **nutrient** that is absorbed and may then be utilized by an animal for physiological function(s). The method of assessing bioavailability depends on the species and its

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physiological state. The animals that are of most interest to nutritionists are usually those that are growing or producing (meat, milk, eggs, etc.). Consequently, growth, efficiency of feed utilization, output of milk or eggs or changes in tissue concentration of some nutrient (e.g. **calcium** in bone) are frequently chosen as parameters of measurement.

In most bioavailability assays the chosen parameter is used to compare a test feedstuff or nutrient to a standard, which is usually the nutrient in its pure and fully available form. The test may use a single measurement (mean ratio method) or a set of several intakes of the standard (slope ratio assay). In the simplest slope ratio assay, a purified or semi-purified standard such as reagent grade compound, crystalline **amino acid**, etc., is fed in a series of diets to give three or more levels of a nutrient that produce a linear increase in the chosen criterion (e.g. **growth**) in response to increasing amounts of the nutrient. The test material is also incorporated into one or more diets at levels that would be expected to yield a linear response but are less than the known or estimated optimum dietary level for maximal response. Provided that there is a linear relationship between the nutrient intake (x) and the animal's response (y) with both the test and the standard nutrient sources, the relationships can be expressed as $y_{test} = a_{test}x + b_{test}$ and $y_{std} = a_{std}x + b_{std}$, respectively, where a_{test} is the slope and b_{test} is the intercept of the regression equation with the test source and where a_{std} and b_{std} are the slope and intercept with the standard nutrient source. It is also assumed that the two lines generated by these equations intersect at 0,0. To ensure the validity

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of the assay, this assumption is tested in the analysis of the results. Therefore the ratio of the slopes, 100 a_{test}/a_{std}, is an estimate of the bioavailability of the test nutrient, when the bioavailability of the standard is assumed to be 100% (Littell *et al*., 1995).

Variations of the slope ratio method include the standard curve and mean ratio assays. In the former case, several data points are generated with the standard nutrient source to obtain a standard linear response. A single level of the test feed is given such that the intake of the nutrient falls within the range of the standard. The response value (y_{test}) is then compared with the value expected from the same amount of pure nutrient, using the regression equation for the standard source. Thus, bioavailability = 100 $y_{test}/(a_{std} \times x_{test})$. In some cases, a direct comparison of a test source of a nutrient is made to a standard source of that nutrient, each having only one data point. In this case, the validity of the assay is heavily dependent on the amount of the nutrient in the test source compared with the standard. If the amount is small, the assay is usually less accurate. It is important to recognize that, in addition to the nutrient of interest, the test feed may contain other constituents that contribute, positively or negatively, to the animal's response. This difficulty can be minimized by arranging that the diets used to establish the standard curve are deficient only in the nutrient being tested and that **antinutritional factor**s in the test feed are inactivated.

Sometimes, the bioavailability of certain nutrients for **fish** is more easily estimated by conducting controlled **digestibility** trials. Although this does not technically fulfil the definition of

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bioavailability it is useful because, for many nutrients, digestibility is the main component of availability.

More accurate estimation of the **true digestibility** of a given nutrient may be determined by the use of isotopes. The method has been particularly useful in determining true **absorption** of various essential minerals, especially of trace minerals. Ideally the source of the nutrient in question is one in which the nutrient has been biosynthesized in the presence of either a stable or a radioactive isotope and is therefore intrinsically labelled with the nutrient. The concentration of the intrinsic label in both diet and faeces can be used to calculate the true digestibility of the nutrient tested. In the presence of another isotope of the same nutrient that has been previously injected into the bloodstream of the subject animal and allowed to reach equilibrium, one can calculate the endogenous loss of the nutrient via the intestine. (JSJr)

See also: Availability; Nutrient bioavailability

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Biogenic amines

Decarboxylation products of **amino acid**s with **hormone**-like actions. **Histamine** is formed by decarboxylation of L-**histidine**.

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Histamine affects cells by binding to histamine receptors (H_1, H_2 or H_3) found in peripheral tissues and the brain. **Tyrosine** is converted to L-dopa (dihydroxyphenylalanine), which is decarboxylated to **dopamine** which, in turn, can be hydroxylated to become **norepinephrine**. These processes are carried out in catecholamine-secreting neurons and in the **adrenal** medulla. The products act on α- and β-receptors. **Tryptophan** is hydroxylated to 5-hydroxytryptophan which is decarboxylated to form **serotonin** (5-hydroxytryptamine), which is found in the brain and in serotonergic neurons. It has its effect through cellular serotonin receptors. In the pineal gland, serotonin is converted to **melatonin**. The **neurotransmitter** γ-aminobutyrate is derived from the decarboxylation of glutamic acid. (NJB)

Biological value (BV)

A measure of **protein quality**. The term has a strict definition but is also used more loosely as a synonym for protein quality. BV is calculated by measuring the faecal and urinary **nitrogen** losses of two groups of growing rats: one given a protein-free diet, the other a diet containing the test protein at a concentration of 10%:

$$BV=100(Ni-(Nu-Nue)-(Nf-Nfe))/(Ni-(Nf-Nfe))$$

where, for the rats given the test diet, Ni is the nitrogen intake, Nu is urinary nitrogen excretion, Nf is faecal nitrogen excretion; and, for the rats given the protein-free diet, Nu_e is urinary nitrogen excretion (endogenous urinary nitrogen), Nf_e is faecal nitrogen excretion (metabolic faecal nitrogen).

Thus, endogenous urinary nitrogen and metabolic faecal

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nitrogen are added to the nitrogen retained to give the total amount of nitrogen utilized. This is divided by the nitrogen truly absorbed (i.e. faecal nitrogen is corrected for endogenous loss) to give the biological value, which is therefore independent of **digestibility**. BV is related to the simpler measure, **net protein utilization** (NPU):

BV=NPU×true digestibility.

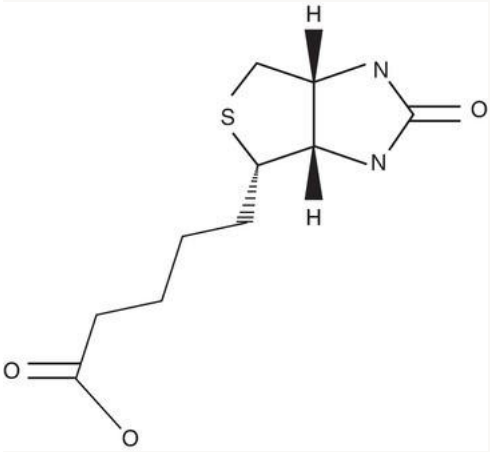
Although originally designed and strictly defined as a test with rats, it has also been adapted for use with other animals. (MFF)
See also: Protein quality

Biotechnology
A technology that uses biological systems and processes to produce substances of medical, biological, nutritional and other commercial significance. It includes use of cell and tissue culture, cell fusion, molecular biology and recombinant **deoxyribonucleic acid** (DNA) technology to generate unique organisms with new traits or organisms that have potential to produce specific products. The most common applications include **fermentation** to produce antibiotics, brewery products and cheese. Genetic engineering allows the isolation of a desired gene and its insertion into the DNA of another organism which is then grown for the commercial production of **insulin**, **hormone**s, vaccines etc. The same technology is used to produce **microorganism**s that degrade hazardous wastes, as well as **genetically modified** plants and animals. (SPL)

Biotin

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$C_{10}H_{16}N_2O_3S$, one of the water-soluble B-vitamins. It is the vitamin co-factor for **pyruvate carboxylase**, which forms **oxaloacetate**, and for acetyl-CoA carboxylase, which is the first step in **fatty acid** biosynthesis. It is also the co-factor for propionyl-CoA carboxylase, which is involved in the conversion of **propionate** to **succinate**, which can be a source of **glucose** carbon. In addition it is a co-factor in the carboxylase step of **leucine catabolism**. It is normally synthesized in adequate quantities by the intestinal bacteria. It occurs normally in a variety of foods. (NJB)



Birth weight

The weight of an animal at the moment it is born. Within species, this weight will depend on the breed of the animal's parents and the genetic material that it inherits from them. The uterine environment also has a significant effect on birth weight. If an embryo is transferred from one female to a smaller one, the birth weight of the resulting newborn is likely to be lower than if it had been carried to term by its own dam. Manipulation of ova and embryos prior to transplanting has been known to increase birth weights by up to 50%, resulting in severe problems at parturition. Fetal requirements for energy, protein and minerals increase

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rapidly, especially during the last third of gestation. Because of this, restricting **energy intake** to the mother can reduce birth weight; while increasing the energy intake of the ewe in the last 6 weeks of pregnancy, for example, can increase the birth weight of lambs. Specific nutritional deficiencies can cause debility, deformation and death of the newborn, rather than reduced birth weight per se. As **litter size** increases, the birth weight of each individual in the litter tends to decrease. Early parturition results in lower birth weights. **Newborn animal**s of lower-than-average birth weight are more likely to die. (PJHB)

Biting

The act of closing the **teeth** around an object are with the aim of consuming or maiming that object. In relation to consumption, biting may be rapidly repeated action in the case of **herbivore**s. In the case of **carnivore**s, biting may be a single action to grasp prey or repeated action to consume parts of the animal. The biting rate of herbivores increases as herbage availability declines and bite size declines, in an attempt to maintain a constant rate of intake. (CJCP)

Biuret

The common name for imidodicarbonic diamide or carbamylurea, $NH_2{\cdot}CO{\cdot}NH{\cdot}CO{\cdot}NH_2$. It reacts with an aqueous solution of copper sulphate and sodium hydroxide to give a purple-coloured complex. Proteins and some **amine**s react in a similar manner to biuret, thus forming the basis of the colorimetric method for the quantitative determination of proteins. The method is simple,

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robust and reliable but lacks selectivity, since all proteins react in a similar manner. Biuret has been used as a source of ruminally available N, and is less toxic than the more widely used **urea**. (JEM)

Black carp (*Mylopharyngodon piceus*)

A carnivorous species that is native to rivers and lakes in East Asia from China to Vietnam. Although it has been widely cultured in South-east Asia, Europe and America and used to control aquatic snails (Ben-Ami and Heller, 2001; Hunter and Nico, 2015), black carp is one of the main freshwater-cultured species in China, mainly in monoculture systems using artificial diets. The total production was 691,500 t in 2018. As a carnivorous species, black carp *M. piceus* are prone to high glycaemia levels when offered feed with a high content of dietary CHO (Cai *et al*., 2009). (QS)

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Black gram

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An annual dicotyledonous plant (*Vigna mungo*), native to central Asia, grown for **forage**, **silage** and **hay**. It is an important feed for livestock in India, with dietary inclusion rates of up to 17% (Saran *et al*., 2000). It is also grown in chicken pastures. **Fodder** is derived mainly from the stem and leaves but the seeds, pods and pod husks are also used. Black gram is usually fed to cattle as a fodder but it may also be consumed by other species, including chickens. The silage of black gram in the dough stage has a dry matter (DM) content of 273 g kg^{-1}, with **crude protein** (CP) at 139 and **crude fibre** (CF) at 191 g kg^{-1} DM. The pods of the black gram plant have much lower levels of CP at 90 and CF at 299 g kg^{-1} DM. Black gram seeds have a CP level of 261–268 and a very low CF level of 53–56 g kg^{-1} DM. The pod husks have a CP level of 166 and CF 246 g kg^{-1} DM. (JKM)

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Black sea bream (*Acanthopagrus schlegelii*)

A euryhaline omnivorous species but preference prey is small animals; it thrives in coastal regions with water of salinity ranging from 4.0 to 35.0 g l^{-1} (Ma *et al*., 2007). It is an economically important food **fish** cultured in Asia, including Japan, Korea, China, and some other countries of South-east Asia (Ji *et al*., 2003). The range of black sea bream in the western Pacific extends from

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Hokkaido, Japan, in the north to Taiwan and Hainan Island in the south. In the coastal waters of China, **spawning** occurs in spring (Zhang *et al*., 1985). The main **nutrient requirement**s are supplied by replacing fish meal with plant protein, also single-cell proteins and mixed proteins The **aquaculture** production yield of black sea bream was 457,000 t in China in 2018, based on China Statistical Fishery Yearbook. (QS)

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Blindness

Nutritional problems that cause blindness in animals generally do so by interfering with the function of the nervous tissue comprising the visual centre of the cerebral cortex, the optic nerve or the retina. **Thiamine** deficiency can result from inadequate dietary

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thiamine in non-ruminants or, in ruminants, from the presence of thiaminases (for example, from eating high-concentrate diets, **bracken fern** or raw fish), which destroy thiamine before it can be absorbed. Polioencephalomalacia, or degeneration of the cerebral cortex, ensues, destroying vision. **Sulphur** toxicity can also induce polioencephalomalacia. Lead **poisoning**, from ingestion of used crankcase oil and grease or discarded lead batteries, results in loss of visual cortex function. **Arsenical** compounds, once used as pig **growth promoter**s and to control swine dysentery, can, in large amounts, cause degeneration of the optic nerve. **Vitamin A** deficiency causes retinal degeneration, leading to **night blindness**. Eventually the optic nerve may become involved and vision lost completely. **Water deprivation** followed by rapid replenishment of water (also known as sodium toxicosis) can cause oedema of the brain tissues, blocking vision. In the nervous form of **ketosis**, blood **glucose** levels may fall to the point at which the function of the visual cortex is depressed, resulting in partial blindness. (JPG)
See also: Lead; Night blindness; Thiamine

Bloat

Most commonly observed in ruminants, as a disorder of **rumen** function that causes swelling or tympanites of the rumen. It sometimes occurs in pigs, when the **small intestine** becomes colonized by gas-producing bacteria. In cattle it can be observed as an acute swelling between the last rib and the hip on the left side. The animals are restless, find lying uncomfortable and may eventually die of heart failure or of suffocation due to inhaling

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rumen contents.

Bloat in ruminants can be obstructive, gassy or frothy. Obstructive bloat is where the oesophagus is blocked, for example by a piece of food that is stuck and the escape of gas during eructation is prevented. This can often be removed by passing a stomach tube to release the gas. Gassy (or feedlot or cereal) bloat is caused by consumption of large quantities of rapidly digested **carbohydrate**. It can be due to the sudden consumption of **cereal**s, particularly if they have been effectively processed, which accelerates bacterial **digestion** of **starch**. This may occur if an animal loses its appetite for a period, and then compensates by overeating. This type of bloat can be treated by releasing the gas with a stomach tube or in an emergency by a rumen trocar and **cannula**. A form of **feedlot** bloat occurs when *Streptococcus bovis* bacteria produce a slime capsule which then traps gas. Frothy (or pasture or legume) bloat occurs when ruminants eat large amounts of pasture or **legumes** that contain **saponin**s and/or soluble proteins, which are released from the plant cells and create a stable foam in the rumen (Majak *et al*., 1995). Pasture bloat is of more economic importance, as it can affect a large group of animals at the same time. **Lucerne** is the most likely of all legumes to cause bloat, with cows sometimes dying within a few hours of entering a field for grazing, but it can also be caused by young leafy grass that has recently received nitrogen fertilizer. Some legumes contain **tannins**, which reduce the speed of **protein digestion** and probably discourage animals from grazing those plants. Tannins are present in sufficient quantities in bird's-foot trefoil to

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prevent the production of a stable foam, and their content in white clover increases sufficiently at flowering to make it safe to graze. If a mixed grass-and-clover sward has enough clover to cause bloat (probably more than 50% of the herbage by mass), it should not be grazed for long periods but should either be conserved, if there is sufficient mass, or rested for a few weeks until the clover inflorescences appear, after which it can be grazed or conserved. Cows are most likely to become bloated in the late evening after a day's grazing, or if they eat quickly after feed has been withheld, or if the pasture is wet. Wet grass reduces **saliva** production, and the saliva contains a **mucin** that disperses foam in the rumen. Herbage that has been frozen is particularly likely to cause bloat, as the rupture of plant cell walls releases a lot of **potassium**. Potassium-rich feeds, such as **molasses**, are notorious for causing bloat, whereas grasses rich in **sodium** appear to be less likely to cause it. The precise mechanism has not yet been determined but may relate to the stimulation of saliva production by sodium-rich feeds, and the foam-dispersing properties of the salivary mucin. Also, sodium encourages drinking and high-Na diets promote less bacterial slime, reduced amounts of bacterial cell lysis, and contribute to less bloat (Cheng *et al*., 1979). Dry **forage** supplements will usually slow down the rate of **digestion** and reduce bloat but, if there is adequate herbage, forage supplements may not be eaten by some cows in sufficient quantities, particularly if they are based on straw or other low-quality forages. Mineral oils also help to disperse the foam and can be added to a concentrate feed or sprayed on to the pasture or the cows' flanks, to be licked

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off as needed. **Linseed** oil is often used. A proprietary product, poloxalene, also breaks up the foam and can be used as a drench for clinical cases or included in **feed block**s as a preventive measure. Often simply walking the cow from the field to the farmstead to receive medication will alleviate the swelling. It is important to keep a bloated cow on her feet if possible, as death can follow soon after recumbency.

There are reported breed differences in the susceptibility of cattle to bloat: Jersey cows are particularly prone to the disorder. Cows can get used to feeds that are liable to make them bloat; this may be by altering their behaviour to spread their meals out more evenly over the day. Lactating cows are particularly susceptible, due to their high intakes. Pasture bloat remains a serious problem in countries like New Zealand, where the cattle graze pasture which may have a high legume content. (CJCP, GMcLD)

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Blood

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The fluid transport system of the body, circulating within the cardiovascular system. It transports **nutrients** from the gut, **oxygen** from lungs, **hormone**s from **endocrine gland**s to body tissues and waste products from the tissues to excretory organs. Blood also aids in the **maintenance** of **pH**, fluid and **electrolyte** balance in the body, aids **temperature** control and is important in defending the body against pathogens.

Blood can be divided into a cellular component and a fluid component. These can be separated by centrifugation. The cellular component normally makes up 30–55% of blood volume, depending on species. The fluid component, plasma, will coagulate on exposure to air, to form serum and a **fibrinogen** clot. With platelets (thrombocytes), and by the action of the coagulation cascade, fibrinogen forms a clot when blood vessels are damaged. This can act as a self-defence mechanism to prevent further blood loss.

Cells that are found in the blood fall into three groups: red blood cells (erythrocytes), white blood cells (leukocytes) and platelets (thrombocytes). There are around 500–1000 times as many red blood cells as white. Erythrocytes are biconcave disc-shaped cells making up around 32% of blood volume. Mammalian erythrocytes have no nuclear material but those of birds, **fish** and reptiles do. They are formed from cells that originate principally in the bone marrow and survive in circulation for 3–4 months. Structurally they are envelopes containing **haemoglobin**, the iron-containing pigment that colours the blood and absorbs oxygen. Oxygen is transported from oxygen-rich areas, the lungs, to

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oxygen-deprived areas where O_2 is exchanged for CO_2, which is then returned to the lungs.

Leukocytes, which are larger than erythrocytes, are nucleated and are involved in body defence. They are divided into two major groups: granulocytes, which originate from bone marrow precursors, and lymphocytes, which come from lymphatic tissues around the body.

Granulocytes include neutrophils (polymorphonuclear leukocytes), which are phagocytic cells that are present in circulating blood but also able to migrate from blood vessels into tissues. Classically, numbers rise in response to bacterial infection. Eosinophils, with red-staining granules, are also phagocytes but are associated with parasitic infections and some allergic conditions. Basophils contain **histamine** that is secreted during allergic reactions. Monocytes are phagocytic and migrate from blood vessels to tissues, where they are called macrophages; they tend to be involved in chronic infections.

Lymphocytes are present in circulating blood but are also found in lymphoid tissues, for example Peyers' patches in the intestinal wall, spleen, tonsils and lymph nodes. They are involved in specific **immunity**, either as B cells in the humeral response (e.g. antibody-secreting cells (plasma cells)), or as part of the cell-mediated immune system.

Blood groups are recognized in animals and are used in thoroughbred identification. Blood transfusions can be used, particularly to treat blood loss or shock, but usually only once, due to the formation of antibodies to the 'foreign' blood group.

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Some of the measurements made on blood include: (i) **haematocrit** or packed cell volume (PCV), which measures the proportion of blood that is in cells; (ii) red, white and total (TBC) blood cell counts; (iii) differential white blood cell counts, which determine the different types of white blood cell present and can give an indication of the morphology; (iv) haemoglobin levels – in total for the blood and, in combination with red cell counts, for individual red blood cells (MCH); and (v) blood chemistry, enzyme and hormone levels.

Disorders of the blood include **anaemia** (lack of red blood cells), leukaemia (a malignant disease of lymphoid tissue that is especially common in the cat, where, unlike in humans, there is rarely an increase in numbers of leukocytes in the blood) and thrombocytopaenia (lack of platelets – causes include **poisoning**). Haemolytic disease of the newborn can result from an incompatibility between the blood of the sire and dam and is thought to be the cause of some late **abortion**s in cattle. In foals, puppies and piglets, **antibodies** in colostrum cause haemolysis of red cells; exchange transfusions have been performed to save severely affected foals. Haemophilia is rare, but is seen in dogs and cats. Haemolysis is the destruction of red cells with the release of haemoglobin; some infections and poisons can cause this. Blood circulation can carry pathogens or pathogenic substances round the body, leading to pyaemia, septicaemia, viraemia or toxaemia. (EM)

Blood flow

The degree to which an organ or tissue, via its network of

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capillaries, is perfused by blood. Blood flow can be measured by the flow (as ml min^{-1}) in the artery supplying it, or in the vein draining it, using various tracer dilution techniques, or by an ultrasonic or electromagnetic flow probe implanted around the blood vessel. (DS)

Blood meal

A deep red/brown granular powder obtained from blood collected at slaughterhouses. It is processed by gentle heating until fully coagulated; the excess water is drained off by pressing and finally the residue is dried and ground. It is occasionally further ground to form a very fine powder known as blood flour, which is more soluble although harder to handle. Blood meal is a good food material that is readily eaten by all animals, although it can be unpalatable at first. Modern drying methods apply heat gently, which allows blood meal to be produced with a minimum of heat damage. The dry matter (DM) is almost pure protein, with high concentrations of essential **amino acid**s except **isoleucine**. Excessive heat substantially reduces its **digestibility** but mild heat improves its value to ruminants by reducing **solubility** in the rumen.

Typical analysis for blood meal

Component (units)	Weight
Dry matter (DM) (g kg^{-1})	900
Metabolizable energy (MJ kg^{-1} DM)	13.2

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Component (units)	Weight
Crude protein (g kg^{-1} DM)	940
Ash (g kg^{-1} DM)	10
Oil (ether extract) (g kg^{-1} DM)	10

Blood meal may potentially carry the prions that cause **bovine spongiform encephalopathy** and its use as an animal feed (especially for ruminants) is banned in many jurisdictions. (MG; GMcLD)

Blood plasma

The fluid portion of unclotted blood consisting of 93% water and 5–7% protein with **electrolytes**, nutrients such as **glucose**, **amino acid**s, **lipids** and some **vitamins**, **hormone**s, metabolic waste products and small amounts of gases. **Albumin**, **fibrinogen** and globulins are the three major proteins. **Globulins** (particularly IgG) are produced by the humeral immune system in response to the stimulus of specific **antigen**s and can be a source of passive **immunity**. (EM)

Blunt snout bream (Wuchang bream) (*Megalobrama amblycephala*)

A herbivorous **freshwater fish** species with a long history of cultivation as a native species in the Yangtze River in China due to its high survival rate, rapid growth and tender flesh. The total production of this species was approximately 783,500 t in 2018. (QS)

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Boar

An entire male **pig**. In the growing phase, boars require higher-quality diets than castrates or gilts because of their higher protein deposition rate. They also have a lower appetite and thus can usually be fed *ad libitum* to slaughter without incurring carcass grading penalties. Their higher protein:fat ratio in liveweight gain makes them the most efficient type of pig in terms of feed utilization, and the preferred option in countries where age at slaughter is low enough to minimize the risk of boar **taint** in the meat. When used as breeding animals, their feed requirements will depend on liveweight, housing temperature and mating frequency. Under practical farm conditions, boars are usually fed a restricted amount of 3–4 kg per day of the same diet as the gestating sows, given in one or two daily meals. Both extreme **overfeeding** and underfeeding can adversely affect libido, while prolonged underfeeding can also reduce sperm production. Adequate levels of **calcium**, **phosphorus** and **biotin** are essential for soundness of legs. Semen quality can be beneficially affected by dietary **supplement**s of n-3 **fatty acid**s and by **antioxidant**s such as **vitamin E** and **selenium**. (SAE)

Body composition

Body composition can be defined either in chemical or tissue-related terms. In an agricultural context, it is not always easy to define what should be considered as 'the body', because there are a number of major components of **liveweight**, such as the **gastrointestinal tract**, that are of little value. The degree to which these are included or excluded in an analysis can cause

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confusion when different results are compared. For some purposes, the empty body, that is liveweight minus gut contents, is an appropriate base line. After slaughter, the empty body minus the major internal organs may be regarded as the eviscerated body. If the skin and hair are removed and an allowance is made for the evaporative loss of cooling, then a '**carcass** weight' is obtained. Carcass weights may be reported with the head on or off.

The simplest chemical description of body composition is in terms of **proximate analysis – dry matter** (or water content), **fat** (**lipid**), **protein** (usually as N × 6.25) and **ash**. With small species, it is practicable to homogenize the entire body and take aliquots for analysis. More detailed analyses can reveal the status of the reserves of macro- and **micronutrient**s.

Studies of tissue-related composition are often undertaken to give a link between the **chemical composition** and the economic value of the carcass. The major differences in body composition amongst animals of the same species usually relates to the ratio of fat (lipid) to fat-free (lipid-free) body, or that of '**adipose tissue** depots' to 'lean tissues'. Elsley *et al*. (1964) showed a remarkable stability between the ratio of bone to muscle and in the ratios of lean parts of the carcass to one another in sheep and pigs that had been grown on profoundly different nutritional regimes. The composition of the fat-free component of the body appears relatively constant both within and across species. This applies whether the fat is defined as chemically determined fat (lipid) or as dissectible fat. Blaxter (1989) gave percentage values for the concentration of water and protein in the fat-free (lipid-free) body

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for a number of species. These were, respectively, for hens 71.9 and 22.1, for rabbits 72.8 and 23.2, for sheep 71.1 and 21.9, for pigs 75.6 and 19.6, for oxen 71.4 and 22.1 and for the horse 73.0 and 20.5. The close similarity suggests a powerful functional relationship across all species.

Factors affecting the proportion of fat in the body

Fatty tissue is late maturing and is characteristically increased in mature animals. Young animals prioritize lean growth and tend to be vulnerable if food becomes scarce, because they have small energy reserves. A feature of early selection for domestic animals was to prize those that had a propensity to fatten easily, because these had a greater survival capability and in adverse times were a ready food source for starving humans. Modern selection techniques have favoured leaner animals to such an extent that some functionality has been lost. For example, in domestic pigs, sows have become so lean that they cannot sustain a normal or extended **lactation**. Hill sheep too are disadvantaged if they are excessively lean, since they lose some of the insulating value of subcutaneous fat when overwintering and the ewes have difficulty maintaining **body condition** if required to **suckle** in the early spring.

Entire males are usually leaner than females, which in turn are usually leaner than male castrates. The quest for carcass leanness has led to a reversal of **castration** policy in some countries and male pigs are left entire in several countries. Bulls too are left uncastrated in some production systems for the same reason, though this can bring management difficulties because of their

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unpredictable aggressiveness.

Nutrition can greatly affect the ratio of fatty tissues to **lean body mass**. Fat proportions are greatly increased in growing pigs and poultry when the diet is deficient in protein or in critical **amino acid**s. Generous feeding on high-energy diets can have the same effect, whilst restricted feeding usually produces a leaner carcass but slower growth rates.

Although changes in nutrition have little effect on the composition of lean tissues, the **fatty acid** composition of the adipose tissue of non-ruminant animals can be profoundly altered by the nature of the dietary fats. Diets rich in **polyunsaturated fatty acid**s such as n-6 **linoleic acid** or **linolenic acid** can transfer high concentrations of these fatty acids to the depot triglycerides. The very long-chain n-3 fatty acids of fish oils (eicosapentaenoic and docosahexaenoic) can also be incorporated in the triglycerides of the adipose depots of pigs and poultry. Some nutritionists believe that this could confer a nutritional advantage to the **animal fat** as a component of human diets. (VRF)

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Body condition

A simple, often largely subjective assessment of the fat and muscle of an animal, to judge its readiness for slaughter or breeding. It

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may be expressed as a body condition score, ranging from 0 or 1 to 5 or up to 9. Key areas to assess are the hip bones of quadrupeds, the ribs and vertebrae. Manual palpation should be used in conjunction with a visual assessment. (MFF; CJCP)

Body condition scoring

A body condition score (BCS) is a simple but effective animal management tool based on a visual assessment of the animal's body shape (especially its **fat** cover) in relation to its frame (skeletal shape). Because the relationship between body condition and frame size is an **indicator** of the animal's nutritional history, BCS can be used to monitor the success of a feeding programme in situations where owners cannot use more direct measures of nutritional status such as feed analysis, nutritional faecal profiling, or monitoring blood chemistry. BCS can be estimated in the paddock without the disruption of mustering, yarding and weighing. There can be consistent differences between scorers but BCS is repeatable, provided that the scorer is experienced.

BCS systems should be tuned to the particular type of animal. For example, temperate dairy breeds and *B. indicus* cattle deposit more fat internally than subcutaneously, compared with temperate beef breeds, and this difference is translated into different relationships between **carcass** fat content and BCS. Several body condition scoring schemes have been developed, including for sheep (Russel *et al.*, 1969), *Bos taurus* dairy and beef cattle (Earle, 1976), *Bos indicus* beef cattle (Nicholson and Butterworth, 1986), *Bos javanicus* cattle (Soares and Dryden, 2011), goats (Ghosh *et al.*, 2019), horses (Carter *et al.*, 2009), pigs (PISC, 2009) and deer

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(Audigé *et al.*, 1998). A 0–5 scoring system is commonly used to assess the BCS of beef cattle, while a 0–9 system is used for dairy cattle.

BCS can predict animal performance. Ovulation rates in sheep increase by 0.13 to 0.56 ova/BCS, and the post-partum **anoestrus** interval decreases in beef and dairy cattle as BCS increases; in dairy cattle, the BCS at calving is positively associated with improved milk yield in early **lactation**. (GMcLD)

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Body density:
see Specific gravity

Body fat
A term used to describe both the amount of **lipid** in the body and the amount of **adipose tissue**, which consists of a matrix of **connective tissue**, blood vessels and specialized cells (**adipocyte**s) in which lipid is stored, mainly as triglycerides. The adipose tissue is subdivided into the subcutaneous, abdominal, intermuscular and intramuscular depots. Subcutaneous **fat** is not uniformly distributed and, in some species, may be concentrated in specialized depots such as the hump or tail. The main abdominal fat stores are the omental and perirenal depots. Fat pads also surround other organs. Inter- and intramuscular fat are important to the cooking and eating qualities of meat. (MFF)

Body fluids
A general term embracing both intracellular and **extracellular** water and including **blood**, **urine**, **saliva**, **sweat** and other secretions, water in the **digesta** and water associated with tissues. The term is particularly used with reference to the maintenance of

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normal hydration and osmotic balance. (KJMcC)

Body temperature:
see Temperature, body

Body water
Body water includes all water contained in the **body fluids** and body tissues of the animal, though the term is sometimes taken to exclude water in the alimentary tract. **Total body water** can be estimated in living animals by dilution techniques (usually using labelled water, $^{2}H_2O$ or $^{3}H_2O$). Body water content can be measured after slaughter by desiccating samples of the homogenized **carcass**. The water content of animals varies inversely with their fat content, generally decreasing with age. The water content of the fat-free body is more constant but also decreases somewhat with age. (MMacL)

Bomb calorimeter
An instrument for measuring the heat of combustion (i.e. the **gross energy**) of a small **sample** of combustible material (e.g. food, body tissue, faeces). The bomb itself is an airtight stainless-steel container inside which the pre-weighed sample (usually compressed into a small pellet) is placed so that it is in contact with a firing device. **Oxygen** is admitted at high pressure through a valve and the bomb is then placed in the **calorimeter** vessel, which is a copper can containing water. This entire system is then placed on an insulated stand inside an outer vessel whose walls form a temperature-controlled water jacket. The temperature of

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the calorimeter and bomb is allowed to equilibrate with that of the water jacket and the bomb is then 'fired' by means of a brief electric pulse. The sample is completely oxidized in its oxygen-rich environment and the heat from its combustion causes a proportional rise in the temperature of the system comprising the bomb, calorimeter vessel and water. An automatic control system is used to cause an equal rise in the temperature of the water jacket, which ensures that there is no heat loss from the calorimeter system; its temperature rise is thus a measure of the heat of combustion of the sample. It is necessary to calibrate the device by means of test firing with samples of a substance of known heat of combustion. The whole procedure takes about 30 min for completion and can yield estimates of heat of combustion accurate to 0.5%. (JAMcL)

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Bone density

The amount of **mineral** per unit of bone volume. The classical method for measurement of bone density is based on Archimedes' principle, requiring weights of the bone in air and in water. Anatomical features of bone such as the medullary cavity, trabecular spaces and the Haversian system create inaccuracies in measurements. Clinical techniques such as dual-energy X-ray absorptiometry (DXA) are used to estimate bone mineral density, but these measurements are based on area (cm^2), not volume

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(cm^3). Estimates of bone density by DXA are highly correlated with **ash** density, but bone mineral density estimates are only weakly associated with fracture incidence in humans. (TDC)

Bone diseases

Nutritionally related bone diseases fall into one of three categories: those affecting the **growth** plate; failure to remodel mature bone properly; and diseases characterized by retention of **cartilage** plugs within bone.

Rickets is the failure to mineralize endochondral cartilage of growth plates; it is usually caused by **vitamin D** or **phosphorus** deficiency in young animals. **Calcium** deficiency may also induce rickets. **Manganese** and **copper** deficiency reduces elongation of growth-plate cartilage by reducing proteoglycan and **collagen** synthesis.

Bone is continuously undergoing **resorption** and replacement by new bone in a process called remodelling. Osteoporosis, primarily the result of calcium deficiency, occurs when bone is resorbed but is not replaced by new bone. Since bone is a major depot of calcium this serves as a means of maintaining calcium **homeostasis**. Osteodystrophy and osteomalacia occur when bone is resorbed and is replaced by bone matrix but not by bone mineral and are typically associated with vitamin D or phosphorus deficiency. In osteochondrosis (mammals) and tibial **dyschondroplasia** (birds), areas of physeal or epiphyseal cartilage fail to mineralize and remain as weak points within the bones. This is associated with diets (and genetics) that encourage very high rates of growth. (JPG)

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See also: Rickets

Bone formation

Bone formation involves a coordinated series of steps including synthesis, secretion, post-translational modifications, and repair (**maintenance**) of a complex extracellular matrix which can become mineralized with hydroxyapatite-like crystals. Pre-**osteoblast** cells proliferate and differentiate as they become embedded in an extracellular matrix. The embedded, fully differentiated osteoblasts are called osteocytes. Signals directing the extent and location of new bone formation are mediated by osteoblasts, but formation is coupled with removal of pre-existing calcified hyaline **cartilage** in growth plates (endochondral ossification), or stimulation of systemic **hormone**s and **growth factor**s that modulate osteoblast proliferation (bone modelling, by endochondral and intramembranous ossification), or removal of existing mineralized bone by **osteoclast**s (bone remodelling). Additional signals may originate with embedded osteocytes that direct localized responses to mechanical loads or fracture healing responses.

The bone extracellular matrix is composed of 40% **collagen** (primarily type 1 collagen) and 10–15% non-collagen proteins, which include proteoglycans (85% chondroitin **sulphate**, 7–12% core protein and 5–7% keratan sulphate), glycosylated proteins and gamma-carboxylated proteins. The helical structure of **collagen** provides tensile strength and, upon mineralization by growth of hydroxyapatite-like crystals within the helix, compressive strength.

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Proteoglycans (also called ground substance) are complex branched polymers with negatively charged side-chains that maintain the hydration state of the matrix.

Mineralization follows secretion of the extracellular matrix with initiation and growth of hydroxyapatite-like crystals ($3Ca_3(PO_4)_2 \cdot Ca(OH)_2$). The mineralized matrix functions in both structural and storage roles. Deposition and **resorption** of **mineral** responds to changes in mechanical loads and to systemic signals involved in **calcium** and phosphate **homeostasis**.

Two systemic hormones, **parathyroid hormone** and 1,25 dihydroxyvitamin D_3, are involved in bone formation through their direct action on **osteoblast** metabolism. Osteoblasts also mediate systemic signals that are transmitted through local signalling pathways to **osteoclast**s. For example, agents that increase bone resorption, such as PTH, bind to receptors on osteoblast cells, which release a localized factor to stimulate osteoclastic activity and hence increased bone resorption. These signalling arrangements function to couple bone formation and **resorption** for modelling and remodelling of bone. (TDC)

Bone meal

Bone meal and products made from bone are most commonly used as sources of **phosphorus**. Phosphates of rock origin (rock phosphate or lime phosphate) may, unless thoroughly treated, contain dangerously high levels of **fluorine**, whereas those from bone are completely safe. Bone meal for use as a phosphorus **supplement** is produced by heating, drying and finely grinding fresh, defatted bones from warm-blooded land animals. This

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extracts most of the protein and fat to leave monohydrogen phosphate ($CaHPO_4 \cdot xH_2O$), also known as mono**calcium phosphate**. This process is now tightly controlled within the EU under *The Processed Animal Protein Regulations 2001* of 1 August 2001 and now includes treatment with dilute **hydrochloric acid** (4%) over a period of at least 2 days, after which the resultant liquor is treated with lime to form a precipitate of **dicalcium phosphate**. Because of these regulations the most common sources of phosphorus now used in animal feed within the EU are from de-fluorinated natural phosphates and composed of equal parts of monocalcium and dicalcium phosphate ($CaHPO_4$-$Ca(H_2PO_4)_2 \cdot H_2O$). (MG)

Bone resorption:
see Bone formation

Boron (B)
A non-metallic element with an atomic mass of 10.811. It does not occur free in nature but combines readily with oxygen to form boric acid, $B(OH)_3$, and borate salts, $B(OH)_4^-$. Boron also forms esters with oxygen-containing compounds, or will link with four oxygen atoms in adjacent hydroxyl groups to form identifiable biological compounds. Some of these B-containing compounds can be isolated from nature, including boromycin, an antibiotic produced by certain bacteria. Certain plant species have an absolute requirement for B, and recent experimental results suggest that B serves a physiological function in animals as well.

Chicks raised on diets marginally deficient in **vitamin D** and

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without B showed more anomalies in bone maturation than chicks fed marginal vitamin D and adequate B (3 mg kg^{-1}). However, B would not substitute wholly for vitamin D. Additional dietary B (5 mg kg^{-1}), compared with no B, enhanced body weight gain in broilers.

Recent studies also have shown that B deprivation is detrimental to normal development of the embryos of the South African clawed frog (*Xenopus laevis*), the zebrafish (*Danio rerio)* and **rainbow trout** (*Oncorhynchus mykiss*). Dietary requirements for farm animals have not been established. (PGR)

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Botanical composition of grasses and food crops

Plants are made up of a number of components, such as leaves, stems and inflorescences. For **herbivore**s, the leaves and young stems of **grasses** are the major source of **nutrients**. Plant material contains several different tissues, of which the most important are mesophyll, epidermis, vascular bundles and schlerenchyma. The first two tissues are important as herbivore food material and are most plentiful in leaves and young stems. Cells of the schlerenchyma and vascular bundles are lignified and have little feeding value. Meristem and parenchymal cells are

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plentiful in storage organs and seeds (e.g. the **endosperm**) and are readily digested.

Grasses and **legumes** are major feed sources for grazing animals. Grasses are divided into temperate (C3) and tropical (C4) types. There are several differences between C3 and C4 grasses which influence their feeding value, but the main difference is in the anatomy of leaves and stems. C3 grasses have a much larger mesophyll:vascular bundle ratio, and are thus more digestible than C4 grasses at a comparable stage of maturity.

Plants with upright stems and aerial buds can only be grazed or cut once, whereas grasses, which have their leaf-growing points protected at the base of the plant can usually be defoliated several times during the growing season. Whereas annual grasses only produce tillers above ground (stolons), perennials can also produce underground tillers, or rhizomes. Provided that there is sufficient soil water and solar radiation, in temperate climates the growing season lasts as long as ambient temperatures are sufficient to maintain growth. However, first flowering is controlled by a combination of the amount of vegetative growth and increasing day length. The grazing season, as distinct from the growing season, is dependent on rainfall being sufficient to allow plant growth, but insufficient to cause damage to plants and soil through treading. In spring, tillers develop rapidly and, if there is no defoliation, this is followed by the growth of tall inflorescence-bearing stems. Vegetative development is arrested at this stage but, if conditions are right, a second flowering occurs in late summer. This is followed by a reduction in tillers during the winter. In the semi-

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arid tropics lack of grazing material, often caused by **drought**, is the major limitation to grazing. For herbivores, leaves and young stems are the major source of nutrients, with conservation of **forage** and supplementary feed gaining in importance as their **nutritive value**, or **availability**, falls.

The nutritive value of a grass sward will depend not only on rainfall and fertilizer applications but also on the frequency of defoliation, either by cutting or by grazing. The more often defoliation takes place, the greater is the proportion of young leaves and shoots in the aerial part of the plant. Lignification of stems will be minimized. Fewer defoliations, whilst resulting in increased lignification, will lead to an increased yield of **dry matter**.

Storage organs in food crops are generally modified stems or roots, with non-lignified secondary thickening. They are normally harvested and stored for use in the winter period. For livestock, this group includes such crops as **fodder beet** and mangels. Modern conservation techniques and a consequent reduction in the use of rotations has reduced the importance of these crops as livestock feed but many are valued as vegetable crops.

Seeds contain only small quantities of **cellulose**, making them edible by humans and other animals. They usually contain very little water and, if kept dry, they remain dormant, allowing long-term storage. The most important crops in this group are the **cereal**s and **oilseed**s. Seeds are valuable sources of **starch**, **protein** and **fats** (**oils**). Many of the crops grown for their seeds for human consumption also contribute valuable **by-product**s for

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livestock feeding (for example: **oilseed cake**s; **bran** and other miller's offals; **straws** and **stovers**). (TS; GMcLD)

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Botulism

Intoxication caused by toxins elaborated by *Clostridium botulinum*, a Gram-positive, spore-forming anaerobic bacterium which inhabits soils, litter, feed and the digestive tract. There are seven types of *C. botulinum*, producing specific toxins: A, B, C, D, E, F and G. Types A, B and E are most important in humans, type C in most animal species and D in cattle. The incidence of botulism is highest in birds. Botulism causes progressive motor paralysis, characterized by progressive weakness and paralysis, and death by respiratory or cardiac paralysis. (PC)

Bovine spongiform encephalopathy (BSE)Also called mad cow disease. A fatal degenerative disease of cattle, related to other transmissible spongiform encephalopathies such as ovine scrapie, and Creutzfeldt-Jakob disease of humans. Neurones in the brain are progressively destroyed, leading to apprehension, hypersensitivity, **ataxia** and coma of affected animals, usually after several years of incubation. BSE can be transmitted to a wide

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variety of mammals by feeding diseased tissues. As the infective agent is not destroyed by cooking, there is concern to avoid human infection. The disease in cattle reached epidemic proportions in the UK in the early 1990s due to the inclusion in **compound feed**s of meat and **bone meal** made from **carcass** offal that included infected material, and it has occurred sporadically in other countries. It was controlled in the UK by banning the use of meat and bone meal in animal feed. Under *The Bovine spongiform encephalopathy (No. 2) Order 1996 (SI 1996 No. 31663),* it was still permitted to feed **blood meal** to both ruminant and non-ruminant animals in the UK and Europe, although this practice was not common. However, following the *Processed Animal Protein Regulations 2001* of 1 August 2001, this practice is no longer permitted in the EU for animals kept, fattened or bred for the production of food. Similar bans on the inclusion of **meat product**s in animal feeds, and regulations excluding older cattle, bovine offals and nervous tissue from the human **food chain**, are now in force in many countries. Animal feeding practices have had to adjust to the loss of these valuable but potentially dangerous feedstuffs. (RFEA; AJFR; MG)

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Bracken fern (*Pteridium aquilinum*)

A perennial rhizome-forming herb found in many parts of the

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world. Its fronds are palatable to livestock but contain several toxins that cause disease syndromes. The toxins include a thiaminase, ptaquiloside, an unidentified bone marrow suppressant, and possibly a cyanogenic **glycoside**. Ptaquiloside is a **carcinogen** that causes urinary tract neoplasms in cattle that have grazed bracken for several weeks. This has been called enzootic haematuria, as affected cattle often bleed into the urinary tract. Poisoned animals also develop leucopenia, thrombocytopenia and **anaemia**. Bracken fern **poisoning** in horses is primarily neurological, probably caused by **thiamine** deficiency. Sheep are relatively resistant to bracken poisoning but some develop bright **blindness** due to degeneration of the retinal neuroepithelium. (LFJ)

Brackish water

Water that is less salty than **sea water** (34–35 g l^{-1}). Brackish waters are usually found in those portions of estuaries where **fresh water** and **salt water** mix. This mixing zone is typically called the middle estuary; it is bracketed by the lower estuary, which is characterized by oceanic influences and is essentially sea water, and the upper estuary, where there is a tidal influence but no intrusion of sea water. (RHP)

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Bran

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The collective name for the layers of tissue (**pericarp**, **testa** and **aleurone**) removed during the processing of cereal **grain**s (e.g. wheat **bran** during **flour** processing). An important **by-product** for animal feeding that is generally low in starch content and **energy value**. (ED)
See also: Cereals

Branched-chain amino acids
The three indispensable **amino acid**s L-**leucine** $(CH_3)_2{\cdot}CH{\cdot}CH_2.CHN^+H_3{\cdot}COO^-$, L-**isoleucine** $CH_3{\cdot}CH_2{\cdot}CH{\cdot}(CH_3){\cdot}CHN^+H_3{\cdot}COO^-$ and L-**valine** $(CH_3)_2{\cdot}CH{\cdot}CHN^+H_3{\cdot}COO^-$. They are closely related in structure and **metabolism**, sharing the same **enzyme** (the **branched-chain keto acid**, **dehydrogenase**) in their catabolic pathway. This enzyme complex is found in both the **liver** and extrahepatic tissues, except for the mature erythrocytes of mammals. The three interact in **metabolism**, such that an excess of leucine alters the utilization of the others: this is called an amino acid **antagonism**. In cases where only one keto acid of the amino acid is used, it will adequately serve as a source of the amino acid. (NJB)

Branched-chain fatty acids
Branched-chain fatty acids are not widely distributed but are found in rumen contents, where they are produced during the **catabolism** of **branched-chain amino acids** by **rumen microorganism**s. Isobutyric acid, $(CH_3)_2{\cdot}CH{\cdot}COOH$, is derived from the catabolism of L-**valine**; and isovaleric acid,

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$(CH_3)_2 \cdot CH \cdot CH_2 \cdot COOH$, is derived from the catabolism of L-**leucine**. (NJB)

Branched-chain keto acids

The **transamination** products of the **branched-chain amino acid**s, **leucine**, **isoleucine** or **valine**. The transamination partner may be one of the other branched-chain **keto acid**s or α-ketoglutarate. The transamination product of leucine is α-ketoisocaproate, $(CH_3)_2 \cdot CH \cdot CH_2 \cdot CO \cdot COO^-$; that of isoleucine is α-keto-β-methylvalerate $CH_3 \cdot CH_2 \cdot CH \cdot (CH_3) \cdot CO \cdot COO^-$; while that of valine is α-ketoisovalerate, $(CH_3)_2 \cdot CH \cdot CO \cdot COO^-$. (NJB)

Brassicas

The brassica family includes **cabbages**, Brussels sprouts, **cauliflowers**, **kales**, **turnips**, **forage rape**, radishes and **mustard**. **Oilseed**s include rapeseed, also known as canola (*Brassica napus*, *Brassica campestris*) and mustard seed (*Sinapis* spp.). All of the brassica family contain **glucosinolate**s which degrade readily to thiocyanates, isothiocyanates, nitriles and their alkyl, alkenyl and aryl residues. These can cause adverse effects such as **goitre** in animals and humans. Some of the **forage** materials, such as kale, also contain *S*-methylcysteine sulphoxide (40–60 g kg^{-1} dry matter) which degrades in the **rumen** to yield dimethyl sulphoxide and then dimethyldisulphide, which causes haemolytic **anaemia**. The glucosinolates and their aglycones smell and taste pungent, flavouring the meat, milk and eggs of animals that consume them. The oils of rapeseed and mustard seeds can

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contain substantial proportions of **erucic acid** but new cultivars have low concentrations of erucic acid (< 50 g kg^{-1} of the **oil**) and glucosinolates (< 10 μmol g^{-1} seed). (TA)

Bread:
see Bakery products

Breadfruit
A round green seedless fruit approximately 20 cm in diameter, produced by the breadfruit tree, which grows up to 20 m high and has large tough lobed leaves. The fruit is cooked and used by people in a similar manner to potatoes, and is a staple food in the Pacific islands. It is related to jackfruit (*Atrocarpus integrifolia*). Breadfruit can be fed to all classes of livestock but is often used for pigs. Dried fruit is ground to make meal for storage. The meal has a pleasant odour and is a good source of energy. Breadfruit meal has low protein, fat and fibre contents but is very high in **carbohydrates** (see table).

Typical composition of breadfruit products (g kg^{-1} dry matter).

	DM (%)	**CP**	**CF**	**Ash**	**EE**	**NFE**	**Ca**	**P**
Breadfruit, ripe	29.8	5.7	4.9	6.8	1.0	81.6	0.12	0.15

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	DM (%)	CP	CF	Ash	EE	NFE	Ca	P
Breadfruit meal	84.9	3.2	5.5	3.1	0.9	87.3	0.08	0.16
Breadnut, fibre and skins	13.4	6.5	18.1	11.2	4.5	59.7		
Breadnut, seeds and shells	31.4	11.1	14.3	4.0	6.0	64.6		

CF, crude fibre; CP, crude protein; DM, dry matter; EE, ether extract; NFE, nitrogen-free extract.

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Breadfruit. Photo courtesy of Phillips Tellis. Licensed under CC BY 2.0.

Breadfruit is seedless but another variety, called the breadnut, contains seeds. Fruits of the breadnut have a rough surface covered in conical spines, unlike the smaller bumps on the surface of a breadfruit. Both the seeds and pulp of the breadnut are edible. The breadnut fruit has higher protein, fat and fibre contents than the breadfruit, particularly so in the case of the seeds. (LR)

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Brewery by-products

Malt culms and brewers' grains are the main **by-product**s of brewing malted or unmalted cereal grains, particularly barley, and other starch-rich products. Other by-products include spent hops, waste beer and brewers' yeast, the latter usually being incorporated with other by-products such as brewers' grains.

Malt culms, also called malt sprouts, comprise the dried radicle (rootlets) and plumule (sprouts) of the germinated barley grains and generally represent approximately 5% of the weight of malted

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barley. They are a good source of protein (290 ± 56.9 g kg^{-1} dry matter (DM)), with a high fibre (556 ± 50.7 g **neutral detergent fibre** kg^{-1} DM) content and an estimated energy (ME) value of 11.1 ± 0.95 MJ kg^{-1} DM. Because of their high fibre content, they are generally fed only to ruminants and then, because of their bitter taste, only at low levels. Wet brewers' grains, also called draff, are the spent grains and the insoluble fraction, including protein, following the removal of the wort, and may also contain residues of **maize** and **rice**. Fresh brewers' grains have a low DM content (250 ± 31.3 g kg^{-1} fresh weight) and high protein and fibre contents (218 ± 34.2 and 618 ± 63.9 g kg^{-1} DM, respectively). They are widely used in **ruminant feeding** as a **forage** or concentrate feed replacer or for **buffer** feeding and have an estimated energy (ME) value of 11.5 ± 0.65 MJ kg^{-1} DM. They can be fed in their fresh state or following ensilage or drying. (ED)

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Broiler breeders

Genetic selection of broilers for rapid growth rate has resulted in the **feed intake** of breeding stock having to be controlled to prevent **obesity**, health problems and reduced reproductive

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efficiency. As reported by Zuidhof *et al*. (2017), over the previous 50 years broiler body weight had increased over 450% but the body weight target considered optimal for reproductive efficiency remained virtually constant. As a result, the gap between the growth potential of broilers and breeder target weight continued to widen. Consequently, the level of broiler breeder feed restriction has increased, creating intense competition during feeding.

Feed restriction is typically accomplished by limiting the amount of feed provided, starting when the birds are 1–3 weeks of age. **Allowance**s during rearing are commonly 60–80% lower than that of birds fed to **appetite** and 25–50% lower during the laying period, resulting in a reduction in the body weight of adults to approximately 45–50% of that of birds fed to appetite. The level of feed restriction imposed is usually dependent on the broiler strain. Among the health problems reduced by restricted feed are bone, joint and foot problems and age-related decreases in tendon elasticity. In addition, feed-restricted birds show improved antibody responses and disease resistance, and significantly decreased mortality.

In spite of these benefits, restricted feeding has negative effects on the **welfare** of broiler breeders, attributed to the fact that they are chronically hungry. The normal behaviour of birds is to spend a considerable portion of their day in activities associated with **foraging**. Jungle fowl spend 60% of their time on eating and foraging, and modern **laying hen**s spend up to 52% of their time on feeding-related behaviour, indicating that the **feeding behaviour** of the modern bird is very similar to that of its

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ancestor. As a consequence of restricted feeding, however, broiler breeders spend less than 15 min per day on eating (de Jong and van Emous, 2017), indicating that these types of birds are not fulfilling their natural feeding motivation. The signs of stress and frustration (including increased aggression, greater activity, **pecking** in feeders, and decreased comfort behaviours, and high rates of stereotyped oral behaviour and pacing) that are observed when broiler breeders are fed restricted amounts indicate that they seek more feed than they are offered.

It is important to provide sufficient space at the feeders to reduce aggression at the time of feeding, since aggression may result in increased levels of feather and skin damage. Also, the speed at which feed is distributed needs to be controlled to allow equal feed intake between individuals, since this helps to promote flock uniformity and minimize aggressive behaviour. Overdrinking (polydipsia) is a common problem in broiler breeder flocks fed restricted amounts of feed, resulting in the need to restrict water intake as well as feed intake in order to maintain **litter** quality, avoid the build-up of intestinal parasites in the litter and maintain good foot pad condition.

Feed withdrawal is known to be a potent physiological stressor in poultry. Domestic chicks fasted for only 24 h show both **adrenal** hypertrophy and a persistent increase in corticosterone secretion which may be indicative of stress, and 48 h of deprivation results in increased susceptibility to *Staphylococcus aureus* infection. The birds also show a high incidence of fault bars in the feathers. Some studies have reported that heterophil to lymphocyte ratios, which

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are often used as an indicator of chronic stress, increase as a result of feed restriction. Persistent basophilia has also been noted in feed-restricted birds, which could be interpreted as indicative of chronic inflammation. Another problem is that flock uniformity is reduced by intense competition for limited feed, and growing the males separately from the females has been shown to be advisable at least with some strains.

Two main approaches have been used to reduce voluntary intake of feed: alteration of the feed composition (for example, by dilution with fibrous ingredients such as oat hulls to improve **satiety** without resulting in excessive weight gain) and quantitative feed restriction. It has been shown that increasing the fibre content of the diet or decreasing the energy and protein contents of the diet can have positive effects on the welfare of broiler breeders, as measured by a reduction in time spent on behaviours indicative of frustration, stress or **hunger** (de Jong and van Emous, 2017; Tahamtani *et al*., 2020). Providing access to fibrous feeds such as **maize** silage and scattering of the feed by use of spin feeders have also been shown to be beneficial.

Quantitative feed restriction is the common approach used in commercial broiler breeder production. Because feeding frustration and hunger are major welfare concerns during rearing, several approaches have been taken to try to decrease the negative feelings of hunger while maintaining suitable growth rates and reproductive health. One of these is non-daily (skip-a-day) feeding schedules, used in some countries to improve satiety on days when feeding is permitted. Not all countries allow skip-a-day feeding,

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due to welfare concerns relating to fasting days. Lindholm *et al.* (2018) compared the effects of raising broiler breeder pullets on a non-daily feeding schedule (2 non-consecutive fasting days per week, 5:2), or on daily feed restriction. Signs of increased physiological stress levels were found in 5:2 birds, including elevated heterophil to lymphocyte ratios (1.00 for 5:2 vs. 0.75 for daily fed at 12 weeks of age), increased adiposity (0.21% lean body weight for 5:2 vs. 0.13% for daily fed), and reduced muscle growth (pectoral muscle 5.94% lean body weight for 5:2 vs. 6.5% for daily fed). At the same time, 5:2 birds showed signs of lower anxiety before feeding times (activity reduced from 10.30 in daily fed to 4.85, activity reduced by 53% compared to birds fed daily), attributed to lower feed competition associated with larger portion sizes. The 5:2 birds generally showed more interest in a novel object in the home pen, which indicated increased risk taking and reduced fear while fasting. The 5:2 birds in this study showed no signs of learning the feeding schedule, and this unpredictability was considered to possibly also increase stress. These and other results suggest that there is no clear and consistent benefit from skip-a-day feeding and that feed restriction of broiler breeder stock according to the feeding pattern recommended by the breeder supply company remains the norm. (RB)

See also: Restricted feeding systems

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Broiler chicken

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Domestic fowl (*Gallus gallus*) produced specifically for **meat production**. The term 'broiler' originally referred to a size of bird that was suitable for rapid oven cooking (as opposed to roasting and frying) but now refers to all strains and sizes of chicken that are reared only for their meat. Broiler chicken strains were first produced around 1950 by crossing White Cornish (also known as Indian Game) with Plymouth White Rock breeds. Continued selection and development of broiler strains has produced birds that grow to market weight within a few weeks, which are then slaughtered at weights that are less than half of their mature body weight. Currently these chickens are grown to various weights to meet specific market demands, namely Cornish Game birds (marketed at approximately 1 kg liveweight), roaster chickens (marketed at 3+ kg), while 'broilers' tend to fall in the middleweight category.

Genetic improvement of meat-type birds is conducted in several countries by specialized companies known as primary breeding companies. These companies also provide expertise in **poultry feeding**, bird management and veterinary care to producers. Commercial birds are generally four-way crosses, which takes advantage of hybrid vigour. Because the breeding period is short for chickens, primary breeding companies can react quickly to changing requirements over a low number of generations. These companies also offer specific bird strains for specific markets.

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Broiler chickens in an intensive rearing system. Photo courtesy of United States Department of Agriculture. Licensed under CC BY 2.0.

Housing systems for broilers vary across the world. Light-tight barns (which allow for control of day–night cycles, **light** intensity and wavelength, and allow ability to provide optimal **temperature** and ventilation for birds at all ages) are common in many parts of the world, particularly in locales in which ambient conditions are a concern. Other areas have open-sided or curtained barns, which allow more ambient air and light into the barn, resulting in less control over the in-barn conditions, and potentially more challenges controlling biosecurity compared with solid-sided barns. Other housing systems may allow free-range access to birds, or windowed houses to allow sunlight into the barn.

Broiler chickens are reared in the same open rearing house from placement to slaughter weight. They are then caught and transported by truck to a slaughter and **carcass**-processing facility. The transport of live chickens requires specially designed vehicles

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and is, therefore, costly. As a result, broiler farms are normally located within a reasonable distance from the processing facility.

Consumption of chicken meat has increased steadily in many countries for a number of reasons, including an ability to cross multiple cultural boundaries, a relatively low cost compared with many red meats, low fat content and recognition as a health-conscious meat. Per capita consumption of chicken meat has increased worldwide, from 9.43 kg in 1999 to 14.7 kg in 2019 (OECD-FAO, 2020).

The US NRC (1994) estimated the nutritional requirements of modern hybrid-type broiler chickens, which are summarized in the table. They demonstrate that these birds require a high dietary content of **metabolizable energy** (ME) and protein in order to support a rapid growth potential. Important **amino acid**s for feather and muscle growth are **methionine** and **lysine**, with other amino acids provided in an ideal balance. Broiler breeding companies later modified these estimates according to the specific requirements of different strains, for the guidance of feed manufacturers. Typically a commercially reared broiler bird (mixed-sex flock) will reach 2.3 kg in 38 days on 3.6 kg of feed, with males growing faster than females.

The diets used in broiler production are based on cereal **grain**s such as **maize** and **wheat**; **protein source**s such as **soybean** meal or canola meal; **mineral** sources such as ground **limestone** and **dicalcium phosphate**; trace **mineral and vitamin supplement**s and other approved additives to enhance gut health of the birds in response to the global phasing-out of **antibiotics in**

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animal feeds.

The feed is usually pelleted, since it flows better through automated feeding equipment, and intake and **feed conversion** efficiency are higher than with **mash** feeds. Another advantage is that the heat used in **pelleting** reduces the level of potentially harmful bacteria such as *Salmonella* spp. in the feed.

Summary of estimated nutrient requirements of broiler chickens, amounts per kg diet (900 g/kg DM basis), from NRC (1994).

	Starting 0–3 w	Growing 3–6 w	Finishing
AME (kcal)	3200	3200	3200
Crude protein (g)	230	200	180
Amino acids (g)			
Lysine	11.0	10.0	8.5
Methionine	5.0	3.8	3.2
Methionine + cystine	9.0	7.2	6.0
Minerals (g)			
Calcium	10.0	9.0	8.0
Phosphorus (non-phytate)	4.5	3.5	3.0
Chloride	2.0	1.5	1.2

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It is usual for broiler chickens to have *ad libitum* access to feed and water throughout the rearing period. Feeders must be distributed evenly throughout the flock with the correct number of feeders for the number and age of birds present.

Whole grain is used in some feeding systems; these systems are closer to the natural poultry feeding situation than the feeding of diets containing ground grain. In addition, the bird is well equipped to digest whole grains. In Europe, Australia and Canada, **wheat** is the most common grain used for this system. **Supplement**s are balanced for blending with whole or coarsely cracked wheat or other cereal grains on farm. For instance, Jones and Taylor (2001) showed that whole **triticale** could be utilized successfully in pelleted broiler diets with broilers, giving production results similar to (or better than) those with pelleted diets containing ground triticale. In addition, proventricular dilatation and mortality due to **ascites** were reduced by feeding pelleted diets containing whole grain. Bennett *et al*. (2002) also demonstrated that with gradual introduction of whole wheat into diets of young broilers and the use of pelleted supplements, broilers performed as well as those not fed whole wheat up to 35% inclusion, with no effects on **carcass** yield and decreased skeletal problems. Current industry practice in Western Canada shows that much higher levels are used with supplements balanced accordingly. This practice is often done to promote gut integrity but is also commonly used to reduce the cost of feed and transportation by allowing a producer to utilize home grown grains.

A modification of whole-grain feeding is **choice feeding** or

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'free-choice feeding', based on the principle that chickens possess some degree of '**nutritional wisdom**', which allows them to select from the various feed ingredients on offer and construct their own diet according to their actual needs and production capacity.

While broilers have traditionally been selected for growth rate, and thus, indirectly, for **appetite**, the primary breeding companies have included many other selection criteria to ensure metabolic health and skeletal integrity of the growing bird. In addition to finely tuned **feed intake** and dietary parameters, water intake is critically important in the growing bird. Clean, fresh water should be provided *ad libitum* and, as stated by Van der Klis and De Lange (2013), **water intake** is affected by factors as diet composition, feed form, intestinal health, stress and environmental conditions. Barn conditions can be negatively affected by dietary components that increase water intake and performance can be negatively impacted by dietary factors that decrease water intake. Maintaining a balance is crucial to keeping the broiler healthy as well as growing to its potential.

Exogenous enzyme supplementation of poultry diets is common and becoming more specialized. Using **enzymes** tailored to the specific types of fibre in the diet can greatly improve **digestion** of specific feedstuffs. **Phytases** release **phytate**-bound **phosphorus** in plant feedstuffs and, allowing a decrease in the use of inorganic phosphates required in **poultry feed**, are commonly used and are even legislated in some parts of the world to decrease pollution. Other enzymes such as proteases and

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mannanases can be formulated into livestock feeds to allow release of bound proteins and **carbohydrates** in other plant-based ingredients.

Ensuring that **water quality** is optimal by minimizing biofilms and bacterial load as well as adjusting diets to the mineral content of water are also important components of broiler nutrition. (KS-L; ENF)

See also: Additives, Chick; Chicken; Choice feeding

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Broken-mouthed sheep

Sheep experience loss and excessive wear of their incisor **teeth**, which farmers will assess in considering whether to keep sheep in their flock. Sheep's mouths should be examined regularly when they reach 5 years of age. Up until that age, after losing their **milk teeth** at 1–2 years of age, sheep typically gain a pair of incisors every year, ending up with four sets of lower incisors. Older sheep typically lose one incisor and one lower jaw premolar per year. Under harsh hill conditions, where pasture is slow growing and short, sheep regularly eat soil and small stones along with the grass, which wears their incisors. Typically 5 kg of soil will be ingested over the winter period, when the grass is short, but it can be up to 10–12 kg in sheep experiencing teeth loss. Excessive **rumination** of coarse feed, dental caries and gingivitis may also contribute to the problem. Broken-mouthed sheep may be sent to lower ground, where taller herbage is available. Many factors contribute to incisor loss in **ewes**, including high stocking rates, internal parasites that deplete **calcium** status, **fluorine** excesses, and breeding the ewes early, which places a nutritional burden on the ewes. Grazing **swedes** and **turnip**s accelerates the rate of wear of incisors. Affected animals lose weight, produce less milk and have reduced **wool growth**. Supplementary feeding during periods of short pasture will help to protect sheep's incisors in hill conditions. Feeding extra calcium during the rearing phase will help sheep to grow strong teeth; and providing calcium **supplement**s during

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late pregnancy and **lactation** reduces skeletal mineralization to provide for **calcium** needs. There is little evidence that the Australian practice of shortening incisor teeth with an angle **grinder** provides benefit in terms of maintaining productivity. It has largely been abandoned, because of concerns for the severe pain that it causes and the immediate setback to the sheep, which lasts about one month. Other problems include spreading teeth and shrinking **gums**. (CJCP)

Brouwer formula

A formula for calculating **heat production**, proposed by Professor E. Brouwer, and recommended for general use in 1965 by an international committee of scientists. As first published the equation relates heat production (M, kcal) to **oxygen consumption** (O_2, litres), **carbon dioxide** production (CO_2, litres), **methane** production (CH_4, litres) and urinary **nitrogen** (N, grams):

$$M=3.666\times O2+1.200\times CO2-0.518\times CH4-1.431\times N$$

In SI units the equation is:

$$M\,(kJ)=16.18\times O2+5.02\times CO2-2.17\times CH4-5.99\times N$$

The equation has become widely accepted for those farm animals that excrete urinary nitrogen in the form of **urea** (i.e. most of them). Slight variations on the formula are more appropriate for use with **poultry** (based on uric acid) and **fish** (based on **ammonia**). (JAMcL)

See also: Indirect calorimetry

Further reading

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Brown adipose tissue (BAT)
A specialized **adipose tissue** found most prominently in some newborn vertebrates. Brown **fat** has mitochondria that can become uncoupled so that the protons produced from substrate **catabolism**, which are normally used for ATP production, are released and the energy that is normally utilized for the conversion of ADP to ATP is lost as heat. This specialized fat participates in **non-shivering thermogenesis** and, because it is highly vascularized, the heat produced is distributed to the body via the blood. (NJB)

Browning
Known as non-enzymatic browning, carbonyl-amine browning or the **Maillard reaction**. Browning occurs when a **reducing sugar** is heated in an aqueous medium with **amino acid**s or proteins. The reaction involves a condensation between the **aldehyde** group of a reducing sugar and a free amino group of an amino acid. In free amino acids or proteins, the ϵ-amino group of **lysine**, the guanidino group of **arginine** and the **amide** group of **glutamine** are involved. The result is a decrease in the **digestion** and **absorption** of dietary **lysine**. (NJB; GW)

Key reference

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Browsing

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Eating of leaves and twigs from trees and bushes. Most livestock species prefer either to browse or to graze, though many (including cattle and goats) are adaptable. In semi-arid **rangeland**s, leaves and fine stems are usually available into the **dry season**, with the new season growth starting just before the onset of the rains. Browse plants often contain **phenolic compound**s. (TS)

Brunner's glands

Small glands in the **duodenum** that produce an alkaline secretion of sodium **bicarbonate** ($NaHCO_3$) that enters the duodenum through ducts located between the **villi**. The secreted bicarbonate, together with that from pancreatic secretions, neutralizes the **hydrochloric acid** in the **digesta** that enter the duodenum from the stomach. The glands are lacking in birds. (SB)

Brush border

The brush-like surface structure, formed by numerous microvilli, on the membrane of the **villi** (the finger-like projections of the gut epithelium). The structure of the brush border substantially increases the absorptive surface area of the **small intestine**. Together with valve-like folds of the intestines, and the finger-like villi, the brush border increases the absorptive surface about 600-fold. A number of specific hydrolytic **enzymes**, including peptidases (**aminopeptidase**s, dipeptidase and **tripeptidase**) located in the brush border and carbohydrases (**maltase**, **isomaltase**, **sucrase**, **lactase**, **trehalase**) attached to the brush border, complete the degradation of proteins and **carbohydrates** into **amino acid**s and **monosaccharide**s, respectively. Entero-

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kinase, which initiates the activation of pancreatic enzymes in the **duodenum**, is also secreted from the brush border. (SB)

Bruxism

A form of oral dyskinesia in which the individual grinds the upper and lower molars. It may also manifest as clenching the **teeth**. It is a common response to pain, stress, anxiety and boredom. Seen primarily in humans, pigs, dogs, cattle and **laboratory animal**s, it can cause significant wear to the enamel and dentine of the teeth, as well as headaches. It can occur during sleep and be treated with intraoral devices. (CJCP)

Buckwheat

Buckwheat (*Fagopyrum esculentum*) is not a cereal but the seeds have similar nutritional characteristics to **cereal** grains. Buckwheat, also called saracen corn, has triangular seeds with a fibrous hull (~20% of seed weight) surrounding a kernel, which is generally used for **flour** manufacture. **By-product**s of buckwheat include buckwheat hulls and buckwheat middlings but only the latter are generally suitable for feeding. Straw is also produced following seed harvest.

Buckwheat may be grown as a green **forage crop**. It is high in **carbohydrates** with, typically, 549 and 129 g **starch** and **crude fibre** kg^{-1} dry matter (DM), respectively. The **protein** content is low (131 g kg^{-1} DM) and both the seed and by-products tend to be deficient in **calcium**. The **grain**s are used for animal feeding and are processed by grinding before feeding to most classes of livestock except poultry, to which they are fed whole. Their low

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palatability means they are generally mixed with other cereals before feeding. Buckwheat middlings have a high feed value and are rich in protein (~300 g kg^{-1} DM) and are generally used as part of the **diet** of dairy cows. The hulls are generally used only as fuel, bedding or packaging. (ED)

Further reading

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Buffalo:

see **Water buffalo**

Buffer

A molecule that controls **pH**, modulating the concentration of protons (H^+) in solution by either releasing or taking up protons. Buffers can be inorganic (e.g. carbonic acid, H_2CO_3) or organic (e.g. acetic acid, $CH_3{\cdot}COOH$) molecules that participate in acid/base reactions, giving off or taking up protons. Buffers vary in the pH they are able to maintain and their capacity to control pH. To work as a buffer the parent molecule must partially dissociate and come into equilibrium with its components, i.e. $CH_3{\cdot}COOH \rightleftharpoons CH_3{\cdot}COO^- + H^+$. It is the capacity of acetic acid in solution to dissociate into an **acetate** anion and a proton that makes it a buffer. (NJB)

Buffer feed

A conserved feed eaten by **herbivore**s in variable quantities, depending on the availability of grazed feed. Buffer feeds are typically **hay** or **silage** and are offered either permanently

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outdoors, or in the case of dairy cows, after milking times for 1–2 h. The buffer feed is offered to counteract variation in **grazing** quality and quantity, weather and other factors that reduce grazing intake. (CJCP)

Bulimia nervosa

An **eating disorder** in which an anxious or stress-prone person alternately binges and purges on food, with a focus on attaining a specific body shape and/or weight. Binges are characterized by excessive eating, without control of intake. Purges are by vomiting, fasting, misuse of medication such as laxatives, and/or excessive exercise. Bulimia nervosa is not known to occur in non-human animals, although rapid consumption of excessive food similar to the human binge occurs after feed restriction in many animals. (CJCP)

See also: Comfort eating

Bulk

Approximately 25% of a typical poultry or pig feed mixture consists of components that cannot be digested. Certain ingredients may be added to increase the indigestible components and decrease the **bulk density** of the feed, and these are described as bulking agents or feed diluents. Examples are sand, clay, ground straw or sawdust and cereal grain hulls such as wheat or oat **bran**.

Birds and pigs respond to a decrease in the bulk density of their diet by increasing their voluntary **feed intake**s, in an attempt to maintain their nutrient intakes. However, this compensation may not be exact and may result in reduced productivity. (SPR; RB)

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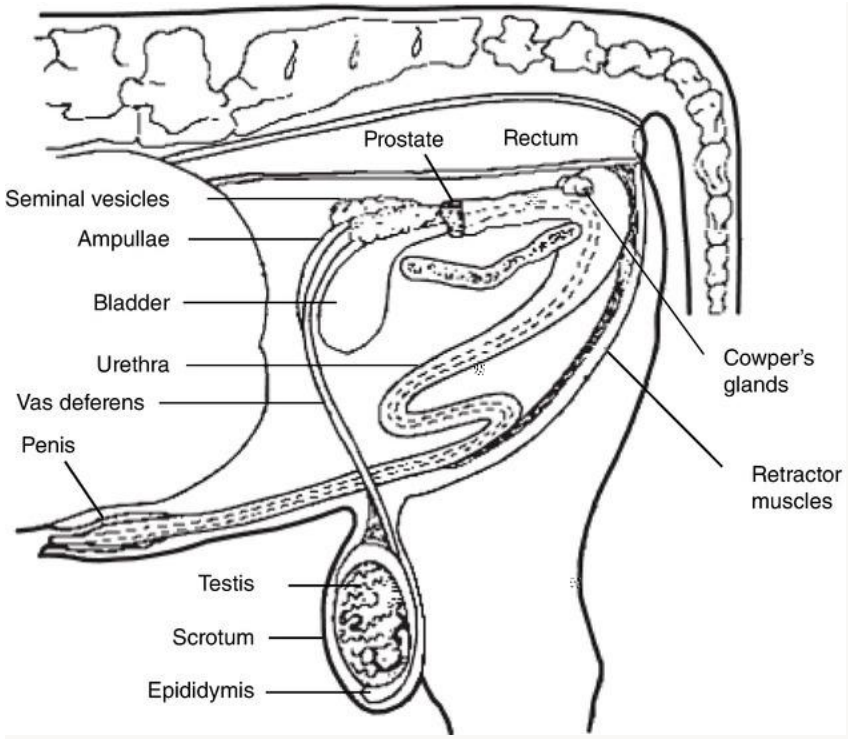
Bulk density

The bulk density of an individual **sample** of a feed such as a cereal is widely used in the feed trade as a measure of its probable **metabolizable energy** concentration, because the starch-containing **endosperm** in a grain has a higher density than the fibrous seed hull. However, there are many confounding factors and bulk density seems to be poorly related to energy concentration or **nutritive value**. Terms used to describe bulk density are bushel weight or specific weight (kg per hectolitre (hl)). The latter is used in international trading of **cereal**s. For example, the accepted minimum for feed wheat is 72 kg hl^{-1} and for bread-making wheat is 76 kg hl^{-1}. (SPR)

Bull

The mature male of any species of Bovinae (cattle and certain other species). The term is usually applied after the animal has reached sexual maturity. The primary function of the bull is to produce spermatozoa and introduce them into the female reproductive tract at oestrus in order to fertilize any ova (sing. **ovum**) that are shed some hours after the end of oestrus. The bull's reproductive tract consists of primary, secondary and accessory sex organs (see figure).

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The reproductive tract of the bull (lateral view).

The primary sex organs consist of a pair of testes, which are suspended in the scrotum between the hindlegs. The testes contain seminiferous tubules, which produce the spermatozoa, and cells that produce testosterone, which gives the bull its libido. The secondary sex organs are made up of the epididymis, where spermatozoa are stored and matured, and the duct system, including the penis, which transport the semen to the cow's vagina at mating. The accessory sex organs comprise the seminal vesicles, prostate and Cowper's (bulbo-urethral) glands, which add buffers, nutrients, hormones and osmo-regulators to the semen.

After **puberty**, semen production is essentially a continuous process, although it can be impaired by severe **malnutrition**, which probably explains why there may be seasonal fluctuations in semen production of bulls living in harsh environments.

The bull's hormonal status means that it grows faster than the

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cow, reaches a higher mature weight and is more active, leading to higher **maintenance** requirements. (PJHB)

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Burdock,*Arctium lappa*, is a large, herbaceous plant with branched stems 0.8–1.5 m long that grows in the plains and humid and shady areas up to a height of 1500–1800 m in the temperate regions of Eurasia. It has a long root about 1 cm diameter, with a spindle-shaped appearance and brown colour externally, white internally. It has wide, drooping leaves and spherical capitula composed of small purple flowers. After ripening, the fruit is shaped like a hazelnut, its color is grey or light brown, and on top there is a bunch of yellow silk threads. The outer surface of the fruit is also covered with fine threads that easily stick to the hand. The fruits stick to the wool and skin of animals, especially sheep, and are transferred to distant areas (Zargari, 1997).



Lesser burdock. Photo courtesy of John McLinden. Licensed under CC BY-ND 2.0.

The plant is also cultivated, being sown in September and

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harvested in March to May. Burdock root contains **inulin**, small amounts of **fatty acid**, carbonate, **nitrate**, **potassium**, various resins, and **glucoside** called lappine or lapposide (Zargari, 1997; Mir *et al*., 2022). The leaves of this plant also contain a substance called arctiopicrine, and active oxidases. In addition to the glucoside in the root, its seeds contain 18% **oil** with a bitter taste, 58% of which is **linoleic acid** (omega-6 fatty acid) and 10% of **oleic acid** (omega-9 fatty acid). The therapeutic properties of its root have been reported to purify the blood, increase bile secretion, act as a diuretic, diaphoretic, and cure gout and rheumatism (Zargari, 1997; Mir *et al*., 2022). Anti-diabetic, antioxidant, liver-protecting, anti-cancer, digestion-protecting, antibacterial, anti-allergenic, antimicrobial, antiviral and anti-inflammatory effects are among the most important claimed effects of using this plant in drug formulations (Mir *et al*., 2022). The medicinal use of this plant is more common for animals, so that in veterinary medicine, a concoction of burdock root (50 parts per thousand) is used to treat scabies and prevent hair loss and severe itching. If its root is used in pieces in the feed of sheep, it may help to treat coughing (Zargari, 1997). Scientific studies related to the feeding of this plant by domestic animals are very limited, but due to the richness of inulin in its root and the prebiotic potential for **inulin**, there may be benefits to improve the health of the digestive system (Itaya *et al*., 2018; Hasted *et al*., 2021). (AS; BH-G; CJCP)

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Butterfat

Also known as milk fat, butterfat is one of the commercial interests and functional constituents of **milk**. At room temperature, milk **lipids** remain as solids and, therefore, are commonly referred to as milk fat, but not oil. Based on nutritional perspectives, butterfat is a major **energy source** to neonates as well as consumers, whereas from an economical perspective, butterfat content directly influences the price of raw milk. Furthermore, the amount of butterfat influences the quality and yield of various processed dairy products. Butterfat is the key ingredient in several dairy products, such as butter, cream (fresh and sour), frozen dairy products such as ice cream and full-fat cheese. In such products, butterfat plays a major role in delivering distinctive flavours, since most flavours and volatiles are fat-soluble. Moreover, physicochemical and organoleptic properties (e.g. melting point, spreadability, firmness,

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meltability, creaminess etc.) of processed dairy products are affected by the composition and amount of butterfat.

In milk, fat globules of 0.1–15 μm in diameter are dispersed in the continuous serum phase and result in an oil-in-water emulsion. Butterfat is secreted as milk fat globules in the endoplasmic **reticulum** of epithelial cells within the alveoli of the mammary tissue and coated with a milk fat globule membrane (MFGM), which consists of proteins and polar lipids. Butterfat is lighter than the milk serum fraction and therefore forms a cream layer in fresh whole milk under gravity. Hence, during the processing of dairy products, homogenization is a crucial step to prevent creaming, i.e. fat layer separation, by decreasing the size of fat globule and creating uniform size distribution. **Lipoprotein lipase** is associated with **casein** micelles in milk, and agitation brings contact of lipase with milk fat globules. Because of the enzymatic degradation of milk fat, a higher level of **free fatty acid**s can be formed, which is undesirable since it confers a rancid taste (mainly due to butyric **fatty acid**) in the final product. The latter effect is seen when milk and **meat product**s from ruminants are low in an **antioxidant** concentration such as **vitamin E** (α-**tocopherol**), which is a fat-soluble compound. Milk fat provides a creamy mouthfeel and pleasant sensory attributes to dairy products, mainly due to its association with **flavour compound**s. Butterfat contributes unique rheological properties to dairy products (e.g. consistency and textural attributes). In general, milk fat is separated by centrifugation and adjusted for fat and protein ratio during the processing/standardization. Nevertheless, in the long

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term, milk fat content can be adjusted through the selective breeding of dairy cows for desired fat levels for processing of raw milk.

The butterfat content of milk varies between species, i.e. ~3.9% in cows, ~4.5% in goats, ~6.7% in buffalo and ~7.4% in sheep. Several factors are known to influence the butterfat content of cows' milk: breed or genetic makeup (for example, for cattle breeds: Jersey ~6.2%, Swedish Red ~4.8%, Zebu ~4.6%, Sahiwal ~4.0% and Holstein ~3.6%); cow health/physiology (for example, mastitis causes a decline in fat content and alterations in composition); and nutrition (see below). Milk fat content is also influenced by a mammal's stage of **lactation**; for example, in the early stages of lactation the proportion of **short-chain fatty acid**s in milk fat is low, due to mobilization of **body fat**. Around 8–10 weeks of lactation, the short-chain fatty acids increase with enhanced *de novo* synthesis. Immediately after calving, cows produce colostrum, which has a very high fat content (~6.7%).

Milk fat predominantly consists of **triacylglycerol**s (~98%) that are synthesized in the **mammary gland**. They have a mixture of fatty acids, ranging in chain length from C4 to C18. Besides these, butterfat contains **phospholipid**s (~1.1%), **cholesterol** (< 0.5%), diacylglycerols (~2.2%), monoacylglycerols (~0.08%), free fatty acids (~0.10–0.28%) and cholesterol esters (~0.02%).

In many ruminants, most of the C4 to C14 and nearly half of the C16 fatty acids are synthesized *de novo* in the mammary gland from acetic acid and β-**hydroxybutyrate**. These are produced as end-products of the **fermentation** by rumen **bacteria** and

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protozoa of plant structural carbohydrates (e.g. **cellulose** and **hemicellulose**s), yielding **acetate** and **butyrate** (which is converted to β-hydroxybutyrate in the rumen wall). These acids are used as **substrates** for *de novo* milk fat synthesis in the mammary gland. The **long-chain fatty acid**s (mainly C18) mainly originate directly from the feed or from mobilized body fats. The **ester** bonds in the dietary lipids (i.e. the bonds between **glycerol** and the fatty acids) are hydrolysed mainly by microbial lipases in the rumen; the released fatty acids are absorbed in the **small intestine** and they are subsequently translocated into milk triacylglycerols.

Nutrition has an important influence on butterfat content of milk. Since acetic acid and β-hydroxybutyrate are major precursors for *de novo* synthesis of milk fat, dietary factors that influence the production of these acids in the rumen, such as digestible fibre intake, have direct effects on the butterfat content of milk. Dairy cows should be fed diets with at least 20% **acid detergent fibre** (ADF), 70% of the ADF should be from **forage** fed either as grazed pasture, **silage** or **hay**, and diets should not contain large amounts of finely chopped forage particles. Milk fat content shows seasonality, where lower milk fat content is apparent when the cows are grazing pasture during summer compared with feeding silage in winter. This is mainly because the **linolenic acid** content in fresh grass is much higher than in silage, and high levels of linolenic acid are associated with the production of long-chain **unsaturated fatty acid**s that inhibit *de novo* **fatty acid synthesis** in the mammary gland and thereby reduce the milk fat

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content. The intake of long-chain fatty acids is positively related to their content in milk; however, if dietary fat content exceeds 6% in the ration on a dry matter (DM) basis, **rumen digestion** of fibre can be disrupted through the physical and detergent effects of long-chain fatty acids on **rumen microorganism**s. This problem can be overcome by feeding rumen-**protected fat** or rumen bypass fat (as **calcium** salts or encapsulated in **formaldehyde**-treated casein) which remains unaffected during microbial fermentation and biohydrogenation in the rumen. Thus, rumen-protected fat enhances the milk fat production of ruminants, without affecting the functions and metabolism of ruminal microorganisms.

Milk fat content is also associated with milking practices, where residual milk (i.e. the milk left in the udder due to incomplete milking) is often high in fat as an effect of the udder emptying pattern (consequently, frequent udder emptying increases the fat yield). Milking frequencies influence the milk fat content, with automatic milking systems being associated with higher milking frequencies compared with milking parlours or tie-stall milking, resulting in lower fat content.

Since the early 1980s, worldwide consumption of butterfat has declined since saturated **fats** are known to adversely affect the serum low-density lipoprotein (LDL) levels of humans and thus increase cardiovascular risks. Butterfat typically contains 60–70% **saturated fatty acid**s and increasing the proportion of unsaturated fatty acids in milk is difficult, because long-chain unsaturated fatty acids in the feed are hydrogenated in the rumen

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unless they are fed in a protected form. On the other hand, studies have shown that omega-3 fatty acids and conjugated **linoleic acid** (CLA) found in milk fat and ruminant meat may be anticarcinogenic, reduce the incidence of **atherosclerosis** and **diabetes**, and partition energy away from **body fat** towards muscle tissue. The main factors that increase the omega-3 fatty acid and CLA content of milk are grazing fresh forages (grass and legumes) and increased intake of **oilseed** meal supplements, such as canola or flax. The concentration of CLA **isomer**s in ruminant milk could be increased by the natural synthesis of CLA isomers (C18:2 *cis*-9, *trans*-11 and C18:2 *trans*-10, *cis*-12) from linoleic acid with the support of linoleate isomerase enzyme, which is mainly found in ruminal bacterium *Butyrivibrio fibrisolvens*.

The Gerber method, Babcock and Mojonnier tests are commonly used to determine the milk fat content. The fat content also can be determined directly by using equipment such as Milko-Tester Minor and Lactoscan milk analyser. For drinking milk (fluid), there are mainly three categories based on milk fat content: whole milk (> 3.5% fat), semi-skimmed milk (1.5–2.0% fat) and skimmed milk (0.3%). The amount of fat in processed dairy products varies; for example ghee ≈ 99.5%, butter ≈ 82%, cream cheese ≈ 47%, full-fat cheese ≈ 30%, cream ≈ 23%, full-fat yoghurt ≈ 3% and skimmed milk yoghurt ≈ 1%). (HP; JKV; ENP; GMcLD)

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Butyrate

A four-carbon **saturated fatty acid**, $CH_3{\cdot}CH_2{\cdot}CH_2{\cdot}COO^-$. It is produced in the **fermentation** of feedstuffs in the rumen and in the lower intestinal tract of both ruminant and non-ruminant animals. Together with the other steam-**volatile fatty acid**s, **acetate** and **propionate**, it forms a major part of the energy supply of ruminants. (NJB)

Butyric acid:

see Butyrate

By-product

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A product of plant or animal production that is incidental to the main product for which the plant or animal is intended. Plant by-products include those from the **milling**, brewing and distilling industries. Animal by-products include those from meat, fish, butter and cheese production. Many feeds (e.g. **oilseed** meals), formerly considered by-products, may be comparable in importance and value to the primary product. (MFF)
See also: Bagasse; Blood meal; Bone meal; Bran; Brewery by-products; Citrus products; Dairy products; Distillers' residues; Dried skimmed milk; Feather meal; Fish products; Hatchery waste; Meat products; Milling by-products; Poultry offal meal; Whey

C

Cabbage

Cabbages (*Brassica* spp.) are members of the **brassica** family commonly grown for human consumption but also used as **fodder** for ruminants. The **crude protein** content of cabbages ranges from about 150 to 250 g kg^{-1} dry matter (DM). The apparent **metabolizable energy** for ruminants is about 10–11 MJ kg^{-1} but

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is very low (< 1 MJ kg^{-1}) for pigs. Cabbages contain **glucosinolate**s (about 20–30 μmol g^{-1} DM). Sheep fed cabbages perform well but tend to have elevated thyroid weights and increased incidence of Heinz bodies in their blood. (TA)

Cadaverine

A bacterial **decarboxylation** product of L-**lysine**, $NH_2{\cdot}CH_2{\cdot}(CH_2)_3{\cdot}CH_2{\cdot}NH_2$. It is found in decomposing **animal protein**. (NJB)

Cadmium

A mineral element (Cd) with an atomic mass of 112.411. It is found naturally in small amounts in rocks, soils and sea water. There is no known metabolic function for Cd and it is generally considered toxic. Certain edible plants may accumulate Cd from the soil. Although the amount accumulated may be small, animals or humans that consume the plant material may obtain enough Cd over time to cause kidney damage. Natural **antagonist**s to the **intestinal absorption** and organ accumulation of Cd are other dietary minerals such as **zinc**, **calcium**, **iron** and **copper**. (PGR)

Cadmium toxicity

Cadmium (Cd) is chemically similar to **zinc** but is not an essential element for animals. It occurs naturally in copper, lead and zinc ores and is potentially toxic in sufficiently high concentrations. However, it is widely used in electroplating, pigments, plastic stabilizers and nickel cadmium batteries. It is a contaminant of

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phosphate fertilizers, and as it is readily absorbed by plant roots and translocated to stems and leaves, it is often consumed by herbivores such as sheep and cattle.

Sewage sludge can have high Cd contents as a result of discharge into waste water, for example following electroplating, which when applied to pastureland are absorbed into the bloodstream of grazing livestock. Despite these risks, there is pressure to utilize sewage sludge as a crop fertilizer because of rising artificial fertilizer prices and growing demand for food. Uptake by livestock can be limited by treating the sludge before application to pasture, injecting it deep into the soil, preventing grazing for at least 3 weeks after application and testing soil regularly. Sewage sludge cannot legally be added directly to animal diets in most jurisdictions.

In highly fertilized pasture, Cd in P fertilizers may be in sufficient concentrations (up to 80 mg kg^{-1}) to potentially cause toxicity in humans consuming animals that have grazed the pasture (Prankel *et al*., 2005). Grazing animals take up Cd directly from the soil or via the plant, either adhered to the leaves or transferred to the stem and leaf from the soil. In the animal's **gastrointestinal tract**, Cd is bound to **metallothionein**s and selectively absorbed by the **small intestine** and sequestered in the kidney and liver. Acute toxicity is rare and focused on the liver. Cd is stored initially in the liver but on chronic exposure is released into the bloodstream to be sequestered by the renal cortex, where the metallothionein Cd complex is degraded by lysosomes. It becomes nephrotoxic if ionic Cd is then released, causing damage to the

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proximal convoluted tubule. Toxic effects on bones are also observed. Maximum concentrations of Cd in offal are between 0.5 and 1 mg kg^{-1} wet weight in the EU. Because of its long half-life, older animals usually have higher concentrations in their organs than young ones. In sheep, although primarily in offal, small amounts of Cd accumulate in muscle when concentration is above 30 μg g^{-1} feed.

Although cattle and sheep offal can have high concentrations, limited consumption by humans means that the biggest dietary source is from plants, primarily cereals and vegetables, especially lettuce. **Absorption** in women with low iron stores is increased to 10% of ingested Cd, whereas in men it may be only 2%. It has a half-life in the human body of several decades. Another major source of Cd intake in humans is from smoking. Inhaled Cd is much more easily absorbed into the bloodstream than ingested Cd. Different methodological and statistical approaches are applied in determining the limit of Cd to prevent toxicity for humans. The European Food Safety Authority and World Health Organization have provisional tolerable weekly intakes of 2.5 and 5.8 μg kg^{-1} body weight, respectively. (CJCP)

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Caecectomy
Surgical removal of the **caecum** or, in birds, usually both caeca. Following laparotomy under general anaesthesia, the caecum is ligated at two points no more than 8 mm apart and as close to the ileocaecal–colonic junction as possible. The caecum is then excised between the two ligatures and removed. The procedure is generally performed in birds to eliminate caecal **fermentation** (bacterial) in experiments involving estimation of **digestibility** based on measurements of nutrient contents of excreta (faeces + urine). The results of such studies have shown variable changes in digestibility, which is reduced for some nutrients. There is decreased uric acid excretion and improved **nitrogen** utilization. (MMit)

Caecum (or blind gut)
A blind sac of the digestive tract located in the pig and ruminants at the ileocaeco–colonic junction of the **small intestine** and **colon**. In birds, two caeca are connected at this junction. In the horse the caecum is connected to the small intestine at the ileocaecal junction and it is a very large comma-shaped structure mainly located on the right-hand side. The relative volume of the caecum varies significantly between species, being much larger in herbivores than in omnivores. Carnivorous animals have a very small caecum, or none (e.g. mink). The size (and capacity) of the caecum in

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omnivores is influenced by **diet**. Prolonged feeding of diets rich in fibre significantly increases both the size and volume of the caecum in the pig.

Together with the colon, the caecum acts as a site for microbial **fermentation** and the absorption of water and **short-chain fatty acid**s produced in microbial fermentation. In the rabbit, specific pellets are produced in the caecum and recycled to the digestive tract after **coprophagy**, which allows the utilization of vitamins and amino acids produced by the microflora of the caecum. (SB)

Caeruloplasmin

A glycoprotein found in the α_2-**globulin** fraction of mammalian plasma. It has a molecular mass of 150,000 kDa and a maximum of eight atoms of **copper** per molecule. It is synthesized in the liver and is the major carrier protein for copper in blood, comprising more than 70% of plasma copper. The concentration of caeruloplasmin in plasma varies with the nutritional copper status of an animal or human. It also has ferroxidase activity and is believed to function in **iron** metabolism by converting Fe^{2+} to Fe^{3+}. (PGR)

Caesium

A highly alkaline metal (Cs) with an atomic mass of 132.9. It occurs in the earth's crust at about 1 ppm. There is no known metabolic function for caesium. The metal is normally associated with radioactive fallout as ^{137}Cs from nuclear explosions and nuclear powerplant emissions. This radionuclide, which can accumulate in

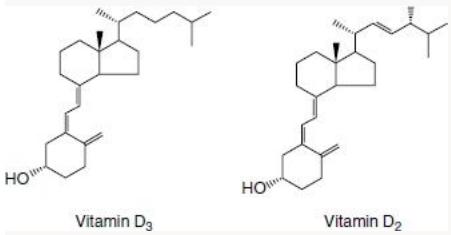
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the tissues of plants, animals and humans, has a half-life of more than 30 years. (PGR)

Caffeine
1,3,7-Trimethylxanthine. It is found in tea and coffee and their **by-product**s. Caffeine stimulates **lipolysis**, which is activated by **epinephrine** and **norepinephrine** through **adenylate cyclase** by production of cAMP from ATP. Increased cAMP activates hormone-sensitive **lipase** and releases **free fatty acid**s from stored **lipids**. The inhibition by caffeine of phosphodiesterase, which breaks down cAMP, results in less degradation of cAMP and maintenance of enhanced lipolysis and free fatty acids. (NJB)

Calbindin
A protein belonging to the superfamily of proteins containing a helix–loop–helix, that binds calcium tightly. (HFDeL)

Calciferol
A general term signifying a compound possessing the ability to cure or prevent the disease rickets. Most often it refers to either vitamin D_2 or vitamin D_3. (HFDeL)



Calcinosis
A degenerative condition of a tissue or organ marked by deposition of **calcium** salts in either an unorganized fashion, or as nodules or

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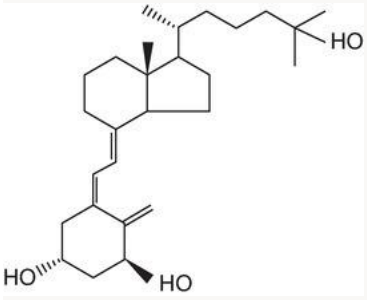
plaques, most frequently in areas of tissue necrosis as seen in the degeneration of skeletal or cardiac muscle related to **vitamin E** or **selenium** deficiency. (DS)

Calcitonin

A 32-amino-acid **peptide** hormone secreted by the 'C' or parafollicular cells of the thyroid gland in response to high concentration of serum **calcium**. It reduces serum calcium by blocking bone **resorption**. (HFDeL)

Calcitriol

A trivial name for the hormonal form of **vitamin D_3**, 1α,25-dihydroxy vitamin D_3 (or 1,25-dihydroxy **cholecalciferol**). It functions in intestine, bone and kidney to elevate serum **calcium** concentration through a nuclear receptor mechanism. (HFDeL)



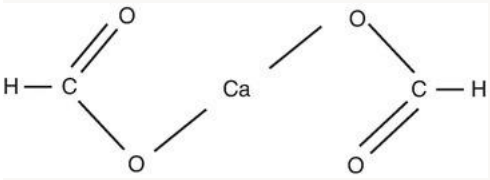
Calcium (Ca)

A divalent metal with atomic mass 40.08. In its ionic form it is required for many functions in the plant and animal world. It is most critically needed for nerve and **muscle** function, for constructing the skeleton, for cellular integrity and cell-to-cell adhesion, but is also required in many other life processes. (HFDeL)

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Calcium formate

The calcium salt of **formic acid** is an off-white crystalline powder that is recognized as a preservative in EU legislation. It is listed as 'E238, Calcium formate, $C_2H_2O_4Ca$, suitable for use in all feeding stuffs'. It is a neutral non-toxic substance, relatively safe and pleasant to handle. In the gut it reduces buffering capacity, selectively stimulates beneficial bacteria and improves gut wall health and absorptive efficiency, appearing particularly beneficial to newly weaned piglets. Calcium formate may also be used as an aid to making **silage** when its selective antimicrobial properties are exploited. (CRL)



Calcium phosphate

Various salts of **calcium** with **phosphorus** are used as **mineral supplement**s for farm livestock. The main two are dibasic calcium phosphate, $CaHPO_4$ (usually anhydrous, though the dihydrate is also available), and monobasic calcium phosphate monohydrate, $Ca(H_2PO_4)_2.H_2O$. Both the calcium and phosphorus from these compounds are readily available to animals. The choice depends upon the proportions of Ca and P required. Pure anhydrous **dicalcium phosphate** contains just over 29 g Ca and almost 23 g P 100 g^{-1} but in practice, depending on the source and method of manufacture, the amounts are 25–27 g Ca and 17–20 g P. Actual levels of calcium and phosphorus supplied by

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'monocalcium phosphorus' monohydrate are 15–17.5 g Ca 100 g^{-1} and 22–23 g P 100 g^{-1}. (CRL)

Calf

The young of any species of Bovinae (cattle) and of certain other species, such as red deer (*Cervus elaphus*). The term is usually applied from birth until the onset of **puberty**. This will occur at around 1 year of age in cattle, depending on season in some species and on **plane of nutrition** in all species. Within a few hours of birth, the bovine calf can walk and see and all of the adult organs are present, although the **mammary gland**s of the female and the sexual organs in both sexes are not functional until puberty. In the female, the ovaries are present and contain all the ova that will ever be produced. In the male, the testes will usually have descended into the scrotal sac.

The newborn calf is almost entirely dependent on its mother's **milk**, not only for nutrition but also for disease **immunity**, since the bovine placenta does not permit the passage of maternal **antibodies** into the fetus. The rumen of the newborn calf is not developed and does not contain the **microorganism**s necessary for its function. A reflex induced by the action of **suckling** stimulates the **ruminoreticular groove** in the rumen to form a tube that delivers milk directly to the **abomasum**, where **rennin** causes coagulation as a prelude to digestion. If milk or **milk substitute** is ingested too fast, which is more likely under artificial rearing conditions, milk can spill from the oesophageal groove into the rumen. In the absence of the rumen microflora of

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the adult, harmful bacteria can feed on this and cause severe digestive upsets.



This newborn calf depends on its mother's milk, not only for nutrition, but also for immunity. Photo courtesy of Mark Gunn. Licensed under CC BY 2.0.

The calf would naturally suckle its mother's milk for the first few weeks of life, after which this is gradually replaced with solid food as the rumen develops. Calves in intensive milk production systems are usually removed from their mothers within the first 2 days after birth and are fed milk or an artificial substitute until they are weaned on to solid food and water alone after 4–8 weeks. It is common for straw, or other **roughage** feed, to be made available to calves from a very early age in order to help to stimulate rumen development and function, but calves under intensive management would also receive concentrate feed. In the wild, calves may continue to suckle their mothers for many months, whilst gradually increasing their intake of solid food, which consists almost entirely of grazed or browsed material. The microorganisms needed for rumen function are picked up from the environment, including the

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calf's mother. The newborn calf is susceptible to cold but has relatively high levels of brown fat, which produces heat for **thermoregulation**. (PJHB)

Calorie

The heat required to increase the temperature of 1 g of water from 14.5°C to 15.5°C. **Kilocalorie** (kcal) and **megacalorie** (Mcal) refer to 10^3 and 10^6 calories, respectively. Unfortunately, the use of the terms Calorie (with an initial capital) and CALORIE (both intended to mean kcal), which are to be found in older textbooks, is still widespread, especially in food packaging. This practice is confusing and strongly to be discouraged.

The calorie is not part of the Standard International (SI) system of units. The SI unit of **energy** is the **joule** (J), which is defined as the work done in moving a distance of 1 m against a force of 1 newton (N). The relationship 1 cal = 4.184 J is known as the mechanical equivalent of heat; it emphasizes the fact that heat, like work, is a form of energy. Even though technically out of date, the use of 'cal' and 'kcal' in the agriculture and food industries is still widespread. In this volume **energy value**s are quoted in both joules and calories whenever needed to avoid confusion. (JAMcL)

See also: Calorific factors

Calorific factors

Calorific factors express the **energy** per unit weight of a substance. It is important to distinguish between two types of calorific factors, namely heats of combustion and food **energy value**s.

The heat of combustion, or **gross energy**, of a substance is the

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energy converted into heat when it is completely oxidized (i.e. burned) to **carbon dioxide** and water. It is a unique property of the substance, which can be measured precisely by use of a laboratory instrument called a **bomb calorimeter**. Although actual heats of combustion (J g^{-1}) vary considerably within each food category (**carbohydrate**, **fat** and **protein**), the heats produced per litre of **oxygen** consumed and per litre of carbon dioxide produced are remarkably consistent within each of the three. This makes it possible to estimate an animal's rate of metabolic **heat production** with high precision by measuring the respiratory gaseous exchange of oxygen and carbon dioxide (**indirect calorimetry**). The table gives heats of combustion of some carbohydrates, fats and proteins.

Heats of combustion (kJ g^{-1})

Carbohydrate	
Monosaccharides (e.g. glucose, fructose)	15.6
Disaccharides (e.g. sucrose, lactose)	16.5
Polysaccharides (e.g. starch, cellulose)	17.5
Fats	34–40
Proteins	22–25

The food energy value of a substance is the **metabolizable**

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energy, or that part of the **gross energy** which is potentially useful to an animal and not discarded as the energy of waste products (i.e. **faeces**, **urine** and combustible gases). Food tables express the metabolizable energy per unit weight of substances. These are not unique properties of the food substance but depend on the digestive processes of the animal. Different food tables are appropriate for **carnivore**s, **herbivore**s and omnivores. Metabolizable energies of different food constituents are generally additive, allowing the overall value of a diet or ration to be assessed. (JAMcL)

Calorimeter:
see Bomb calorimeter; Calorimetry; Direct calorimetry; Indirect calorimetry

Calorimetry
The measurement of heat. A calorimeter is the instrument used for its measurement. The **bomb calorimeter**, a laboratory bench instrument, is used to measure the heats of chemical reactions, especially the heats of combustion of foods and individual food components. Animal calorimetry is the measurement of the heats produced by and given off from living animals and it has been used with animals ranging in size from mice to horses. Distinction must be made between **direct calorimetry**, which is the physical measurement of heat given off by the animal, and **indirect calorimetry**, in which the measurements are of the chemical quantities involved in **metabolism**; the heat generated is calculated from the heats of combustion of the end-products.

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Indirect calorimetry thus measures **heat production**, whereas direct calorimetry measures heat loss by the animal to its environment. In the long term the two must agree, but over short periods there may be an imbalance between heat production and heat loss with a consequent change in body temperature. (JAMcL)

See also: Heat balance

Further reading

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Camelids

The Camelidae (camels and llamas) belong to the suborder Tylopoda, closely related to, but distinct from, the Ruminantia. Today there are only six species. The two larger camels, the one-humped dromedary, *Camelus dromedarius,* and the two-humped Bactrian camel, *C. bactrianus,* originated in Arabia and Iran–Turkestan, respectively. The four smaller species, the llama, *Lama glama,* the alpaca, *L. pacos,* the guanaco, *L. guanicoe*, and the vicuna, *Vicugna vicugna*, came from South America.

Only the guanaco and vicuna remain wild, although small feral populations of the other species may be found. The llama and alpaca have been domesticated for some 4000 years and the dromedary and Bactrian camel for 3000 years (Clutton-Brock, 1981). They have all served as general farm stock and as pack and draught animals in the arid lands to which they are so well adapted. So successful was the dromedary as a pack animal in the desert that wheeled vehicles were seldom seen in North Africa until

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200 years ago. They provide excellent meat and their milk resembles cow's milk in composition (see table). The milk is greatly prized by camel herders, who may rely on it for water and nourishment for many days on end. The animals are often shorn for their wool. The alpaca remains the chief provider of wool in Peru while the vicuna has an exceptionally fine and valuable coat. In Arabia the dromedary is bred and trained for racing, showing remarkable endurance, and this calls for special diets (Allen *et al.*, 1992).



Vicuna, a wild relative of the camel that was domesticated by South Americans and bred into the modern alpaca. Photo courtesy of Thomas Quine. Licensed under CC BY 2.0.

Composition of milk of the dromedary compared with the dairy cow (g kg^{-1}) (source: Narjisse, 1989).

	Protein	**Lactose**	**Fat**	**Ash**	**Total solids**
Camel	40	42	43	8	134
Cow	38	49	44	7	138

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There are some 17 million dromedaries and Bactrian camels in the world; India, China and Ethiopia have about 1 million each. They may live for up to 40 years. **Puberty** is reached at 2–5 years, depending on health and nutrition. The **gestation period** is from 12 to 13 months and the interbirth interval 2 or 3 years. The shorter-lived **South American camelids** have an 11-month gestation period. They can interbreed and produce fertile hybrids. Much research has been done on the control and manipulation of **reproduction** and embryo transfer (Allen *et al*., 1992).

The dromedary is particularly well adapted to dry savannah and scrubland pastures (Rutagwenda *et al*., 1990). It takes **forage** from ground level to 3 m high and eats from a wide variety of plants. Its divided prehensile upper lip allows it to select green shoots from among thorny twigs and it also strips off leaves by pulling twigs through its mouth. Its long legs and ability to travel without water for some days give it a wide grazing radius around a water supply. It has wide footpads, not sharp hoofs, and so can walk easily over soft ground.

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The camel is well adapted to eat shrubs and bushes on drylands. Photo courtesy of D. Stanley. Licensed under CC BY 2.0.

The camel's **digestive system** is functionally very similar to that of true ruminants, although anatomically distinct (Wilson, 1984). In place of the ruminant's upper dental pad, the camel has two incisors and one canine **tooth**. **Rumination** and the vigorous secretion of the parotid salivary glands resemble that of the ruminant. The forestomach is divided into three compartments, analogous to the **rumen**, **reticulum** and **omasum** but covered in a mucous non-papillated epithelium. This is followed by an acid-secreting fourth compartment resembling the **abomasum**. The forestomach shows a strong repetitive contraction at intervals, differing from the minute-by-minute contraction of the reticulorumen. Despite these differences in structure and **motility**, the camels ferment their food microbially in the forestomach, and produce and absorb **volatile fatty acid**s as a result, in much the

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same manner as ruminants. Fibrous particles are selectively retained in compartments 1 and 2 for prolonged **fermentation**. A gutter-shaped structure running from the cardiac orifice of the oesophagus to the entrance to compartment 3, resembling the **ruminoreticular groove**, allows milk sucked by the calf to bypass the rumen.

The **metabolism** of water and salt by the dromedary has been thoroughly investigated (see Farid, 1989, for summary). The animal shows many **adaptation**s to hot, dry conditions and tolerates long periods of **water deprivation**. Concentrated **urine** (up to 3 osmolar) and dry **faeces** (up to 60% **dry matter**) reduce excretion of water; heat storage by diurnal fluctuation of body temperature (37–40°C) reduces the need for **evaporative heat loss**; a furry coat protects against solar radiation; and appropriate behaviour reduces **heat production** by day. The camel appears to have a higher requirement for **salt** than sheep or cattle, 1% NaCl in drinking water being beneficial but 2% has a deleterious effect.

Much has been published on the management, feeding habits, nutrition and diseases of camels in books and in the proceedings of international conferences. The nutritional requirements of camels under various conditions (work, **lactation**, etc.) and the composition of preferred camel browse plants were conveniently summarized by Wilson (1989a). (RNBK)

See also: South American camelids, effects of nutrition on meat quality

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Candida (*Candida albicans*)

A yeast-like fungus that is a normal inhabitant of the nasopharynx, digestive tract and external genitalia. Disruptions of mucosal integrity may result in *Candida* infections, most commonly in birds. Infection of the oral **mucosa** is known as thrush. In poultry, lesions are most common in the crop, resulting in a condition known as 'sour crop'. Thrush is common after use of therapeutic levels of antibiotics or unsanitary drinking facilities. Young chicks and poults are most susceptible. Candidiasis may be treated or prevented with copper sulphate in the drinking water or with the inclusion of an anti-fungal agent such as nystatin in the feed (where approved locally). Chlorination of the drinking water may also be effective. For prevention, it is important to provide fresh clean feed and water at all times, uncontaminated by fungi. (RB)

Cannabis (*Cannabis sativa* L)

A dioecious and herbaceous annual plant with a height of 1–3 m and a strong smell, depending on the variety.

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Cannabis plant. Photo courtesy of Brian Shamblen. Licensed under CC BY 2.0.

It has opposing leaves along the stem, although closer to the end of the stem the leaves become single. It also has male and female flowers on two separate bases. The male flower is complex and hanging and appears at the end of the stem and has five stamens inside its flower cover. The female flowers have the same appearance as the male flowers, but are without peduncles and have leaf-like bracts. The fruit of the plant is hazelnut-shaped and dark brown in colour. Cultivation of this plant is possible in poor and calcareous lands, but the water requirement is high and it is also grown in warm and temperate regions. About 1200 kg seed are produced per hectare, and after China, France is the largest seed producer (about 5000 t of seeds per year) (Zargari, 1997; Krist, 2020). The mass production of this plant is under strict control in many countries in order to make proper and optimal use of its beneficial nutritional and medicinal benefits and to prevent its

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misuse. The active ingredients of this plant include cannabene (liquid with a very strong smell) and hydrocannaben (odourless and amber coloured). The aerial part of the herb contains the resin substance of cannabis (cannabine) or hashish (hachichine). Cannabiol can be extracted from its leaves (Zargari, 1997).

The most important active compounds are found in the flowering branches and the base fruits of the plant material, which, respectively, include tetrahydrocannabinol (tetrahydrocannabinol) (THC) ($C_{21}H_{30}O_2$), cannabinol (cannabinol) ($C_{21}H_{24}O_2$) and cannabidiol ($C_{21}H_{31}O_2$).

THC is the main constituent of marijuana. Due to the concern about the harmful effects of this compound, the European Union gives subsidies to producers if they cultivate species containing less than 0.2% THC (Zargari, 1997; Krist, 2020).

The seeds of this plant contain 30–35% **oil**, which contains 50–70% **linoleic acid** (omega-6), 20–30% **linolenic acid** (omega-3) (therefore the ratio of omega-6 to omega-3 **fatty acid**s is ideal). Also, 2–4% of omega-6 fatty acids contain the valuable compound, gamma-linolenic acid (GLA). The consumption of the oil of this plant is beneficial for reducing cholesterol and arteriosclerosis. In general, due to the appropriate amounts of **polyunsaturated fatty acid**s and their optimal ratios, the consumption of its seeds in the form of **nuts**, as well as its oil for salads, sauces and cooking, is useful for human health. This oil should not be used for frying, due to its smoke point of 165°C.

Due to the large amount of triacyl-glyceride, the oil can be used as the raw material of cleaning products, for example in soap

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making, softeners, ointments, massage oil, shampoo, lacquer colour and printing ink. Considering the **solubility** of THC and the concern about the consequences of consuming THC, as well as the effects of this stimulatory, toxic and hallucinogenic compound on the mental characteristics of consumers, it is always important to control the amount of THC in food and pharmaceutical formulations to less than 0.3% (Krist, 2020).

In addition to **lipids**, cannabis seed contains 24% **crude protein** and 25% fibre, along with phenolic and **flavonoid** compounds and catechins (as antioxidant compounds), like rapeseed. Compared with soy, cannabis provides more fat and contains more fibre, arginine and **unsaturated fatty acid**s, which indicates the high potential of this valuable vegetable food source (as a source of protein and lipid) in animal nutrition (Franek *et al*., 2022). (AS; BH-G; CJCP)

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Cannibalism

Consumption of all or part of a conspecific. Commonly associated with consumption of offspring or partner in insects. It is also

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prevalent in stressed, intensively housed animals, such as pigs and chickens, in which body parts such as the tail or vent are cannibalized. In chickens it is distinguished from **feather pecking** by the tearing at the underlying skin. Sows may savage their piglets. Feeding animals members of their own species carries significant disease risks, such as the development of encephalopathies. (CJCP)

Cannula

A tube introduced surgically into a duct or cavity of the body. A narrow cannula is more commonly called a **catheter**. Cannulation is performed in order to **sample** repeatedly **body fluid**s such as **digesta**, blood or secretions or to introduce material into the body.

Cannulas in the digestive tract may be simple, by which only samples of digesta are obtained, or re-entrant, by which the entire flow is collected from the proximal cannula, measured, sampled and returned via the distal cannula. Because a simple T-cannula, although less invasive than a re-entrant cannula, allows only sampling with no estimate of total flow, it requires the inclusion in the diet of an indigestible **marker** which follows the flow of the nutrient. A further problem, common to both types, is that the cannula is relatively small and may give unrepresentative samples, especially with fibre-rich feeds. Nonetheless, cannulation at the terminal **ileum** is routinely used for determining the ileal **digestibility** of one or more nutrients, in particular **amino acid**s. A more advanced technique, the post-valvular T-cannula, has a large cannula placed in the **caecum** opposite the ileocaecal valve. Using a nylon cord it can be steered in such a way that, during a

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collection, virtually all the digesta passing through the ileocaecal valve is directed into the cannula. Ileal digesta can be collected without cannulation by slaughtering animals and sampling digesta post mortem or by a surgical modification such as ileostomy or ileorectal anastomosis. However, results indicate that the terminal ileum alters in its physiology and microbiology to assume some of the roles of the **large intestine**.

Cannulas (catheters) can be guided under X-ray into particular blood vessels via superficial veins or arteries. Cannulation of the cardiovascular system may be combined with flow measurement in order to quantify the flow of a component of interest. Cannulation of secretory ducts, for example those of the salivary glands, **pancreas** or gall bladder, may be used to follow changes during development and responses to feeding, diet composition, etc.

Cannulation may influence the composition or flow of the fluid being sampled; thus, results need to be evaluated carefully. (SB)

Canola:
see Rape

Canthaxanthin:
see Carotenoids

Capric acid
Decanoic acid, $CH_3{\cdot}(CH_2)_8{\cdot}COOH$, a saturated **medium-chain fatty acid**, shorthand designation 10:0. It is found in **coconut** and palm kernel oils. (NJB)
Key reference

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Caproic acid

Hexanoic acid, $CH_3{\cdot}(CH_2)_4{\cdot}COOH$, a saturated **medium-chain fatty acid**, shorthand designation 6:0. It is found in **coconut** and palm kernel oils. (NJB)

Caprylic acid

Octanoic acid, $CH_3{\cdot}(CH_2)_6{\cdot}COOH$, a saturated **medium-chain fatty acid**, shorthand designation 8:0. It is found in **coconut** and palm kernel oils. (NJB)

Carbohydrate

The most abundant group of **organic compound**s in the world. There are three classes: **monosaccharide**s, **oligosaccharide**s and **polysaccharide**s. Plants produce carbohydrates by photosynthesis for their own needs, simultaneously providing a stored form of solar energy. Higher animals and **microorganism**s use carbohydrates as **energy source**s and as precursors of more complex compounds.

The term carbohydrate was originally coined because these molecules were believed to be hydrates of carbon, having the general formula $C_n(H_2O)_n$. Structural characteristics common to carbohydrates are: (i) the carbon skeleton is unbranched; (ii) all but one carbon bears a hydroxyl group; and (iii) one carbon exists as a carbonyl group which, if on a terminal carbon, gives rise to an **aldehyde** but if on an internal (centrally placed) carbon, typically

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carbon 2, it creates a **ketone**. These compounds are known as aldoses and ketoses, respectively. **Sugars** of five or more carbons in length have a strong propensity to form a ring structure through the reaction of a hydroxyl group on one carbon with the aldehyde or ketone to produce an internal hemiacetal or hemiketal and thereby a **furanose** or **pyranose** ring. In so doing, a new asymmetric or chiral centre is generated. This carbon is known as the anomeric carbon and the hydroxyl group generated may exist in an α or β configuration (Fig. 1).

The smallest molecules generally termed carbohydrates are glyceraldehyde and dihydroxyacetone, also the only possible three carbon sugars, or trioses. The most abundant naturally occurring carbohydrates are the five-carbon (**arabinose**, **xylose** and ribose) and six-carbon (**glucose**, **fructose**, **mannose** and **galactose**) **monosaccharide**s (Fig. 2) and polymers of these. Monosaccharides have the general formula $(CH_2O)_n$.

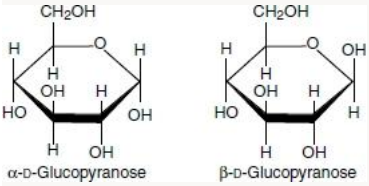


Fig. 1. Alpha- and beta-D-glucose are anomers whose sole configurational difference resides in the sterid arrangement about carbon atom 1; this 'carbonyl' carbon is also called the anomeric carbon atom. The plane of the ring projecting from the plane of the paper is the thicker edges. In the alpha configuration, the hydroxyl group on carbon atom 1 is below the plane of the ring and is so projected on a flat surface. In the beta configuration, the hydroxyl group on carbon atom 1 is above the plane of the ring and is so projected on a flat surface.

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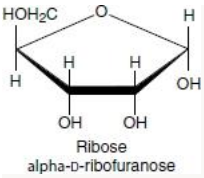


Fig. 2. Most abundant naturally occurring monosaccharides in their most common structural forms.

Natural sugars are optically active (i.e. rotate the plane of polarized light) because they contain one or more asymmetric carbon atoms, so that the number of stereoisomers can be considerable. Laevorotatory sugars are indicated by a small capital L or a minus (–) sign, and dextrorotatory sugars by a small capital D or plus (+) sign. Since the sign of rotation of plane-polarized light provides no information about the configuration or the centres of asymmetry of the molecule, a convention of nomenclature has been devised to indicate configurational properties. This consists of using D or L to indicate the centre of asymmetry most remote from the aldehydic end of the molecule. Further distinction is required to identify the asymmetry of carbon atom one, which is designated as α or β orientation. The linear and cyclic structures of sugars can be depicted in a variety of ways on a plane surface. The International Union of Pure and Applied Chemistry and the International Union of Biochemistry have recommended carbohydrate nomenclature that indicates structure, configuration and linkages, although many of the more common carbohydrates have deeply entrenched trivial names.

Monosaccharides are commonly joined together through a glycosidic linkage to produce di-, tri-, oligo- and polysaccharides. This is formed between the anomeric carbon atom of one

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monosaccharide and any hydroxyl group on another monosaccharide through formation of an acetal. A common linkage, which produces a linear chain, is between carbon 1 of one monosaccharide and carbon 3 of the adjacent monosaccharide, denoted as (1→3); a branch on this linear chain may be between carbon 1 of the branching monosaccharide and carbon 6 of the monosaccharide in the chain, indicated as (1→6). Several derived monosaccharides have very important metabolic functions. Reduction of the **aldehyde** groups of an aldose gives a polyhydric alcohol, or alditol. Sugars are phosphorylated as the first step in animal **metabolism**. **Amino sugars** have a hydroxyl group, usually on the carbon 2 atom, replaced by an amino group. Replacing a hydroxyl with a hydrogen, usually on carbon 2 or 6, produces deoxy sugars.

The α(1→4) and (1→6) links between glucoses, such as in **starch**, are hydrolysed in the small intestinal lumen of mammals by **amylase**s. Disaccharides from the diet, for example **sucrose**, **lactose** and **maltose**, as well as maltose and **isomaltose** produced by the action of amylase on starch, are hydrolysed to constituent monosaccharides by specific disaccharidases in the mucosal **brush border** of the **small intestine**. Of the monosaccharide products, glucose is actively absorbed, whereas galactose and fructose are absorbed from the small intestine by facilitated **diffusion**.

None of the β-linked **pentoses** or hexoses are susceptible to the digestive **enzymes** of animals, nor certain α-linked **polysaccharide**s such as **fructans**, but they can be degraded by

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microbial enzymes in the gut. **Fermentation** of these carbohydrates, which are collectively known as **dietary fibre**, is an important source of energy for ruminants and a minor source for non-ruminant species. (JAM)

Carbohydrate digestion by non-ruminant and ruminant mammals

The primarily chemical classification of dietary **carbohydrates** is by composition of **sugar** monomers, the type of linkage (α or β) and molecular size (degree of polymerization) (DP). This approach divides the carbohydrates into three main groups: sugars (DP 1–2); **oligosaccharide**s (DP 3–9); and **polysaccharide**s (DP ≥ 10). The sugars can further be subdivided into **monosaccharides** and **disaccharides**, and sugar alcohols. Oligosaccharides and polysaccharides can be subdivided into **starch** and **non-starch polysaccharide**s (NSPs). For non-ruminant mammals, oligosaccharides are further subdivided into digestible and non-digestible oligosaccharides; and starch is divided into digestible starch and **resistant starch** (RS). The linkages between the carbohydrate components, the way the different carbohydrate molecules are organized and the linkage to other non-carbohydrate cell wall components, **lignin** and **protein**, have a great impact on where the carbohydrates are digested.

Non-ruminant mammals

Almost all the α-linked carbohydrates are degraded to monosaccharides (**glucose**, **fructose** or **galactose**) by endogenous enzymes that are either secreted into the intestinal lumen or located on the epithelial **brush border**. Others, those

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with β-linkages, have to be degraded by microbial enzymes and are further processed through different metabolic pathways to **short-chain fatty acid**s (SCFAs) (primarily **acetate**, **propionate** and **butyrate**) and gases. These processes all occur in the lumen or on the interface between the lumen and the gut epithelium.

Monosaccharides and disaccharides are present in plant and dairy products. **Sucrose** is the most abundant sugar in plant products (vegetables, fruit, etc.), whereas the monosaccharides (glucose, fructose, galactose) are usually present in low concentrations. **Lactose** constitutes the major part of the carbohydrates in milk and dairy products. While sucrose is well digested even at very high intake levels, the intestinal capacity to absorb fructose can be restricted, and the intestinal capacity to digest lactose in, say, pigs is age dependent. Sugar alcohols/polyols are usually not present to any larger extent in natural ingredients but commonly used as low-caloric sweeteners in human foods.

The DP of oligosaccharides has been variously defined as including everything from 2 to 19 monosaccharide units, but it is mostly restricted to DPs between 3 and 10 based on the IUB-IUPAC Joint Commission on Biochemical Nomenclature (JCBN). Oligosaccharides can be present as malto-oligosaccharides produced by the enzymatic **hydrolysis** of starch or in sprouted grains. However, more common in plants are the non-digestible oligosaccharides, α-galactosides (**raffinose**, **stachyose**, **verbascose**) and fructo-oligosaccharides. α-Galactosides are homologous series consisting of 1 to 4 galactose α-linked units linked to sucrose present in a wide variety of plant materials,

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legumes in particular. Fructo-oligosaccharides are homologous series consisting of 1 to 7 β-linked fructose units with a terminal sucrose unit. They are found in cereals, grasses and in roots of **chicory** and tubers of **Jerusalem artichoke**, in the latter as a mix with higher DP **inulin**. Other types of oligosaccharides are *trans*-galacto-oligosaccharides produced by enzymatic conversion of lactose, xylo-oligosaccharides produced by enzymatic hydrolysis of high-molecular-weight arabinoxylan, and isomalto-oligosaccharides produced by enzymatic hydrolysis of starch. Common for most of the oligosaccharides is that they are not digested by the endogenous mammalian enzymes, but some may have specific effects on the microbiota, thereby differentiating them as **substrate** from NSP.

Native starch is water-insoluble semi-crystalline compounds synthesized as roughly spherical granules in plant tissues and with a form that characterizes the plant in question. Plant starch generally contains 20–30% by weight of **amylose** and 70–80% by weight of **amylopectin**. Amylose contains linear chains of approximately 300–3000 glucose monomers in length connected by α (1-4)-bonds. Linear α (1-4)-bonds make up approximately 95% of the amylopectin molecules, the remaining approximately 5% is made up of α (1-6)-bonds. This organization results in a molecule with many branching end-points and a more open structure on which α-**amylase** can act more easily compared with the more compact structure of amylose. While it was earlier suggested that the amylose content was the most important factor determining the rate of starch digestion, recent studies point to a more complex

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interaction between the molecular and granular structure (helix formation, number of pores, size of the molecule, amylopectin sidechain length distribution and crystalline structure) for the *in vitro* rate and extent of **digestion**. *In vivo* the majority of starch is digested and absorbed before the end of the **small intestine** but for some starch sources a certain fraction (known as RS, i.e. resistant starch) may resist digestion. Four different forms of RS are recognized: resistant because of physically entrapment of starch within intact cell wall structures (RS_1); resistant because of the starch granular structure (RS_2); resistant because amylose is forming irreversible re-crystallization during cooling of gelatinized starch (RS_3); and resistant because the starch is chemically modified (RS_4). Irrespective of the reason, RS will provide substrate for the microbiota in the **large intestine** and be fermented into SCFAs.

NSPs are the most complex composed carbohydrate fraction and consist of a series of soluble and insoluble polysaccharides, primarily present in plant cell walls (CW). The building blocks of NSP are the **pentoses arabinose** and **xylose**, the **hexoses** glucose, galactose and **mannose**, the 6-deoxyhexoses **rhamnose** and **fucose**, and the **uronic acid**s **glucuronic** and **galacturonic acid**s (or their 4-*O*-methyl esters). The monosaccharides that make up the polysaccharides can exist in two ring (**pyranose** and **furanose**) forms and can be linked through glycosidic bonds at any one of their three, four or five available hydroxyl groups and in two (D or L) orientations. As a result, NSP can adopt a huge number of three-dimensional shapes and,

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thereby, offer a vast range of functional surfaces. Charged groups on monomers, i.e. the acid group of uronic acids, can further affect the ionic properties and may be esterified to variable degrees. Additionally, the NSP can be linked to non-carbohydrate molecules like lignin and suberin, which creates hydrophobic surfaces.

The most important NSPs present in plant foods for non-ruminant mammals are **cellulose**, mixed linkage (1→3; 1→4)-β-glucan (β-glucan), arabinoxylan, **xyloglucan**s, **galactomannan**s and **pectic substance**s (homogalacturonan, rhamnogalacturonan types I and II, xylogalacturonan, and **arabinogalactans** types I and II). These CW polysaccharides are present in various proportions in different plant tissues and isolates; pectic substances are commonly added to foods as stabilizers or hydrocolloids. NSPs are not degraded by non-ruminant mammals' endogenous enzymes but may impact the rate and extent of nutrient digestion because of the potential influence of soluble NSPs on **gastric emptying** and the digestion processes in the small intestine. NSPs are the most important substrate for the microbiota in the large intestine, where it is degraded and fermented into SCFA in a fashion related to the structural composition and cross-linkages of the cell wall polysaccharides. A common feature is that the soluble NSPs are degraded faster than the insoluble NSPs and that insoluble NSPs from non-lignified tissues are degraded to a larger extent than NSPs in lignified tissues. NSPs in lignified tissues provide the major part of the non-degraded NSPs found in **faeces** and are the main contributor to faecal bulking.

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Ruminant mammals

Carbohydrate digestion in ruminant animals is primarily through microbial fermentation in the rumen. The linkages (α and β) in dietary carbohydrates are degraded by rumen microbes (bacteria, fungi and **protozoa**) and further processed through different metabolic pathways to produce ATP for these organisms to use for **protein synthesis** and their own growth, and SCFAs and gases (CO_2, CH_4, H_2, H_2S). SCFAs are absorbed through the rumen wall and are utilized by the animal as an **energy source**. Depending on the dietary carbohydrate composition, a variable amount of the resistant starch bypasses the rumen and is degraded in the small intestine.

In the ruminant literature, it is a common practice to classify the **feed** carbohydrates into: insoluble or soluble CW NSPs; starch; and water-soluble carbohydrates (WSCs). In ruminant nutrition systems, CW insoluble NSPs are classically characterized as the fraction insoluble in a neutral detergent solution, called neutral detergent fibre (NDF). It consists essentially of cellulose, insoluble **hemicellulose**s and lignin, whereas it does not include CW soluble polysaccharides, such as pectins, mixed linkage β-glucan, soluble arabinoxylan, and other soluble NSPs.

The different carbohydrate fractions are degraded to a variable extent in the rumen; the mono-, di- and oligosaccharides present in WSC are the most readily degraded carbohydrates, with starch being intermediate. Insoluble CW is the fraction with the lowest degradation rate but with considerable variation within the different sub-fractions. It is generally assumed that WSCs are

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fermented in the rumen almost instantaneously after being released from the plant cells, with disappearance rate of WSC from the **rumen fluid** of > 400% h^{-1} depending on the dose. The fractional disappearance rate of starch in the rumen is less (5–60% h^{-1}) but variable, with the total degradation of starch in the rumen varying between 25% and 100% of starch intake. Factors influencing the total degradation of starch in the rumen are starch sources (for example, higher digestibilities for **wheat**, **triticale** and **rye** than **maize** and **sorghum**), **particle size** and feedstuff processing. The lowest degradation rate in the rumen of dietary carbohydrates is for the insoluble CW NSPs, varying between 2% and 8% h^{-1}, depending on the composition of the insoluble NSPs and the extent and nature of lignification. Since the digestion of insoluble CW in the rumen apparently starts after a lag phase, the extent of **rumen digestion** of insoluble CW NSPs is highly dependent on the residence time of particles in the rumen but is also influenced by the ratio between the readily fermented carbohydrates (WSC, starch, soluble CWs) and insoluble CWs. Insoluble CWs escaping digestion in the rumen are not digested in the small intestine but to a variable extent in the large intestine. The contribution of the large intestine to insoluble CW digestion, however, is only around 10% of the total tract digestibility of insoluble CWs. As for non-ruminant mammals, lignification of the CWs plays a significant role for the total tract digestibility of CWs.

The SCFAs as well as gases are end-products of microbial fermentation of primarily carbohydrates but also of other substances in the rumen. The SCFAs consist mainly of acetate,

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propionate and butyrate and to a lesser extent of valerate, caproate, iso-butyrate and iso-valerate. The composition of SCFAs, and the loss of C in gases, are mainly determined by the composition of the microbial population, and thus largely determined by the intake and composition of carbohydrates and their degradation. Typically, feeding high levels of insoluble CWs stimulates fibrolytic microorganisms and induces high levels of acetate, whereas the feeding of high levels of starch stimulates amylolytic microorganisms and increases the proportion of propionate. Concentrate diets and diets rich in WSC may stimulate the development of protozoa that promotes the production of butyrate in the rumen. Irrespective of the dietary carbohydrate composition, SCFAs contribute to the major part of absorbed energy to ruminant mammals in contrast to non-ruminant mammals, where glucose is the main energy contributor. (KEBK)

See also: Feed composition table and analysis; One-carbon metabolism in animals

Carbon dioxide

A diatomic gas, CO_2, that makes up ~0.033% by volume of air. In photosynthesis, plants use atmospheric CO_2 in the biosynthesis of all the organic components in their cells. In animals, carbon dioxide is an end-product of the **catabolism** of **fatty acid**s, **carbohydrates** and **amino acid**s. In solution in the body, carbon dioxide becomes carbonic acid: this is rapidly converted enzymatically to **bicarbonate**, which is part of the blood and tissue **buffer** system.

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Metabolism
can be likened to a slow burning in which fuel (food) is combined with **oxygen** to provide the **energy** for life processes together with the release of carbon dioxide and waste energy in the form of heat. The amount of carbon dioxide produced is similar though slightly less than the amount of oxygen consumed, being approximately 0.35–0.47 l for every **kilojoule** (kJ) of energy converted into heat. The table gives crude estimates of the carbon dioxide production (l per day) of growing farm animals at different body weights. For pregnant animals these estimates should be multiplied by approximately 1.5, for **laying hen**s by 1.75 and for lactating animals by 2, or even 3 for a high-yielding cow. For **maintenance** conditions they should be reduced to about two-thirds. (NJB; JAMcL)

Carbon dioxide production (litres per day) of growing farm animals.

Body weight	Chickens	Sheep	Pigs	Cattle
50 g	2			
100 g	4			
200 g	7			
500 g	10			
1 kg	16			
2 kg	27	50		
5 kg		70	60	

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Body weight	Chickens	Sheep	Pigs	Cattle
10 kg		100	120	
20 kg		180	220	200
50 kg		300	400	400
100 kg			600	650
200 kg			800	1000
500 kg				1600

Carbon–nitrogen balance

Apart from **fat**, which can represent 5–40% of the total body mass of farmed animals, the remainder or 'fat-free body' consists of 20–23% **protein**, 70–75% water and small amounts of minerals and carbohydrate. Carbon and **nitrogen balance** is a technique for measuring energy retained in the body (as growth, milk, eggs etc.) by assuming that all retained energy is in the form of protein and fat. Energy retained as protein and as fat is the product of their masses retained and their heats of combustion. Since protein is 52% carbon and 16% nitrogen, whilst fat has 77% carbon and no nitrogen, the quantities of retained protein and fat can be calculated from the retained carbon and nitrogen. These in turn may be measured as the differences between the quantities of the two elements in the food consumed and in the faeces and urine excreted, with allowance for the carbon lost in **carbon dioxide** and **methane** during respiration. The necessary calculations are encapsulated in the equation for retained energy (RE):

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RE (kJ)=51.83% C+19.4% N

where C and N (g) are retained masses of the elements. To use the technique it is necessary to collect, weigh, sample and analyse all food, faeces and urine over at least one 24 h period, as well as measuring the quantities of carbon dioxide and methane expired. (JAMcL)

See also: Indirect calorimetry; Respiration chamber

Carbon sequestration

Grazing multispecies pastures by livestock at low stocking densities may make an important contribution to carbon sequestration into the soil. Grazing cattle can stimulate plant growth, encouraging CO_2 sequestration. However, **methane** emissions from the cattle currently counteract these benefits to make the overall impact on climate change negative. Stocking density, nutrition of the cattle and the soil–pasture relationship can influence the overall greenhouse gas emissions and impacts on climate change. Overgrazing can reduce carbon sequestration if plant biomass is depleted. However, given the right balance, livestock grazing may help to offset some of the CO_2 released into the atmosphere, both historically and currently, from burning fossil fuels. The maximum benefit will be obtained when unproductive cattle graze on tall pasture at low stocking densities. However, if there is little or no production from the livestock, it is unclear why this option would be utilized, since more carbon would be sequestered in a natural ecosystem, with many biodiversity benefits. (CJCP)

Carboxylases

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A group of **enzymes** involved in incorporation of **carbon dioxide** into metabolic intermediates involved specifically in **gluconeogenesis** (e.g. **pyruvate** carboxylase) and **lipogenesis** (e.g. acetyl-CoA carboxylase) and in the **catabolism** of **leucine**. In all these examples the vitamin **biotin** is involved as the enzyme co-factor. (NJB)

Carboxypeptidase
An **exopeptidase**, hydrolysing **peptide** bonds from the C-terminus of proteins. Carboxypeptidase A (carboxypolypeptidase; peptidyl-L-**amino acid hydrolase**; EC 3.4.17.1) and carboxypeptidase B (protaminase; peptidyl-L-**lysine** [L-**arginine**] hydrolase; EC 3.4.17.2) are secreted as inactive procarboxypeptidases from the **pancreas** and activated in the **duodenum** by **trypsin**. The liberated products are free amino acids or di- or tripeptides. Carboxypeptidase A hydrolyses all linkages except those in which the terminal amino acid is **arginine** or **lysine**, whereas carboxypeptidase B only hydrolyses bonds with terminal arginine or lysine residues. (SB)
See also: Protein digestion

Carcase:
see Carcass

Carcass
Although the term may be used to describe a dead animal, particularly in the wild, in animal production systems it normally refers to animals that have been prepared for human consumption.

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This usually implies the removal of the digestive tract and contents and sometimes other internal organs. However, the extent of preparation varies between animal species and is also affected by religious and cultural restrictions. Poultry, for example, may be sold intact, or with feathers removed, or eviscerated with head on, or (in most modern processing situations) plucked and eviscerated with head and legs removed; however, parts such as heart, liver, **gizzard** and neck may be returned to the eviscerated carcass (often in a separate plastic bag). Pigs are normally eviscerated and shaved; the head may be removed or left attached. Cattle and sheep are normally skinned and have the head and lower parts of the legs removed. Depending on consumer demand, a variable amount of subcutaneous and visceral **fat** may be removed. In Europe, as a result of **bovine spongiform encephalopathy**, it is now necessary to remove all spinal cord material to minimize the risk of **contamination**.

As a consequence of these different practices, the proportion of 'carcass weight' to pre-slaughter weight varies. This ratio, described as 'kill-out proportion', is also affected by the breed and stage of **maturity** of the animal and by pre-slaughter feeding or fasting. There is also a difference between 'hot carcass weight', i.e. weight at time of evisceration, and 'cold carcass weight', which is the weight after a period of hanging in a refrigerated room. Typical kill-out proportions are: broilers, 0.7–0.75; turkeys, 0.8–0.85; cattle, 0.5–0.6; pigs, 0.75–0.8; sheep, 0.5. (KJMcC)

See also: Meat production; Meat yield

Carcinogens

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Substances that cause cancer. Most carcinogens in feeds are secondary carcinogens, requiring metabolic activation by hepatic **cytochrome** P450 enzymes. Examples of carcinogens in feed include **aflatoxin**, **fumonisin**s, pyrrolizidine **alkaloid**s in *Senecio* spp. and ptaquilosides in **bracken fern** (*Pteridium aquilinum*). The commonest dietary cause of cancer in livestock is bracken fern, causing urinary tract cancer (enzootic haematuria) in cattle. This is a significant problem in parts of Western Europe (especially Britain), Asia, New Zealand and Central and South America. Bracken-induced tumours may also occur in the nasopharynx, oesophagus and forestomach of cattle. Infection with bovine papilloma virus type 4 is a predisposing factor. **Rainbow trout** are especially sensitive to aflatoxin-induced **liver** cancer, caused by dietary levels of aflatoxin as low as 1 ppb. (PC)

Carnitine

Carnitine, $(CH_3)_3{\cdot}N^+{\cdot}CH_2{\cdot}CH(OH){\cdot}CH_2{\cdot}COO^-$, is essential for the transport of **long-chain fatty acid**s across the impermeable inner mitochondrial membrane. The role of carnitine palmitoyltransferase is to control the rate of mitochondrial **fatty acid** catabolism but **medium-chain fatty acid**s (up to C-8) are thought not to require carnitine for entry to the mitochondrion and thus their rate of **catabolism** is not dependent on carnitine. The precursor of carnitine biosynthesis is **trimethyllysine**, produced by **methylation** of protein-bound **lysine** by ***S*-adenosylmethionine**. (NJB)

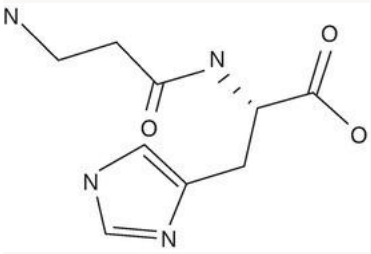
Carnivore

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Carnivores survive mainly by eating the flesh of animals. Obligate carnivores survive solely by this means. Predators are carnivores that eat prey animals as their main source of nutrients. They typically have forward-facing (rather than sideways-facing) eyes and they have **teeth** and **claws** to capture animals. They also have keen senses, capabilities for rapid movement and strength to restrain other animals. Other carnivores are scavengers that consume dead animals and plants. (CJCP)

Carnosine

A **dipeptide**, $C_9H_{14}N_4O_3$, of β-**alanine** and L-**histidine** (β-alanylhistidine). It is found in both brain and **skeletal muscle**. The enzyme carnosine synthetase is widely distributed in tissues. Tissue carnosine can be depleted in dietary histidine deficiency and this complicates studies on histidine requirements. (NJB)



Carob

Carob seeds are a product of the leguminous Mediterranean tree *Ceratonia siliqua*. The pods and seeds are sweet and palatable. The **fat** content is ~5 g kg^{-1} and the **protein** content 50–100 g kg^{-1}. The apparent **metabolizable energy** for poultry is 5–6 MJ kg^{-1} and 10–12 MJ kg^{-1} for ruminants. Although palatable due to the relatively high **sugar** content (about 200–300 g kg^{-1}), the meal

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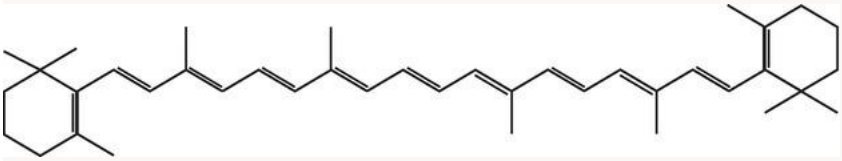
tends to contain tannic acid, which reduces **nutrient digestibility** and probably apparent metabolizable energy. Recommended concentrations in poultry diets are less than about 50 g kg^{-1} while adult ruminants may accept levels as high as 100 g kg^{-1}. (TA)

Carotenes:
see Carotenoids

Carotenoids
A group of plant pigments of which a small percentage give rise to **vitamin A** activity and thus are called provitamin A carotenoids. β-Carotene (see figure) is the most active provitamin A carotenoid. Provitamin A carotenoids such as α, β and γ carotenes are found in pasture **grass**, **silage** and **hay** as well as in **lucerne** and green and yellow vegetables such as **carrot** and **sweet potato**. Cryptoxanthin and β-zeacarotene, which contribute provitamin A activity, are also found in yellow **maize**. The common **potato** and white maize and other grains are virtually devoid of provitamin A activity. Although a number of carotenoids can serve as vitamin A precursors, they are not all bioequivalent. For example, β-cryptoxanthin and β-zeacarotene are reported to be 50–60% and 20–40% as biopotent as is β-carotene, respectively. In addition, not all carotenoid-like structures have provitamin A activity. For example, xanthophylls found in green leaves and **lycopene** found in **tomato**es do not have provitamin A activity. The biopotency of provitamin A substances is also affected by a number of additional factors. The physical matrix in which the carotenoids exist within

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food plays a role in limiting their availability. Heating of plant foods prior to ingestion improves their bioavailability but may also lead to isomerization of the naturally occurring all-*trans* configuration to *cis* configurations, which can reduce their **biological value**. Appreciable amounts of carotene (and vitamin A) may be degraded in the **reticulum** and **rumen** of grazing ruminants. In addition, carotenoids are unstable to **oxygen** and **light** exposure. Loss in green forages may occur during field curing (up to 80%), and hay stored for 2 years is estimated to contain less than 10% of the original carotenoid content.



Structure of all-*trans* β-carotene.

The **digestion** of **fat** substances (including carotenoids) in non-ruminant animals takes place largely in the **small intestine**. Once released from foods, carotenoids in bulk **lipid** droplets in the intestine are acted on by **bile salts** and pancreatic lipase, forming mixed lipid micelles. The capacity of micelles to incorporate carotenoids may be one factor that limits carotenoid **absorption** at higher intakes. Without micelle formation, carotenoids are poorly absorbed. Carotenoids are thought to be absorbed by intestinal mucosal cells by a mechanism involving passive **diffusion**. Once inside the intestinal enterocyte, the carotenoid may be converted to vitamin A or absorbed as such. There is variability in the ability of animals to absorb carotenoid unchanged into the body. For example, birds convert carotenes into vitamin A

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with only trace amounts of carotenoid passing unchanged into the tissues. Most species do not absorb carotenoids intact. Sheep, goats, pigs and rabbits contain virtually colourless **body fat**. In contrast, β-carotene can be found in the body fat of cows, horses and humans.

More is known about the **metabolism** of all-*trans* β-carotene than of any other carotenoid. Much of the conversion of β-carotene is presumed to occur in the enterocyte of the small intestine through the action of a dioxygenase which can cleave between the 15 and 15′ carbons yielding retinaldehyde as the primary product in a 1:2 ratio, respectively. Evidence has also been provided for the eccentric or non-central cleavage of β-carotene yielding β-apo-carotenals which are then oxidized to β-apo-carotenoic acids and retinoic acid. The extent of conversion of β-carotene to vitamin A is highly species dependent. The vitamin A activity (1 IU = 0.3 μg all-*trans* retinol) available as carotene is estimated at 1667 IU mg^{-1} in the chicken and at 400 IU mg^{-1} in horses and cattle. Pigs may be even less efficient. High intakes of retinyl **ester** have been shown to reduce intestinal β-carotene cleavage activity, though the manner in which the conversion of β-carotene to vitamin A is regulated is unclear. Retinaldehyde resulting from β-carotene cleavage is reduced to retinol followed by **esterification** with **long-chain fatty acid**s in the intestinal enterocyte. Retinyl esters are the major lymphatic product of β-carotene metabolism. Carotenoids (in a few species) and retinyl esters are transported by **chylomicron**s from the intestinal mucosa to the bloodstream via the lymphatics. **Lipoprotein lipase** acts on the chylomicron to

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release **free fatty acid**s that are taken up by the liver and ultimately other tissues. (MC-D)
See also: Retinyl palmitate

Carp:
see Black carp; Common carp; Crucian carp; Grass carp

Carrageenan (Irish moss)
A **polysaccharide** extracted from red **algae** in **seaweed** (*Rhodophyceae*) used as a thickener and vegetable **gum**. It is composed mainly of **potassium**, **sodium**, **magnesium**, **calcium**, **sulphate** esters and 3,6-anhydro-**galactose** co-polymers. Commercial carrageenan is frequently standardized by dilution with **sugars** and mixed with **salt** to obtain food-grade gelling or thickening agents. (JKM)



Irish moss drying in Prince Edward Island. Photo courtesy of Larry. Licensed by CC BY 2.0.

Carrot (*Daucus carota*)

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Annual or biennial herb widely distributed throughout the world's temperate zones. The larger-rooted late varieties of carrot are used for stock **feed**. Surplus supply and reject carrots from the food industry are used to provide energy for livestock. Carrots contain β-carotene, **vitamin A** and phytochemicals. Their high vitamin A content makes carrots a particularly valuable **supplement** for hay and straw.



Carrots are a good food for rabbits and other herbivores. Photo courtesy of Jennifer C. Licensed by CC BY 2.0

Carrots can be fed to cattle, sheep, horses and companion animals such as rabbits. They are low in protein but enhance **forage** intake levels. Prolonged use of carrots at high levels can produce a yellow colour in the milk fat of dairy cattle or carcass fat of beef cattle. Typical inclusion rates are 10–15 kg per day for cows, 5 kg 100 kg^{-1} body weight for beef cattle and up to 5% of the diet in ewes. Carrots are usually fed in their fresh state but may be dried and ground into a meal for inclusion in compound **supplement**s. The dry matter (DM) content of carrots is 110–130 g kg^{-1} and the nutritive composition (g kg^{-1} DM) is **crude protein** 92–95, **crude fibre** 110, **ether extract** 15–17, **ash** 70–75 and **neutral detergent fibre** 200–210, with ME 11.9–12.8 MJ kg^{-1} DM.

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(JKM)

Cartilage
A type of non-vascular supporting **connective tissue** composed of **chondrocyte**s and **collagen** fibres embedded in a firm chondrin matrix. Cartilage is elastic, translucent, bluish white and gelatinous in nature. Temporary cartilage present in the fetal skeleton is later replaced by bone but permanent cartilage remains unossified. (MMax)

Casein
A group of proteins found in **milk**, which precipitate under acid conditions (pH < 4.6) to form a clot or curd. Casein constitutes about 80% of the total proteins in cows' milk and is the main ingredient of cheese. Casein is also precipitated by the action of **rennin** on milk, either in the animal's **stomach** or added during cheese manufacture; this curd is softer than that precipitated by acids.

The five major classes of casein found in milk are α_{s1}-, α_{s2}-, β, κ and γ, comprising 43, 10, 31, 11 and 5% of total casein, respectively, on average. Most casein is aggregated with **calcium phosphate** in large micelles ranging in diameter from 30 to 300 nm; more than 90% of the calcium in milk is associated with casein micelles. Spray-**dried milk** powder can be reconstituted with water because the casein–calcium micelles retain their structure and redisperse. (PCG)

Cashmere goats

Cashmere is one of the finest and most luxurious animal fibres and is the undercoat of a number of goat breeds selected over many years for the production of this highly valued fibre. The name derives from Kashmir where, in former times, the fibre was traded. Like all domesticated goats (*Capra hircus*), cashmere goats are thought to be descended from the bezoar or Persian wild goat (*Capra aegagrus*). All are double-coated, carrying their fine cashmere undercoat, produced by the secondary **hair** follicles, beneath an outer coat of coarse guard hair that grows from the primary follicles. Both fibre types are found all over the body, except on the face and legs; the term 'undercoat' is frequently misinterpreted as meaning that the cashmere fibres are found only on the undersurface or belly of the goat. The main populations of cashmere goats are found in China and Mongolia and through the southern parts of Russia to Afghanistan and Iran. In recent decades small populations of cashmere goats have been established in the USA, Australasia and in Europe, the last being based on a new synthetic breed, the Scottish cashmere goat.



Cashmere goats in Himachal Pradesh, India. Photo courtesy of Jelle Visser. Licensed under CC BY 2.0.

Cashmere goats are generally small: adult females (does) weigh some 40–50 kg and the males (bucks) about 60–70 kg. The fibre characteristics of the many breeds of cashmere goat have been reviewed by Millar (1986). Cashmere mean fibre diameters are in the range 13–18.5 microns (μm). Coarser mean diameters are not regarded by the textile industry as conforming to the generally accepted definition of cashmere. Within a fleece having a mean fibre diameter of, say, 15 μm, individual fibres may range in diameter from less than 8 to about 28 μm. The best-quality cashmere has a mean fibre diameter of 14–15 μm; it is dull, with no lustre, and is highly crimped, i.e. the fibres have a tight spiral form. Cashmere is generally white, but grey, brown and fawn cashmere is also produced. In coloured goats the cashmere fibres are lighter in colour than the guard hair. The weight of cashmere produced per goat varies widely from about 150 g or less in animals producing

the finest cashmere, to around 400 g or more in those with coarser fibre. Cashmere fibres are the goat's protection against cold winters and they grow seasonally. It is generally believed that growth is initiated by the shortening day length following the summer solstice and that it ceases at the winter solstice. There is evidence, however, that in some breeds the period of cashmere growth is longer than 6 months. The cashmere fibres are shed or moulted in the spring, at which time the cashmere is generally harvested by combing the goats.

Cashmere goats are seasonally polyoestrous. Does come into heat at 21-day intervals during the breeding season which, in the northern hemisphere, extends from about August to February. Gestation length averages about 150 days. (AJFR)

Reference

Millar, P. (1986) The performance of cashmere goats. *Animal Breeding Abstracts* 54, 181–199.

Cassava (*Manihot esculenta* Crantz)

A herbaceous shrub up to 4 m high with finger-like leaves, also known as manioc, tapioca, Brazilian arrowroot and yuca. Cassava can develop into a small tree. It is widely grown in the tropics and subtropics for its tuberous **starch**-filled roots. The mature cassava plant (12 months old) contains 6% leaves, 44% stem and 50% tubers. **By-product**s of root processing are 8% peel and 17% pomace. The tubers contain a **glycoside**, **linamarin**, concentrated in the skin which is hydrolysed by linamarinase, an **enzyme** also present in the plant, to release hydrocyanic acid (HCN). Bruising the roots activates the enzyme. The HCN can be removed by

heating, soaking or prolonged sun drying. Bitter varieties contain more than 0.02% HCN and require thorough processing before feeding. Most commercial varieties are sweet, with < 0.01% HCN, and can be used raw. Slicing, soaking and drying removes much of the HCN, as does cooking. Mortalities have been reported in animals drinking water used for soaking cassava.



Cassava
production in Colombia. Photo courtesy of Neil Palmer, CIAT (International Center for Tropical Agriculture). Licensed under CC BY-SA 2.0.

Both fresh and dried cassava roots are fed to ruminants. Dried cassava roots can be used as a replacement for grain as an **energy source** in the rations of dairy cattle, fattening beef animals and lambs. Although an excellent source of energy, cassava is deficient in protein, **fat**, **trace element**s and vitamins. Cassava protein is particularly low in the **sulphur**-containing **amino acid**s (**lysine**, **methionine** and **cysteine**). The inclusion of **supplement**ary sulphur in the ration, along with a source of degradable protein or **non-protein nitrogen**, allows rumen microbes to manufacture

the necessary balance of **amino acid**s. This also assists in the **detoxification** of HCN in the rumen and liver. Replacement of **maize**, **oats** or **barley** by cassava in dairy rations has no effect on milk yield and can reduce production costs.

Grain in poultry rations can be partly replaced by cassava chips or root meal, with supplementary methionine (0.2–0.3%) for layers. Up to 20% inclusion in poultry rations allows satisfactory production levels. Cassava tubers, with a digestible dry matter (DDM) of 92%, can replace up to 75% of cereal in pig rations, provided that the final ration contains no more than 100 ppm HCN, producing leaner carcasses than grain-based diets. As with poultry rations, attention must be paid to balancing the energy:protein ratio in the ration.

Cassava leaves can also be used as feed, especially to provide **undegradable dietary protein** (UDP) to ruminants. Unlike the roots, the leaves are a good source of protein, containing 25% **crude protein** (CP) and producing up to 6 t CP ha^{-1}. The CP content, and hence feeding value, decreases as the leaves become older (see Tables 1 and 2). **Leaf protein** has a high **lysine** content but is low in sulphur-containing **amino acid**s. In labour-intensive production systems, leaf stripping can be practised to provide supplementary **fodder** for ruminants. However, removal of leaves can reduce root yields, and the use of leaves from bitter varieties can result in HCN toxicity. Sun drying of leaves may reduce the HCN content. Cassava foliage is usually used as a **supplement** to grass fodder to increase dietary protein levels. The use of 0.5% leaf in layer rations will provide carotene for enhanced yolk colour.

Inclusion rates of up to 150 g kg^{-1}, and 300 g kg^{-1} for growing pigs, can be used with the addition of methionine and an **energy source**. Dried leaf meal is bulky, and **pelleting** is recommended for **chick feed**.

Table 1. Typical composition of cassava products (g kg^{-1} dry matter).

	DM (%)	**CP**	**CF**	**Ash**	**EE**	**NFE**	**Ca**	**P**
Fresh leaves, 4 weeks	15.3	24.8	18.3	8.5	5.2	43.2	0.98	0.52
Fresh leaves, 8 weeks	16.1	24.1	26.0	8.0	5.0	39.9	0.99	0.56
Stem		10.9	22.6	8.9	9.7	47.9	0.31	0.34
Fresh roots	32.1	3.9	4.9	4.8	1.0	85.4	0.09	0.12

	DM (%)	CP	CF	Ash	EE	NFE	Ca	P
Fresh peel	27.9	5.3	21.0	5.9	1.2	66.6	0.31	0.13
Pomace	83.5	2.2	26.9	3.4	0.6	66.9	0.68	0.05

CF, crude fibre; CP, crude protein; DM, dry matter; EE, ether extract; NFE, nitrogen-free extract.

Table 2. Digestibility (%) and ME content of cassava.

	CP	CF	EE	NFE	ME (MJ kg^{-1})
Ruminants					
Leaves	57.0	39.0	54.0	71.0	9.18
Tubers	–	53.0	51.0	90.0	12.23
Poultry					
Leaf meal	63.0				7.80
Pigs					
Leaf meal					9.70

	CP	CF	EE	NFE	ME (MJ kg^{-1})
Tubers	91.6				14.57

Silage

can be made from the whole cassava plant. Cassava peel, a by-product from the processing of roots for human use, can also be used for animal feed. Peel is rarely fed fresh, because of high levels of **cyanogenic glycosides**, which are reduced by sun drying, ensiling and **fermentation**. Rumen DM degradability of dried or ensiled cassava peel is > 70% after 24 h. In rations, peel is offered primarily as an **energy source** with a **protein supplement**. Optimum value is obtained with a rapidly degradable protein to synchronize energy and nitrogen release.

Cassava pomace, the residue after extraction of starch from cassava roots, has a **crude fibre** (CF) content similar to leaves but is low in protein, fat and minerals. Although it can be used as a ruminant feed, it is more commonly fed to non-ruminants. (LR; JKM)

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Castor bean (*Ricinus communis* L.)

A variable species, appearing as an annual herb in temperate climates and, in tropical areas, as a perennial tree with leaves deeply divided into six fingers. Each spiny outer shell contains three seeds (beans) which can be removed after drying. The bean is the source of castor oil, with a mechanical extraction rate of around 66%. Approximately 60,000 t of castor bean meal are produced annually in India. Castor bean meal contains 0.22% **ricin**, a toxin, which can be deactivated by steam treatment (5 kg cm^{-2} for 15–30 min). Alternatively the meal can be boiled for 10 min in three times its own volume of water, the water discarded and the process repeated. The wet meal can be air dried at 70–80°C. Detoxified meal is a good source of protein and energy for ruminants (see Tables 1 and 2) and can be included in concentrate mixtures for sheep at a level of 10%. Poultry appear to be less affected by ricin than mammals, and up to 40% of detoxified meal can be included in their rations.

(LR)

Table 1. Typical composition of castor bean products (% dry matter).

	DM	CP	CF	Ash	EE	NFE	Ca	P
	(%)							

	DM (%)	CP	CF	Ash	EE	NFE	Ca	P
Castor bean meal, mechanical extraction		34.8	33.2	10.4	10.6	32.2		
Castor bean meal, solvent extraction	92.0	38.5	32.3	7.1	1.0	21.1	0.76	0.87

CF, crude fibre; CP, crude protein; DM, dry matter; EE, ether extract; NFE, nitrogen-free extract.

Table 2. Digestibility (%) and ME content of castor bean.

	CP	CF	EE	NFE	ME (MJ kg^{-1})
Ruminants					
Castor bean meal	80.8	8.9	92.9	43.4	7.75



Castor beans are not actually beans, but they are the seeds of the castor oil plant (*Ricinus communis*), from which castor oil is produced. A minor cash crop in central India. Photo courtesy of Coshipi. Licensed under CC BY SA 2.0.

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Castration
Removal of the testes of a male animal by surgery or by chronic interruption of the vascular and nerve supply to the testes and scrotum. Rendering the testes dysfunctional by surgical or chemical means. (MMit)
See also: Sex differences

Cat (*Felis catus*), essential nutrients
The cat is an obligate (true) **carnivore** and evolved lacking many of the key **enzymes** of biosynthesis and **metabolism** that are present in other species. Cats consume a diet containing animal tissues to meet their requirements for **amino acid**s, **fatty acid**s, **vitamins**, **minerals** and water. Today, as cats have become the most popular indoor pet in many countries, **obesity** and sarcopenia are two major health concerns linked to their diets.



Obesity has become a major health problem in domestic cats. Photo courtesy of Josbert Ionnee. Licensed under Public Domain Mark 1.0

Protein and taurine

Cats use proteins as a dispensable source of energy. The National Research Council (NRC) has recommended that cats require a minimum of 1.9 g protein kg^{-1} body weight per day, or ~23% **metabolizable energy** (ME) from protein, to maintain basal **nitrogen balance** as well as normal body repair, **immunity**, plasma proteins, **protein turnover** and to prevent amino acid deficiencies. The amino acid requirements of cats reflect their need for animal-based protein, and inability to synthesize or derive from other sources certain amino acids (e.g. **taurine** and **arginine**). When given the opportunity to choose, cats prefer diets with most ME from protein, some from fat, and less than 5% from **carbohydrates** (CHO). While the protein concentrations of commercial dry feline diets are safely over the NRC minimums, most are less than 50% ME from protein. In fact, most feline diets contain less than 40% ME, which recently was found to be the amount of protein needed to prevent loss of **lean body mass** (e.g. muscle) in adult cats. The quantity of protein in feline diets is one important factor, but the quality (**digestibility** and amino acid composition) of the protein in the diet is also critical. The average **protein digestibility** of good-quality dry cat foods ranges between 80% and 85%, but the protein digestibility of some commercially available dry cat foods is less than 80%. This means a diet that is 80% digestible, containing 35% protein, is providing only 28% protein to the cat. Feline diets specially formulated with protein concentrations less than 30% ME are typically found only in veterinary prescription diets developed for use in specific disease conditions (e.g. kidney failure) and are well documented to

result in significant loss of lean body mass in cats. Finally, feline diets formulated with a lower protein concentration replace that protein with a CHO source.

Taurine is a nutritionally essential amino acid in cats, i.e. they must consume all of the taurine needed in their daily diet, the only source of which is from animal tissues. Cats fed commercial diets containing inadequate taurine (from loss during processing and interactions with carbohydrates in dry diets) develop a fatal form of heart muscle failure, called dilated cardiomyopathy. The increased popularity of cats as household pets, along with the shift to feeding cats only dry commercial diets for convenience, led to a subsequent increase in diagnosis of taurine **deficiency diseases** in cats (**blindness**, cardiomyopathy). Researchers subsequently confirmed that these diets did not contain sufficient taurine to survive processing of the food and particularly in dry foods with inadequate meat-source proteins. The addition of additional meat-source protein and supplemental taurine to feline diets has made this once serious heart condition rare.

Energy (fat and carbohydrate)

Obesity

is a complex, multifactorial disease, but nutrition, and particularly excess intake of **energy**, is an important factor. Control of **calorie** intake (energy) in indoor cats is very challenging when they are fed only dry calorie-dense foods – the most common diet for indoor cats. Diet composition and the tendency to overfeed are key factors in development of obesity, but other factors that impact on the energy needs of indoor cats, including inactivity, neuter status and

boredom, also contribute significantly. The **energy requirement**s (in kcal per day) for **maintenance** of intact cats have been estimated by a number of different equations, including the standard $100 \times BW_{kg}^{0.67}$, but a general approximation frequently used for intact cats is 55 × BW (in kg). However, the vast majority of indoor cats are not sexually intact, and data show that while the onset and mechanisms are different, both male and female cats require a significant reduction in their daily **energy intake** of ~15–25% post neutering (35–40 kcal BW_{kg}^{-1}) to avoid rapid weight gain. To illustrate, an intact 4 kg female cat whose maintenance energy requirement is 240 kcal per day will require a decrease in calories to 160 kcal per day (or 40 kcal BW_{kg}^{-1} per day) or less to prevent rapid weight gain or obesity. The caloric density of commercial dry cat foods ranges from 300 to 600 kcal per cup; thus, an exceedingly small amount of food must be fed to prevent **overfeeding**, which can result in undesired food-seeking behaviours. Recent data suggest that feeding cats canned foods or whole-food diets, which are 75–80% water, not only provides the cat with a greater volume of food (which increases **satiety**) but importantly also increases water intake.

Dietary fat is a highly efficient **energy source** in feline diets, but it is also important because food preferences in cats are triggered by the types and amount of **animal fat** present. Cats will refuse diets that are low in animal fat (or supplemented with plant oils), an important consideration when enticing sick or anorectic cats to eat. Cats require animal fats in their diet to provide the essential **arachidonic acid** and omega-3 fatty acids

(docosahexanoic acid (DHA) and eicosapentanoic acid (EPA)), which cats cannot synthesize from plant source precursors. These **essential fatty acid**s are critical in cell membrane health and function, normal regulation of inflammation and platelet function, and normal **reproduction**, and are essential for healthy organ and brain function.

The other major energy source in feline diets is **starch** or other complex **carbohydrates** from grains, legumes or other plants. Cats have no nutritional requirement for carbohydrates in their diet, and adult cats consuming a diet of prey (birds, mice or other small mammals or insects) will consume less than 5–10% of their total intake as CHO. In fact, cats are not anatomically, physiologically or metabolically adapted to consume large amounts of CHO in their diet. It does not mean that they are unable to digest, absorb or utilize CHO, but there are significant inefficiencies and challenges for them. There are multiple examples of their unique characteristics nutritionally: (i) cats lack significant numbers of functioning **amylase** and **disaccharidase** enzymes in their mouth or intestinal tract (< 10% of that in dogs) – the enzymes most responsible for CHO **digestion**; (ii) the intestinal tract of the cat is much shorter, compared with similar sized omnivores – reducing the capacity to efficiently digest large quantities of CHO or dietary CHO that have lower **digestibility**; and (iii) cats have a greatly reduced capacity to facilitate the uptake of post-prandial **glucose** from the blood into cells (for example, post-prandial **hyperglycaemia** is prolonged) because they have significantly reduced numbers of inducible **glucokinase**, the

enzymes on liver and muscle cells that activate GLUT receptors to increase glucose uptake into cells. Tangible evidence that cats are physiologically and metabolically challenged by high-CHO diets is demonstrated by the persistence of elevated blood glucose concentrations for 8–12 h following a high-CHO meal (e.g. dry food with 35% CHO content). This prolonged increase in blood glucose is not observed in cats consuming high-protein, low-CHO diets, as their body's glucose needs are met through breakdown of protein and **gluconeogenesis**. Even mildly elevated post-meal blood **sugar** concentrations are detrimental to long-term health, having important impacts on **appetite** and **insulin** secretion (significant in the pre-diabetic state), and result in increases of pro-inflammatory **cytokines** that contribute to ageing and development of chronic disease.

Dietary fibre

The majority of complex CHOs present in pet foods are highly digestible starches with alpha linkages: energy sources that can be easily digested by the gastrointestinal enzymes present in simple-stomached animals (dogs and cats). Complex CHOs present in diets containing structural beta linkages are plant-based materials like **cellulose** that are generally known as **dietary fibre**s. These complex CHOs require bacterial **fermentation** to break down their carbon structure to be used for energy – a process that only occurs in the **rumen** of cattle or large **colon** of horses. Dietary fibres must be present in small amounts in commercial processed foods because they are important to the health of the gastrointestinal (GI) microbiome (the bacterial ecosystem of the

gut) and to normal cells of the colon that require them for energy and proper function. Dietary fibres are present in two basic forms: digestible (soluble) and poorly digestible (insoluble) fibre. Soluble fibres come from a variety of plant sources, such as **inulin**, **guar gum**, beet pulp or other plant germ sources (**oat** fibre). Soluble fibres are also called **prebiotics**, as they represent a source of nutrients for commensal bacteria in the intestinal microbiome/ecosystem. Insoluble fibres (e.g. cellulose) are not digested to any appreciable extent in cats (or omnivores), due to their very short GI tract and the brief dwelling time of ingesta in the colon that prevents significant opportunity for bacterial fermentation. Insoluble fibre sources such as cellulose are added to feline diets in small (< 1–3%) quantities to provide a bulking action that promotes normal colonic **motility** and assists with complete defecation. However, if insoluble fibres are added to diets in large amounts (> 8–10% in weight loss or 'hair-ball' diets) the result can be very deleterious, as these fibres significantly decrease the digestibility of many nutrients (protein, vitamins and minerals). They also increase the risk of constipation by resulting in production of larger, drier faeces that are difficult to expel. This is a particular risk in obese, sedentary indoor cats.

Vitamins

The vitamin needs of cats are also unique in that they have a greater need for many of the water-soluble (B vitamins), and they lack the ability to synthesize fat-soluble vitamins (especially A and D) from typical plant source precursors. Water-soluble B vitamins must be part of the cat's daily diet, as they are not stored in any

significant quantity. The requirement for B vitamins is high in cats because many (**thiamine**, **pyridoxine**, **niacin**, **riboflavin** and **cobalamin**) are important co-factors in critical metabolic pathways. Both pyridoxine (vitamin B_6) and cobalamin (vitamin B_{12}) are required in the feline diet at four times that of omnivores, due to their function as essential co-factors in transaminase reactions – the process of converting protein to metabolic energy. Cats that are not eating can develop a wide range of clinical signs, from deficiency of B vitamins, including profound neck ventroflexion and weakness that can develop rapidly in cats with thiamine deficiency. As with their need for animal tissues to provide essential fatty acids, cats also require vitamins A and D to be present in their diet in their biologically active forms (**vitamin A** as retinol and **vitamin D** as **calcitriol**), because they lack the enzymes necessary to convert β-carotene to vitamin A or vitamin D precursors in skin to deoxycholecalciferol. **Vitamin E** and **vitamin K** are also present in high levels in animal fat and do not require a conversion pathway to achieve their active form. Deficiency of these vitamins in cats is less common, unless they are not consuming a diet with animal tissues present or have severe and prolonged **anorexia**. Extreme deficiencies of these vitamins are rare, as they are stored to a degree in liver and fat tissues, but cats consuming **vegetarian** or **vegan** diets, dog food or other inadequate diets will develop deficiencies of almost all of the amino acids, fatty acids and vitamins we have discussed here.

Water

The water needs of cats reflect their development as strict

carnivores, as they are programmed to obtain most of their water requirements from eating prey (~70% water). Cats have a less sensitive response to thirst and **dehydration** than dogs and adjust their water intake to the **dry matter** content of their diet (not the moisture content). Based on **total body water** studies, cats eating only dry cat foods consume 10–15% less water daily as compared with cats eating canned foods (75–80% water). Feeding cats canned or whole foods increases both water intake and **urine** volume – two physiological priorities vital to health and prevention of urinary and **kidney disease**s but also a key factor in **calorie** control and **satiety**. (DLZ)

Catabolism

Cellular metabolic processes leading to the systematic enzymatic breakdown of molecules. These processes differ from the extracellular breakdown of molecules called **digestion**, which occurs in the **gastrointestinal tract**. For example, the catabolism of **amino acid**s in the **liver** leads to the recovery of **amino nitrogen** in **urea**, while the digestion of protein in the intestinal tract leads to free amino acids. (NJB)

Cataract

A common degenerative condition of the ocular lens in which the crystalline lens becomes opaque to varying degrees. It commonly arises during **diabetes** or some forms of **poisoning**. Cataracts are defined relative to the portion of the lens that is opaque, aetiology, degree of change over time, degree of opacity and relationship to other intraocular pathological changes such as adhesions between

the lens capsule and iris. Cataracts result from degeneration of the lens epithelium or changes in the osmotic status of the lens cortex allowing excess water to invade the lens crystal. (DS)

Catecholamines

A group of neuroactive **amine**s. **Dopamine**, **norepinephrine** and **epinephrine** are derived from **tyrosine** via its hydroxylation to L-DOPA (L-dihydroxyphenylalanine). Further **metabolism** of L-DOPA leads to the production of these three catecholamines. They are synthesized mainly in the **adrenal** medulla but norepinephrine, for example, is made in other organs and in nerve endings. In Parkinson's disease there is a deficiency of dopamine synthesis. (NJB)

Catfish

A large group of (principally) **freshwater fish** characterized by a body with no scales, or else covered with bony plates, and a head with up to four pairs of barbels. Catfish of the families Ictaluridae and Clariidae are the major species established in **aquaculture** with the total production 4.12 million tonnes in 2018.



Red-tailed catfish (*Phractocephalus hemioliopterus*). Photo courtesy of Shankar S. Licensed under CC BY 2.0.

The channel catfish (*Ictalurus punctatus*) is native to North America and has constituted a major aquacultural enterprise in the USA. The striped catfish (*Pangasianodon hypophthalmus*) is native to South-east Asian regions and cultured in the regions for over five decades; in 2018 the total production in the world was 2.36 million tonnes. Walking catfish of the genus *Clarius* had a total production yield of 1.25 million tonnes in 2018 and are native to Africa and Asia, being cultured in these continents, as well as in Europe. The yellow catfish (*Pelteobagrus fulvidraco*), with relatively smaller body size and a yellow colour, is native to China and the total production in 2018 was 509,000 t. The nutritional requirements of channel catfish have been extensively studied, with as many as 40 nutrients in all of the major groups having been demonstrated to be necessary for normal metabolic functions. Catfish in both families are omnivorous in their **feeding behaviour** and will consume a variety of food organisms in nature. As such, these fish generally can thrive on prepared diets composed of plant-derived feedstuffs with relatively low protein concentrations ranging from 28% to 32% of diet for juvenile and subadult fish. Their diets typically contain relatively high levels of soluble **carbohydrate** from **cereal grain**s and grain **by-product**s. (DMG; QS)

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Catheter
A tube introduced into a body cavity for the withdrawal of fluid or for the introduction of substances. A catheter is commonly placed in a vein to obtain repeated blood samples, or in the bladder for the complete collection of **urine**. A larger tube introduced into the gut is normally called a **cannula**. (DS)

Cation:
An ion with a positive charge. (NJB)
See also: Acid–base balance

Catla (*Catla catla*)
One of the economically important carp species used in composite culture throughout India, Pakistan and South-east Asian regions. Catla is a surface feeder and zooplanktivore species (FAO, 2017). Catla, also recognized as thaila, is a column feeder and is popular in polyculture systems, cultured with other species (Aslam *et al*., 2016). Catla production increased through the first decade of the 21st century and was nearly 2.8 million tonnes per year in 2012 (FAO, 2015). India dominates catla production, contributing 71% of global production (FAO, 2012). (QS)

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Cattle

Cattle belong to the order Artiodactyla (even-toed ungulates), suborder Ruminantia, family Bovidae, subfamily Bovinae and tribe Bovini. Bovinae are characterized by the presence of hollow horns and Bovini by their large size. Commercially important species among the tribe Bovini are found in the subtribe Bovina (mainly *Bos* genus). Humpless cattle (*Bos taurus*) predominate in northern temperate latitudes, whereas humped cattle (*Bos indicus*) inhabit the more tropical regions of the world. These two species can interbreed to produce fertile offspring. Other species in this genus include *Bos grunniens* (domestic yak), *Bos javanicus* (Bali cattle) and *Bos frontalis* (domesticated gayal), found in Asia.



Cattle play a major rôle in subsistence agriculture in developing countries, as seen in this boma in Ethiopia. Photo courtesy of D. Stanley. Licensed under CC BY 2.0.

Domestication of these species involved selection for functional traits such as docility, mature size, draught, milk production and muscularity, as well as type traits such as coat colour and polledness. Differential selection for such traits resulted in the formation of breeds, i.e. animals of common origin with certain distinguishing characteristics passed uniformly from one generation to the next. **Adaptation** to local environmental conditions through natural selection also occurred. For example, the N'Dama breed (*Bos taurus*), resident in West Africa, developed resistance to trypanosomiasis (sleeping sickness) spread by the tsetse fly, and *Bos indicus* cattle have tolerance of heat and cattle ticks (*Haemaphysalis longicornis* and *Rhipicephalus* spp.).

Cattle have been classified by utility, where selection has favoured the production of either **meat** (**beef cattle**) or **milk** (**dairy cattle**) (Buchanan and Dolezal, 1999). Some breeds are dual-purpose meat and milk producers. Mature size can vary

considerably within each class and this, together with the genetic potential for milk production, can have a significant bearing on the animal's **metabolizable energy** (ME) requirements for **maintenance** (0.40–0.55 MJ ME kg^{-1} $W^{0.75}$ for non-lactating beef cows; 0.50–0.65 MJ ME kg^{-1} $W^{0.75}$ for lactating beef cows; and up to 0.77 MJ ME kg^{-1} $W^{0.75}$ for lactating dairy cows) (where W = **liveweight**, kg), so determining their suitability to specific nutritional environments (Sinclair and Agabriel, 1998). (KDS; GMcLD)

See also: Beef cattle production systems

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Cauliflower

Cabbage flower (caulis), *Brassica oleracea*, of which there are many varieties, has a compact white head of fleshy flower stalks and is eaten by humans as a vegetable. Cauliflowers are available year-round and are particularly plentiful in spring and autumn. They have a very high **vitamin C** content and are rich in

potassium, fibre and **folate**. Surplus production can be fed fresh to cattle and sheep. Cauliflower is a good source of **protein**, has no **fat** but contains high levels of natural **sugar** and **dietary fibre**. Typical dry matter (DM) content of cauliflower is 120–130 g kg^{-1} and the nutrient composition (g kg^{-1} DM) is **crude protein** 230–240, **crude fibre** 120–125, **ether extract** 20–25, **ash** 115–120, **neutral detergent fibre** 290–295 and **starch** 5–8, with ME 11.5–12 MJ kg^{-1} DM. (JKM)

Celery (*Apium graveolens* L.)
Plant of family Apiaceae widely grown for human consumption. Celery has recently been introduced into the tropics for cultivation at higher altitudes. Surplus production may be available for use as animal feed. The leaves are rich in protein and carotene; they have been used up to a rate of 10% of the diet in chickens and can effectively replace **lucerne** meal. In Africa, the dry matter (DM) content of fresh leaves is 110 g kg^{-1} and the nutrient composition (g kg^{-1} DM) is **crude protein** 272, **crude fibre** 35, **ash** 190, **ether extract** 69, **neutral detergent fibre** 434, **calcium** 27 and **phosphorus** 17. (JKM)

Cell walls
Heterogeneous macromolecular structures that are exterior to the plasma membrane and give rigidity and shape to the cell. Bacteria, fungi and plants have cell walls of different compositions. Plant cell walls are composed of a mixture of **polysaccharide**s, **protein**, **lignin** and cutin. The cell walls of **grasses** also contain **silica**. The principal polysaccharides are **cellulose**, **arabinoxylans** and

pectin, but there is large diversity in polysaccharide composition among plant species. Plant extensin is a fibrous protein associated with the deposition of the cell wall. Lignin is a **polyphenolic compound** that imparts rigidity to the cell wall. Cutin is composed of higher-molecular-weight alcohols and gives the surface of the cell wall a waxy appearance.

The compositions of the cell walls of grasses and **legumes** differ. In general, grasses usually have a higher percentage of cell wall in the above-ground biomass than legumes at a similar stage of **maturity**. However, legumes usually have a greater percentage of lignin in the cell wall than grasses. The polysaccharides in the cell walls of grasses are composed of approximately equal ratios of cellulose to arabinoxylans and other heteropolysaccharides, whereas in legumes the ratio of cellulose to other heteropolysaccharides is much higher. The composition of the cell wall also varies widely among specific plant parts and cell types within each cell tissue. Cells that are involved in photosynthesis have thin primary cell walls with little or no lignin. Cells that have a structural role have thickened secondary cell walls that are highly lignified.

At an early stage of development, the plant cell wall has a low content of lignin and the cell wall polysaccharides are highly degradable by microbial **enzymes**. As the plant cell matures, the contents of lignin, cutin and silica increase and the degradability of the cell wall polysaccharides decreases. These changes in the composition and degradability (**digestion**) of the cell wall are responsible for decreases in **digestible energy** as forages mature.

Mammals and other animals do not have enzymes that hydrolyse cell wall polysaccharides but obtain energy from cell walls through **fermentation** of polysaccharides by symbiotic, anaerobic **microorganism**s that reside mainly in sacculated organs of the digestive tract, such as the **rumen**, **colon** or **caecum**. These microbes possess a diversity of enzymes that break down the cell wall polysaccharides. The **monosaccharide**s undergo fermentation to **volatile fatty acid**s (VFAs) that are absorbed and used by the host for **energy metabolism**.

'Cell wall' and 'fibre' are often used as synonyms. This may lead to confusion: many non-fibrous polysaccharides that do not occur in plant cell walls are referred to as '**dietary fibre**' in the human nutrition literature because they are not digestible by mammalian enzymes but require fermentation to yield energy. Therefore, caution is required in the use of the terms. (JDR)

Cellobiose

A **disaccharide**, 4-*O*-β-D-glucopyranosyl-D-glucose, $C_{12}H_{22}O_{11}$, the basic structural unit of **cellulose** and a product of the **hydrolysis** of cellulose by **cellulase**. The stereochemistry of cellobiose allows the formation of two intramolecular **hydrogen** bonds. Cellobiose is often used as a **substrate** in microbiological tests for cellulase activity. (JDR)

Cellular agriculture

Production of animal-sourced products from cell culture, applying a combination of **biotechnology**, tissue engineering, molecular biology and synthetic biology to food production to create and

design new methods of producing proteins, fats and tissues that are molecularly identical to those made via traditional animal agriculture conventional methods. The technology aims to produce edible animal-based products more ethically and with a reduced environmental footprint compared with conventional farm production. The most common cell types used to produce cell-based products are muscle-derived cells called myocytes. Serving as a proof of concept, the world's first cultured **beef** hamburger was created by Dr Mark Post in 2013 using established tissue engineering methods of growing organs for human medical use. The first commercially available cultured '**meat**' was muscle cells grown on a scaffold, but without the fat and **connective tissue** that meat from animals may have. The first **chicken** substitute was released in Singapore in 2020 after the country gave regulatory approval for the world's first 'clean meat' that does not come from slaughtered animals. The cellular agriculture novelty is the process of the large-scale application of the technology. (DB)

See also: Cultured meat

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Cellulase

An **enzyme** that hydrolyses the β(1→4)-*O*-glycosidic linkages in **cellulose**. Cellulases occur in bacteria, fungi and plants but not in animals. In bacteria and fungi, cellulases degrade plant cellulose to **glucose**, cellobiose and oligoglucans to derive energy for growth and reproduction. Cellulase in bacteria is located in protuberances on the cell surface called cellulosomes. These structures are involved in the attachment of bacteria to plant cell walls and are required for normal cellulase activity. (JDR)

Cellulolytic microorganisms

As no mammal secretes an **enzyme** complex capable of degrading **cellulose**, the symbiotic relationship between the enteric fibrolytic microflora and **herbivore**s is vital to the utilization of fibrous plant material. Plant cell walls are degraded by a combination of bacteria, fungi and protozoa, the first two groups accounting for about 80% of the activity. The main cellulolytic bacteria are *Fibrobacter succinogenes*, *Ruminococcus albus*, *R. flavifaciens* and *Butyrivibrio fibrisolvens*. Among the fungal species are *Neocallimastix frontalis*, *N. patriciarum*, *Orpinomyces bovis* and *Piromyces communis*, while ciliate protozoa of the genera *Diplodinium* and *Eudiplodinium* degrade cellulosic material by engulfment (phagocytosis). In contrast to the weak opportunistic

interaction of protozoa with plant material, the majority of cellulolytic bacteria and fungi form strongly associated colonies. This strategy allows the cellulolytic enzymes to be concentrated on the **substrate**, restricts access to the site of **hydrolysis** and end-products and protects the enzymes from ruminal proteases. Electron micrographs of fibrolytic bacteria and fungi adhering to plant cell walls show the material being gradually eroded. Considering the highly complex nature of the substrate involved, this implies that a range of specific fibrolytic enzymes are released simultaneously. In ruminants, the primary site of cellulolytic activity is the reticulorumen, followed by the **caecum**, while in horses and pigs this occurs in the enlarged **colon**. (FLM)

Cellulose

A homopolysaccharide of **glucose** in which glucose residues are linked between carbon 1 of one glucose residue and carbon 4 of the adjacent glucose (β-D-glucopyranose–β-D-glucopyranoside linkages); this linkage is written as β(1→4). Cellulose is the main **polysaccharide** in the plant cell wall. It is the most abundant natural polymer on the earth's surface and, were it not degraded and converted to CO_2 by **microorganism**s, atmospheric CO_2 would be rapidly depleted by the fixation of CO_2 into cellulose by plants. The macromolecular structure of cellulose is formed by intramolecular and intermolecular **hydrogen** bonds that give cellulose its fibrous properties. Cellulose is organized into bundles of microfibrils that form a network around the plant cell. At early **stages of growth** this network is flexible and the cell structure is maintained by turgor pressure and the resistance of the network.

After the cell has elongated and **lignin** is deposited in the cell wall, the shape of the cell may become fixed.

Animals do not have digestive **enzymes** that are capable of hydrolysing β(1→4)-**glycoside**s (**cellulase**s) but symbiotic microorganisms of the digestive tracts do have cellulases and degrade cellulose to **volatile fatty acid**s. These acids are absorbed and metabolized by the host. The rate of degradation of cellulose is slow compared with other polysaccharides. Microbial attachment to the surface of the cellulose microfibrils is required for cellulose degradation to proceed. (JDR)

Cereals

Those members of the **Gramineae** (**grass**) family that are cultivated for their **grain**, which is primarily used for human and animal food. The cereals most commonly cultivated are **barley** (*Hordeum sativum*), **maize** (*Zea mays*), **oats** (*Avena sativa*), **wheat** (*Triticum aestivum*), **rice** (*Oryza sativa*), **rye** (*Secale cereale*), **triticale** (hybrid of wheat and rye) and **sorghum** (*Sorghum bicolor*). Most of the proteins of cereal grains are found in the **endosperm** (e.g. 72% in wheat) and their overall content is influenced by a range of factors, including species, variety, fertilizer application, soil fertility and **climate**. Protein concentrations are typically 97–160 g kg^{-1} dry matter (DM) for barley and wheat but lower for maize and oats. Cereal proteins are generally deficient in essential **amino acid**s, especially **lysine**. In all cereal species the **starch**-rich **endosperm** is the most important fraction, both nutritionally and economically. The starch comprises **amylose** and

amylopectin and their ratio determines the quality of the starch. The cell wall content (as neutral detergent fibre) (NDF) ranges from about 124 g kg^{-1} DM for wheat to 310 g kg^{-1} DM for oats. The animal **feed** industry represents a major market for cereal grains, which contribute a large proportion of the energy supply to pigs, poultry and young ruminants. Generally cereals make a lower contribution to the diets of ruminants. Cereal **by-product**s arise from a number of industries, including **milling**, brewing, distilling and starch manufacture. Cereal by-products play an important role in the diets of ruminants, owing to their greater capacity to degrade fibre. (ED)

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Ceruloplasmin

The US spelling of **caeruloplasmin**.

Cetoleic acid

cis-11-Docosenoic acid, $CH_3{\cdot}(CH_2)_9{\cdot}HC{=}CH{\cdot}(CH_2)_9{\cdot}COOH$, molecular weight 338.6, shorthand designation 22:1 n-11, a long-chain 22-carbon monounsaturated **fatty acid** found in the oils of cetaceans (whale and dolphins) and fish. (NJB)

Chelate

An association of two or more independently existing molecules or ionic species to form a heterocyclic ring compound. The new compound formed by this association exhibits chemical and physical characteristics distinct from those of either parent compound or element. In biological systems chelates typically involve a **metal** cation such as **iron**, **cobalt**, **copper**, **magnesium** or **zinc** bound to an **organic compound** via **oxygen**, **nitrogen** or **sulphur** elements. Examples include chelates such as **haemoglobin**, **chlorophyll** and **vitamin** B_{12}. Ligand bonds vary from relatively stable covalent bonds to very unstable, highly ionic bonds between molecules. In animal nutrition, chelating compounds are used to sequester or stabilize metal ions. A common chelating agent is ethylenediaminetetraacetic acid (EDTA). (TDC)

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Chemical probiosis

The control of the **gastrointestinal microflora**, especially of bacterial pathogens, by dietary substances that interfere with microbial adhesion. Many bacterial pathogens adhere to the gut surface by the binding of their fimbriae to **sugar** moieties on the epithelial surface. The fimbriae contain specific **lectins** called adhesins: this binding mechanism is essential for adhesion and infection by many pathogenic bacteria that need to resist **peristalsis** in the intestine in order to colonize it.

Lectins are proteins capable of specific and reversible binding to sugar moieties. Suitable lectins for inhibition of bacterial adhesion can be isolated from bacteria, for example from those pathogenic bacteria that cause infections. Certain plant lectins have similar affinities to those of the specific bacterial lectins involved in adhesion of the bacteria to intestinal epithelial cells and these can also be isolated and used to inhibit bacterial adhesion. On the other hand, lectins themselves may have a major influence on the **turnover** of the intestinal cells and the effect of lectins in relation to infection by pathogenic bacteria depends on the specificity of the lectin as well as its concentration. Thus, dietary lectins can both enhance and reduce colonization by pathogenic bacteria.

In an alternative form of chemical probiosis, bacterial adhesion is inhibited by feeding simple or complex **carbohydrates** that have a terminal structure that closely mimics the carbohydrate side-chains of the bacterial receptors on the gut wall. While dietary lectins actually occupy the same sites as the bacterial adhesins, the complementary saccharides act by competing with them.

Chemical probiosis is an alternative to probiosis by the addition of live bacteria (called **probiotic**s) which also function by a competitive exclusion of pathogenic bacteria. Thus, both methods may help to maintain normal commensal flora (the resident non-pathogenic flora). (SB)
See also: Prebiotic

Chemical score
An evaluation system used to assess the relative value of a single **protein** or mixture of proteins (and **amino acid**s) to be used in a

diet. A value is obtained by assessing the amino acid pattern (usually mg amino acid g^{-1} N) of the protein(s) in relation to an established reference amino acid pattern. This pattern may be developed from the estimated amino acid requirements of the animal in question, or from the pattern of high-quality protein, such as egg protein. The value of a protein is not constant, because amino acid requirements vary with species and with purpose (**maintenance**, **growth**, **milk** or **egg production**). The score is calculated by dividing the amount of each indispensable amino acid in the diet by the amount of the same amino acid in the reference pattern: the score is the lowest of these ratios. For example, if the lowest score is for **lysine** (making it the first limiting amino acid) and the amount of lysine (mg g^{-1} N) in the diet is 80% of that in the reference pattern, the chemical score is 80%. This protein evaluation scheme assumes accurate estimates of the amino acid content of the proteins involved and that dispensable amino acid nitrogen is not limiting. (NJB)

Chemical treatment of feeds Straws,high-moisture **grain**s and forages may be chemically treated when making **hay**, **silage** or alkalage to ensure preservation without deterioration, or to improve **nutritive value**, or both.
Alkali treatment in the form of **sodium** hydroxide, **ammonia** or **urea** has been used on a number of low-quality forages, including straws, husks and hays. It is carried out in an enclosed container and results in an end-product with a pH of 10–11. Alkali reduces the number of **ester** linkages between **lignin** and cell wall

carbohydrates and increases the **digestibility** from *c.* 55% before to 65% after treatment. Urea is also used in the production of alkalage from whole-crop cereals. This product is akin to silage with the exception that it is alkaline and not acidic. The urea preserves the crop by releasing ammonia, which inhibits the activity of undesirable **microorganism**s within the clamp.

Hydrochloric acid, **sulphuric acid** and **formic acid** are used in the preservation of green crops as silage. These inhibit microbial activity within the silo, preserving the **forage** by direct **acidification**.
Recently the longer-chain **organic acid**s (propionic, caproic and acrylic) have been included in acid mixtures to inhibit **yeasts** and moulds associated with the aerobic spoilage of silage. **Propionic acid** is used in the storage of high-moisture **cereal grain**s (moisture content 20–30%) for the same purpose. **Sodium** benzoate is used in the preservation of a variety of feeds for its anti-microbial activity. Sulphites and bisulphites are also used in the preservation of silages. These generate sulphur dioxide, which is toxic to many spoilage microorganisms. *See also*: Alkali treatment, ammonia treatment of straws(DD)

Chestnut
The reddish-brown edible **nut** of sweet chestnut (*Castanea sativa*), primarily harvested for human consumption. When used as animal **feed**, chestnuts may be ground or crushed and made into meals or occasionally pellets. They can be fed to most species of livestock but the level of inclusion for ruminants is limited by the

high **oil** content. Like all nut products, they can be contaminated with **aflatoxin**s and are therefore subject to feed regulations. Treatment may be required to remove such **contamination**. The typical dry matter (DM) content of chestnuts is 920–930 g kg^{-1} and the nutrient composition (g kg^{-1} DM) is **crude protein** 12–16, **neutral detergent fibre** 180, **lignin** 41, **acid detergent fibre** 146, **ether extract** 70, WSC 95 and **starch** 53, with ME 13.7 and **gross energy** 20.6 MJ kg^{-1} DM. (JKM)



Chestnut, the fruit of the sweet chestnut. Photo courtesy of William Warby. Licensed under CC BY 2.0.

Chewing

Chewing or **mastication** of the food is the process of masticating the food in the buccal cavity, which begins the digestive process and facilitates swallowing. Chewing breaks down the food particles, mixes the food with **saliva** and adds the salivary **enzymes**, which start the chemical process of **digestion**, and **pH** buffers, which counteract the acidity in **gastrointestinal tract** that is either an end-product of microbial digestion or is secreted to break down food. Inadequate fibre in the diet is common in managed animal populations, particularly those that are kept intensively in automated facilities. Farmed animals that have been genetically

bred for high productivity are fed high-energy diets, which release **energy** and **protein** quickly to allow for high intakes. These diets usually have low fibre content because it is slow to be digested. There is evidence in a wide variety of species that chewing helps to alleviate **welfare** problems associated with high-energy diets, and hence animals chew if there is adequate fibre in their diet. They may chew the bars of their cages, their bedding or just the air (**sham chewing**). Dogs have a specific need to chew, especially during puppyhood, and cats chew their fur in stressful situations to create fur balls.

A specific form of chewing in **ruminant animal**s is **rumination** behaviour, in which animals regularly regurgitate partially digested **feed**, returning it to the buccal cavity for further mastication before swallowing the bolus again. Also known as 'chewing the cud', this is performed on food boluses that have been regurgitated into the buccal cavity from the **rumen** by a process called reverse **peristalsis**. In this way the food particles can be further comminuted into those that are small enough for digestion by microbes in the rumen. Adequate time spent ruminating is associated with contented ruminant animals. (CJCP)

Chick
A young bird, especially one that has recently hatched. The term is frequently used to describe young birds that are still covered by down and have not yet developed a complete feather cover. (SPR)
See also: Broiler chickens

Chicken Domestic fowl bred for **meat** and/or **eggs**. Chickens

belong to the genus *Gallus* of the family Phasianidae and are commonly classified as *Gallus domesticus*. They are descended primarily from the red junglefowl (*Gallus gallus*) (Lawal *et al*., 2020). Archaeological evidence indicates that they were first domesticated over 5000 years ago in Southeast Asia, possibly as fighting cocks. Following domestication they were brought to Europe and then to Oceania and the Americas. Some hybridization of the domestic chicken with related junglefowl has taken place. For instance, breeders have incorporated a gene from the grey junglefowl (*G. sonneratii*) that results in yellow skin, a feature of meat birds that is preferred in regions such as North America.



Red jungle fowl, from which chickens were domesticated. Photo courtesy of Glenda and Ken. Licensed under CC BY 2.0.

Chickens are uniquely different from other farm livestock in several ways. Their **digestive system** is relatively simple (except for a **gizzard**) and their skeleton light, related probably to an evolutionary need for a light body weight to enable flying. Although light in weight, the skeleton is strong and has many hollow bones that are connected to the respiratory system and aid in **temperature** regulation. In addition chickens possess medullary bone that allows storage of **calcium** deposits, which is particularly important in **laying hens** as a readily available source of calcium

for **eggshell** formation when calcium intake is insufficient.

They have a high rate of **metabolism**, breathe rapidly and have a rapid rate of **digestion**. The absence of **sweat** glands and presence of feathers, comb and wattles aid in the regulation of body temperature, which is higher than in other farm livestock. Application of the knowledge related to these factors allows farmed chickens to be provided with the correct environmental conditions, and an ability to be utilized successfully as a producer of meat and eggs under a range of husbandry conditions worldwide.

Under natural conditions it is usual for a hen to lay a clutch of up to 12 eggs and then to stop laying and incubate the eggs by sitting on them in a nest. At this stage the hens are described as broody. Modern breeds developed for **egg production** have generally lost this ability. While brooding, the hen maintains the nest at a constant temperature and humidity, as well as turning the eggs regularly. Fertile chicken eggs hatch at about 21 days. The hens usually remain on the nest for a few days after the eggs hatch, during which the newly hatched chicks feed by absorbing the internal **yolk sac**. Later the chicks are taught to find food and water.

In commercial production the correct conditions for **incubation** are replicated in artificial incubators. An unfortunate aspect of layer production is that about half of the chicks hatched are unwanted males, which have to be disposed of humanely. Originally these chicks formed the basis of a chicken **meat production** system, which later developed into the broiler industry, i.e. chickens raised exclusively for meat. An active area of

research in the 21st century is to sex eggs from egg-type chickens prior to incubation so that only female eggs hatch.

Chickens are gregarious and usually live together in flocks, with a communal approach to the incubation of eggs and raising of young. It is usual for individual chickens in a flock to dominate others, establishing a '**pecking** order', with dominant individuals having priority to food and nesting locations and birds low in the pecking order being attacked. Removing hens or roosters from a flock causes a temporary disruption to this social order until a new pecking order is established.

Nutrition

Chickens are omnivores and in outdoor conditions scratch at the soil to obtain seeds as well as soil arthropods, earthworms etc. They have a modified gut, in comparison with other non-ruminant species such as pigs or humans. The digestive system is relatively simple, probably due to an evolutionary need for a light body weight related to the ability to fly. The mouth is modified into a narrow, pointed **beak** to facilitate seed-eating, and does not allow for the presence of **teeth** to permit grinding of the feed into smaller particles for swallowing. Instead, mechanical breakdown of feedstuffs is performed mainly by a grinding action in the gizzard (which is attached to the **proventriculus**) and contractions of the muscles of the gastrointestinal walls. The function of the proventriculus is analogous to that of the **stomach** in the pig. Chemical breakdown of the feed particles is achieved by **enzymes** secreted in digestive juices and by gut microflora. The digestive process reduces feed particles to a size and **solubility** that allows

for **absorption** of digested nutrients through the gut wall into the portal **blood** system.

Laying hens

Modern commercial layer production involves two main types of birds: white-egg breeds and brown-egg breeds (*see* Laying hens). White-egg breeds are predominant because most of the eggs consumed worldwide are white. Also, the white-egg layer is a more efficient and prolific **genotype**. Most modern breeds produce over 20 kg of egg mass by 76 weeks of age with a **feed conversion ratio** (FCR, weight of feed/egg mass) of just over 2.0. Brown-egg hens can also produce about 20 kg of egg mass output over the same time period but require more feed to do so. They are typically heavier birds and therefore have a higher **maintenance** requirement. The other consequence of being heavier is that they lay larger eggs; but, as the total mass of egg they lay is similar to that of white birds, they lay fewer eggs. Egg production usually starts at 16–21 weeks of age and is continued for about 12 months when production is low and the birds have to be replaced.

Environmental conditions are often automatically controlled in egg-laying systems. For example, the duration of the lighting phase is initially increased to prompt the beginning of egg-laying at 16–20 weeks of age and then mimics summer day length which stimulates the hens to continue laying eggs all year round. Under these conditions hens can produce over 300 eggs a year.

Broiler chickens

The modern **broiler chicken** industry grew out of the egg

industry. Selective breeding for meat traits, production efficiency and hybrid vigour have taken place, resulting in the commercial bird commonly being a four-way cross. These birds are marketed at around 4–6 weeks of age and weighing around 2 kg, depending on the market in question. Records indicate that due to continued genetic improvement they achieve market weight 1 day sooner each year. Their FCR under barn conditions with controlled environments is high at around 1.5–1.9. An 'all-in, all-out' management system aids in disease control and allows several flocks to be raised consecutively throughout the year.

Bird welfare

Early poultry production was based on backyard flocks of dual-purpose chickens. Later the industry developed into a year-round enterprise with most of the production of eggs and **poultry meat** taking place globally under intensive conditions. However, since the 1980s **welfare** concerns and consumer attitudes have resulted in international regulations being introduced to restrict the use of conventional cages in egg production and to allow chickens access to outdoor conditions. An active area of research is to develop systems that enable chickens to display their natural behaviours such as pecking order, **foraging**, perching and dust-bathing without exposing them to disease and predator risks, feather-pecking, vent-pecking and **cannibalism**. Raising chickens under outdoor conditions results in more expensive eggs and chicken meat, due mainly to a higher amount of feed needed and a lower stocking capacity, and it appears to be supported by consumers. (RB)

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Chickpea

A **legume**, *Cicer ariatinum*, grown primarily for human consumption. The seed varies considerably in colour (from black to beige or white), shape and composition, depending on the cultivar. Chickpeas have been fed to pigs and poultry: they contain about 200 g **protein** kg^{-1}, about 300 g **starch** kg^{-1} and about the same quantity of **non-starch polysaccharide**s. They contain small amounts of **trypsin inhibitor**s. They also contain **tannins**, at low concentrations in the light-coloured varieties; black cultivars contain about 2 g kg^{-1}. Such low levels would be unlikely to cause detrimental effects in animals. The apparent **metabolizable energy** for poultry is about 12 MJ kg^{-1} and that for ruminants about 14 MJ kg^{-1}. Chickpeas are reported to contain phyto-**oestrogen**s. (TA)

Chicory

A Mediterranean herb (*Cichorium intybus*) of the family Asteraceae. It is a hardy plant, the roots of which are used in

coffee substitutes and blends. The curled dandelion-like greens are used as potherbs, and true endive (*C. endivia*) is grown for salad. **Forage** chicory is grown in New Zealand and more recently in the USA for feeding to ruminants. Forage chicory is a perennial plant, producing leafy growth, which is higher in nutrient and **mineral** contents than **lucerne** (**alfalfa**) or temperate **grasses**. Having a taproot, it is **drought** tolerant but it can be damaged by overgrazing and frost. Chicory pastures have a lifespan of 5–7 years and yield 7.5–15 t ha^{-1} under **rotational grazing**, provided that they are maintained with a minimum stubble height of 38–50 mm and given rest periods of 25–30 days. The **digestibility** of forage chicory leaves is 90–95% with a **protein** level of between 100 and 320 g kg^{-1} **dry matter**, depending on plant **maturity**. (JKM)

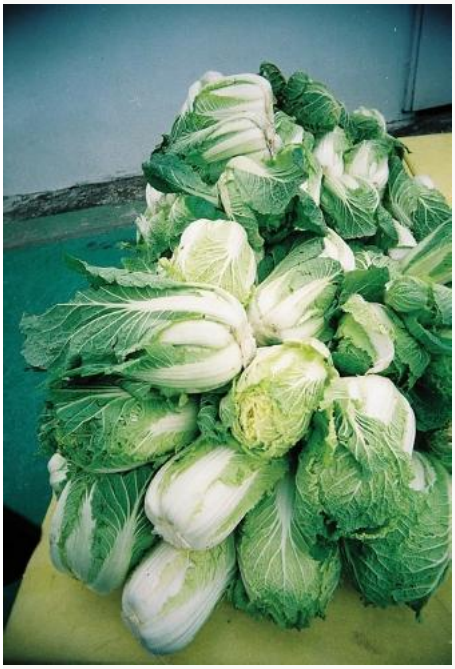


Wild chicory. Photo courtesy of J. van Cise. Licensed under CC BY 2.0.

Chinese cabbage

Brassica rapa (subspecies *pekinensis* and *chinensis*), also known as celery cabbage, pak-choi, pe-tsai and wong bok. It has a mild flavour similar to that of **celery**. Chinese cabbage is more closely

related to **turnip** and **swede** than to other varieties of **cabbage**, its leaves being thinner and more delicate than cabbage leaves. Cultivation practices are the same as for regular cabbage but Chinese cabbage matures faster and may be ready in as little as 60–65 days after sowing. It is used fresh in salads or cooked like regular cabbage and may become available for animal feed due to either oversupply or inferior quality. It is suitable for ruminants and can be fed to dairy and beef cattle at 30% and to ewes at 20% of their total diets. The dry matter (DM) content of Chinese cabbage is 90–110 g kg^{-1} and the nutrient composition (g kg^{-1} DM) is **crude protein** 210–230, **crude fibre** 100–120, **ether extract** 17–20, **ash** 105–115 and **neutral detergent fibre** 275–285, with MER 11.5 MJ kg^{-1}. (JKM)



Chinese cabbage. Photo courtesy of Film forever. Licensed under CC BY-ND 2.0.

Chinese mitten crab (*Eriocheir sinensis*)

Over the past decades, the Chinese mitten crab, *Eriocheir sinensis*,

has rapidly become an important **aquaculture** species in China (Zhang and Li, 2002; Yang and Zhang, 2005). Because of its high **meat yield**, delicate flavour and high nutritional value, market demand and price for the crab have been very high in China (Chen *et al*., 2007). With the decline in natural resources and a breakthrough in artificial **reproduction**, *E. sinensis* cultivation began in 1980s. Since then, the *E. sinensis* cultivation industry has increased rapidly in response to growing demand in international and domestic markets. The yield of cultivated *E. sinensis* reached up to 757,000 t (8.1% of cultural crustaceans) in the world in 2018.



Chinese mitten crab. Photo courtesy of Bj. Schoenmakers. Licensed under CC0 1.0.

The technology of raising crabs in **rice** fields assists the planting, breeding and ecological functions of the rice fields, and opens up new ways for the sustainable development of rice and aquatic products. Crab farming in rice paddies can pollute the water body, but the combined effect can have a certain purification effect on the water body (Sun *et al*., 2014). Rice provides a favourable living environment for crabs; the crabs prey on weeds and pests, reducing the incidence of field diseases (Zhao *et al*., 2018). The manure produced by the crabs provides fertilizer for

rice and promotes the growth of rice. In recent years, with the development of eco-agriculture, rice–crab breeding has become an effective agricultural production and income-increasing model, and hence rice–crab farming has developed rapidly in China. (QS)

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Chitin

A linear **polysaccharide** chain of β(1→4)-linked *N*-acetyl-D-glucosamine $(C_8H_{13}NO_5)_n$ units. It is similar in structure to **cellulose**, but the C-2 hydroxyl group is replaced with an acetylated amino group. Upon acid **hydrolysis**, chitin yields glucosamine and acetic acid. It is insoluble in water, dilute acids or bases and is resistant to bacterial hydrolysis. It is a major constituent of the exoskeleton of crustaceans (crabs, **lobster**s etc.),

insects and spiders, comprising 20% of their **gross energy**, and is also found in some **fungi**, **algae** and **yeasts**. In animal **feed**, if undigested, it represents a major loss of energy and can reduce **nutrient digestibility**. This may be due to its ability to bind water, **bile** and **fatty acid**s. **Chitinase** activity, and hence chitin **digestibility**, varies between **fish** species (Krogdahl *et al*., 2005), being low in salmonids (Olsen *et al*., 2006). Chitin reduces nutrient digestibility and growth in **rainbow trout**, hybrid **tilapia**, *Oreochromis niloticus* × *Oreochromis aureus* and **Atlantic salmon** (Olsen *et al*., 2006). Chitin has immunostimulatory activity in some aquatic species. (TDC; QS)

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Chitinase

An **enzyme** that liberates *N*-acetyl-D-glucosamine from **chitin**. Chitinase is produced in the gastric **mucosa** as well as by the enteric microflora. An industrial preparation of chitinase (chitodextrinase; poly(1→4-α-(2-acetamido-2-deoxy-D-**glucoside**)) glycanohydrolase; EC 3.2.1.14) is purified

from *Streptomyces griseus*. (SB)

Chitosan
Deacetylated chitin, i.e. a polymer of D-glucosamine rather than of *N*-acetyl-D-glucosamine. In **feed** ingredient analysis, chitosan is classified as **dietary fibre**, isolated with the **acid detergent fibre** fraction. In the **digesta** it is positively charged and mimics cholestryamine in sequestering **cholesterol** and other **bile** acids. (TDC)

Chlorella
A single-celled freshwater blue alga, which ranges from 2 to 8 μm in diameter, with an unusually high content of **chlorophyll**. Chlorella completes its reproductive cycle in 17–24 h and is rich in **protein**, **vitamins**, **minerals** and other bioactive substances, including compounds referred to as 'chlorella **growth factor**'. It is used as a **feed** for **fish larvae** and in nutritional **supplement**s for humans. (SPL)

Chloride
The ion of the inorganic element chlorine. It is required by living systems, and in **metabolism** is usually found as a counter anion to the cations **sodium** and **potassium**. The distribution of chloride between extracellular and intracellular fluid varies with the tissue. For example, the extracellular concentration relative to the intracellular concentration in neurons is 13, in **skeletal muscle** 31, but in cerebrospinal fluid only 1.14. In regard to plasma osmotic pressure (290 mOsm), chloride is the major anion to counter

sodium. The other significant anion is **bicarbonate**. In renal function, the reabsorption of sodium and chloride plays a major role in body **electrolyte** and water metabolism. **Laboratory animal**s fed chloride-deficient diets respond within hours by markedly reducing urinary excretion of chloride. Poor **growth** and reduced efficiency of **feed** utilization (gain/feed) are seen within weeks of feeding a deficient diet. However, a chloride deficiency is not expected under normal feeding conditions. (NJB)

Chlorophyll

A generic name applied to plant pigments involved in photosynthesis. The chlorophylls trap **light** energy and direct it through chemical reactions to the production of ATP. Chlorophyll-*a* is a **magnesium**-containing porphyrin and is the major chlorophyll in **algae** and higher plants: it absorbs light at wavelengths of 400–450 nm and 640–680 nm. Chlorophyll-*b* absorbs light at wavelengths of 430–500 nm and 640–700 nm. Both absorb essentially no light at wavelengths of 450–600 nm. Thus, green light passes through the tissue, giving plants their characteristic colour. (NJB)

Choice feeding

The provision of two or more types of food, either simultaneously or sequentially, in order to investigate feeding preferences or specific **appetites**, or allow self-adjustment of nutrient intake to meet specific requirements of individual animals. Selection of specific food items may be on the basis of **taste**/flavour, learned behaviour or a metabolic response to one or more nutrients in the

ingested food, while the selection of sources of certain mineral elements such as **salt** (**sodium**), **calcium** and **phosphorus** may be part of a more innate control (specific appetite) to prevent deficiencies. Information gained from such choice feeding studies can be used to develop feeding programmes for food-producing livestock and poultry, as well as animals in zoos and other confinement environments.

Specific appetites

Under natural conditions, herbivorous and omnivorous animals usually select their (balanced) diets from potential food supplies that vary greatly in terms of their nutritional contents. Such selection involves meeting specific requirements for particular nutrients, based on 'specific appetites' for those nutrients. Evidence for specific appetites can be obtained in a two-choice situation, either by offering the nutrient concerned in one position and an otherwise balanced diet that is lacking that nutrient in another position, or by offering two versions of the same diet that are sufficient and deficient in the nutrient concerned. Alternatively, soluble nutrients can be provided in drinking water, and subjects eating a diet deficient in such a nutrient can be given a choice between water with and without that nutrient. Specific appetites may be in response to a short-term demand, as for example the demand for dietary calcium for **eggshell** formation when an **egg** enters the shell gland of a **laying hen**. This has been demonstrated by offering hens a choice between a low-calcium diet and a separate calcium source such as **oyster shell**. Other specific appetites may be in response to a long-term demand, as for

example when physiological requirements change prior to an annual breeding season, or when an animal is suffering from a long-term deficiency in a particular nutrient. Thus, some specific appetites have been demonstrated experimentally by feeding subjects on a diet deficient in the nutrient concerned for a week or so before the choice trial. Most appetites are learned and it may take many days for subjects to arrive at a balance between the foods on offer that is sufficient to meet the requirement. In **domestic fowl**, specific appetites have been demonstrated for three minerals (calcium, **zinc** and phosphorus), one **vitamin** (**thiamine**), **protein** in general and two specific **amino acid**s (**methionine** and **lysine**). In addition, heat-stressed fowls have been shown to develop an apparent (learned) specific appetite for **vitamin C**, which is known to alleviate the consequences of **heat stress**. In other words, these birds learned that they felt better when they ate more of the vitamin C-supplemented food.

Choice trials need to be designed carefully, with adequate **sample** sizes, for the following reasons.

1. Individual variation. Unless a preference or avoidance is very marked (for example, rejection of food or water tainted with a bitter substance such as quinine), there is great individual variation in preference. Hence, large numbers of animals are needed to demonstrate a difference.
2. Positional preference. Animals can learn to associate differences in food composition with the position in their pen of the food containers. The position of foods offered should be represented equally in all positions, and positions should not be switched for

any particular animal even if the foods are easily distinguished by other means, e.g. colour or flavour. To allow for social influences on choice, animals should be far enough apart for a neighbour's presence not to interfere with the subject's choice.

3. Colour and flavour preference. An obvious way to enhance a food's identity is to flavour or colour it uniquely. Although some animals have inherent flavour or colour preferences, these are easily overridden by the relative nutritional value of the foods. However, if the food preference itself is weak and if novel flavours or colours are aversive to some animals (because of neophobia) more than others, it is important to use colours that are easily distinguished by the subjects, for which there are no marked preference or avoidance, and to distribute the colours equally among the foods being offered. Generally speaking, mammals learn to use food flavours more readily than colours as cues to **nutritive value**, while with birds the reverse is true.
4. Feeding preferences. Animals demonstrate neophobia – a fear of new things – and this applies to foods. Preference or avoidance of particular foods may be apparent in the short term, perhaps because of some novelty effect, without being so in the longer term. Just because one food is eaten in greater quantities than the other does not mean that the second is less palatable, simply that to make a balanced diet the animal should eat less of the second. The term '**palatability**' is frequently, but wrongly, taken to be a property of a food, when in fact it is a property of the food, the animal, and the animal's previous experience of eating this, or similar, foods.

Regulation of food intake

Poultry

Although the **chicken** has relatively few taste buds and does not possess a highly developed sense of smell, it is able to discriminate between certain food sources on the basis of colour, taste or flavour, when a choice is available. As shown by Dove (1935) (see Table 1), birds possess some degree of '**nutritional wisdom**' which allows them to select from the various **feed** ingredients offered and construct their own diet according to their individual needs and production capacity. Discriminating between nutritious and harmful feeds is learned differently in birds than in mammals since chicks are not fed directly by the parents. This learning process is assisted in traditional production systems involving natural rearing, by the presence of the parent birds during the early life of the **chick**. Birds appear to rely to a large extent on visual appearance in selecting various feedstuffs, refusal or acceptance of food on its first introduction being determined by colour and general appearance (El Boushy and van der Poel, 2000). According to the evidence reviewed by the latter authors, chickens preferred yellow-white **maize** followed by yellow, orange and finally orange-red maize. Red, red-blue and blue seeds were eaten only when the birds were very hungry. Preference tests showed also that less was eaten of black and green diets. Some of the research indicated that chicks show a preference for diets of the same colour as that fed after hatching. Colour is important also in teaching birds to avoid feeds that produce illness after ingestion. The review cited above indicates that birds possess a keen sense of taste and can

discriminate between feeds on the basis of sweet, salt, sour and bitter. **Rancidity** and staleness have been shown to reduce intake of feed. However, there appear to be genetic differences in taste discrimination among poultry species. The finding that **sucrose** in solution appears to be the only **sugar** for which chickens have a preference may be of use in helping to prevent 'starve-outs' in baby chicks or to help birds during disease outbreaks or periods of stress. Current evidence suggests that most flavours added to poultry feed are ineffective in stimulating intake of feed. A sense of smell is probably less important in birds than in mammals, birds lacking the behaviour of sniffing. Other factors identified by El Boushy and van der Poel (2000) as being involved in control of **feed intake** include **temperature**, **viscosity**, osmotic pressure of water, salivary production, **nutritive value** of feed and toxicity of feed components.

Table 1. Dietary self-selection by chicks and effect on nutrient intake (Dove, 1935).

Feed ingredient offered	Intake (% of total)	Nutrient content of selected dietary mixture	NRC estimated requirements (1994)
Yellow maize	52.8	Crude protein 179 g kg^{-1}	180 g kg^{-1}
Oat meal	8.9	ME 2729 kcal kg^{-1}	2880 kcal kg^{-1}

Feed ingredient offered	Intake (% of total)	Nutrient content of selected dietary mixture	NRC estimated requirements (1994)
Wheat bran	21.3	Calcium 13 g kg^{-1}	9.0 g kg^{-1}
Fish meal	11.4	Phosphorus 11 g kg^{-1}	4.0 non-phytate P
Bone meal	2.9		
Dried skimmed milk	2.1		
Oyster shell	0.6		

As noted above, birds have been shown to possess some degree of 'nutritional wisdom' or 'specific appetites', eating less of diets that are inadequate in nutrient content (see Table 2). Laying stock have the ability to regulate feed intake according to the **energy** level of the diet; therefore, it is important to adjust the concentration of other nutrients in relation to energy level when intake is affected. Modern broiler stocks appear to have lost the ability to regulate intake according to dietary energy level, which means that breeding stock have to be fed rationed amounts. Broilers, on the other hand, appear to have a greater ability than laying stock to select feeds that result in a balanced intake of protein when presented with a variety of feeds (Forbes and

Shariatmadari, 1994). Use can be made of this information in planning choice-feeding systems for poultry. The findings reviewed by El Boushy and van der Poel (2000) indicated that **wheat** and **sunflower** seeds, polished **rice**, cooked potatoes, **potato** flakes and fresh **fish** are very palatable feedstuffs. **Oats**, **rye**, rough rice, **buckwheat** and **barley** are less palatable, unless ground. **Linseed** meal appears to be very unpalatable. Among the physical factors affecting feed intake is **particle size**. For instance, it has been shown that feed particles are selected by broilers on the basis of size (El Boushy and van der Poel, 2000), intake being greatest with particles of 1.18–2.36 mm. As the birds aged the preference was for particles greater than 2.36 mm. Social interaction is another factor influencing intake, chicks being known to eat more in a group situation.

Table 2. Estimated feed savings by adopting choice feeding with laying hens (from Henuk and Dingle, 2002).

Reference	Conventional diet (g per hen per day)	Choice feeding (g per hen per day)	Saving in feed intake (%)
Henuk *et al.* (2000b)	123.8	120.3	2.9
Blair *et al.* (1973)	116.2	108.9	6.7
Leeson and Summers (1978)	114.4	107.2	6.7

Reference	Conventional diet (g per hen per day)	Choice feeding (g per hen per day)	Saving in feed intake (%)
Leeson and Summers (1979)	118.4	110.7	7.0
Henuk *et al.* (2000a)	126.5	114.6	10.4
Karunajeewa (1978)	132.5	118.5	11.8

Pigs

Studies on the ability of growing pigs to select a balanced diet have concentrated mainly on energy and protein, with the aim of optimizing growth rate and carcass leanness. For instance, Henry (1985) showed that voluntary feed and **energy intake**s were dependent mainly on energy concentration of the diet, intake being adjusted to allow the pig to maintain its **energy requirement**, although the level of energy intake declines slightly as energy concentration decreases. This was explained by a progressive limitation of gut capacity before energy demand is met, as diet bulkiness becomes more important. A further modulation of feed intake was provided by changes in the ratio of protein (or **amino acid**) to energy around the optimum level for growth. A liberal protein supply allows a self-limitation of feed consumption in the pig, with a resulting beneficial effect on carcass leanness, while a marginal deficiency in the limiting amino acid or total protein

supply induces a compensatory increase in feed intake to meet more closely the corresponding requirement, but at the expense of increased carcass fatness. These findings indicated that continued genetic improvement for lean **meat production** should allow more liberal feeding than very restricted feeding in the later **stages of growth**, with a progressive move to feeding relatively high-energy diets (balanced correctly for protein and amino acids) to appetite without adverse effects on carcass quality.

Further data on the ability of growing pigs to select a balanced diet were provided by Kyriazakis *et al*. (1990). Four diets (L, A, B and H) with similar energy content, but different concentrations of **crude protein** (125, 174, 213 and 267 g CP kg^{-1} air-dry basis, respectively) were formulated. The four diets were offered *ad libitum* either singly or as a two-way choice using all the six possible pairs, to individually caged pigs from 12 to 30 kg **liveweight**. Food intake fell from 1001 to 971 to 961 to 868 g per day ($P < 0{\cdot}05$) as the protein concentration of the foods increased from L to H. Growth rate followed an opposite trend (492, 627, 743 and 693 g per day respectively, $P < 0.01$). When the pigs had to select between two diets limiting in protein (L and A), the less limiting one was preferred; and when the choice was between the diet adequate in protein or containing an excess of protein (B or H), the lower-protein diet was preferred. When the pigs were given a choice between two diets, a combination of which was non-limiting (pairs LB, LH, AB and AH), the protein concentrations of the selected diets were not different between treatments (208, 204, 202 and 205 g CP kg^{-1} respectively) and they also declined

systematically with time and weight. The growth rate of the animals on these pairs was 752, 768, 769 and 763 g per day ($P > 0.05$), which were not significantly different from the highest growth rate achieved on a single diet. The results suggest that growing pigs, when given a choice between a suitable pair of foods, are able to choose a balanced diet and to alter its composition to reflect their changing requirements.

Research has also been conducted on the preferences of growing pigs for certain feed ingredients, particularly with a view to enhancing the voluntary intake of pigs just after **weaning** when appetite for solid food is low and there is commonly a growth lag. For instance, Solà-Oriol *et al*. (2009) conducted a series of experiments to investigate the preferences of weaned pigs for 15 **protein source**s, six fat sources, and three fibre sources, in relation to **soybean** meal, sunflower oil and wheat **bran**. Preference was affected by feedstuff type and by its inclusion rate in the diet. At practical levels of inclusion, it was found that soybean meal containing 440 g CP kg^{-1} was preferred over soybean meal containing 480 g CP kg^{-1}, sunflower **meal** or rapeseed meal; no distinct preference was found between extruded soybeans and **lupin** seed; soybean protein was preferred over wheat **gluten** or potato protein; fish meal and dried porcine plasma were preferred over spray-dried porcine plasma; and **dried skimmed milk** and sweet milk **whey** were preferred over acid milk whey. Storage for 10 months prior to usage had a negative effect on preference, particularly for potato protein. The results also showed that the diet containing palm **oil** was preferred over the reference diet, and

that the diets containing **linseed** oil or soybean oil were avoided; also that the pigs had a higher preference for the diet containing **carob bean** meal as a fibre source and lower preference for the diets containing dehydrated **lucerne** and **sugarbeet** pulp. This research group also studied the preferences for **cereal** types in relation to a reference diet based on white broken rice as the cereal source. Results showed that extruded rice, naked (dehulled) and extruded naked oats were preferred over other cereal grains when included in **mash** diets. Barley had a higher preference when the diet was pelleted. A related area of research has been the use of **sucrose** or human high-intensity sweeteners, particularly saccharin as appetite enhancers in young pigs (Roura and Fu, 2017). Another aim of this research was to test the hypothesis that the pig might be a suitable model of the human in its taste responses to certain dietary components. One of the main findings of this research was the limited perception of human high-intensity sweeteners by pigs. It was also shown that a long-term exposure to sucrose and **maltodextrin**s reduced feed intake and increased innate preferences for protein solutions.

The taste system in pigs is now known to be very complex, involving a relatively large tongue and one of the highest number of taste buds (n = 19,904) in mammalian species (Roura and Fu, 2017). Findings reviewed by these authors indicate that a network of chemosensory cells in the tongue, gut and brain appears to mediate the hormonal responses controlling the **hunger–satiety** cycle. Dietary essential **amino acid**s (e.g. Lys, Met, Trp and Thr) have also been shown to be important drivers of food selection and

intake in pigs. In addition, glutamic acid has been reported to enhance feed intake in young pigs. However, the long-term effect of sugars, amino acids and **fatty acid**s on feed intake in pigs remains unclear. In particular, the effect of excess nutrients such as amino acids in the diet has received little or no attention in relation to food preferences, according to this review.

The commercial application of the findings on food preferences in pigs appears to be different from that in poultry. Whereas a practical application of the data in **poultry feeding** has been to devise systems that allow the birds to make appropriate food choices, the main application of the pig data has been to allow a nutritionist in collaboration with the farmer to formulate appropriate diets and feeding systems that result in the optimal intake of food, particularly at a critical stage such as **weaning** time.

Ruminants

Although the published data on choice feeding by ruminants is not as extensive as for poultry or pigs, there is evidence that ruminants are capable of selecting from a range of feedstuffs in order to ingest a balanced diet. For instance, Atwood *et al*. (2001) compared the intake and growth performance of beef calves offered a choice or no choice among foods. Diets consisted of *ad libitum* access to either a chopped, mixed diet of rolled barley (31.3%), rolled maize (31.3%), maize **silage** (15.5%) and lucerne **hay** (18.9%) or a choice among those feedstuffs offered individually. During the first week of the trial, cattle that selected their own diets ate more than animals fed the mixed diet, attributed to their ability to choose

from a variety of ingredients with different flavours and nutrient contents. However, for the remainder of the trial, animals offered a choice tended to eat less than animals offered a mixed diet (102 vs. 109 kg DM per day) and rate of gain was similar on both feeding regimes (0.89 vs. 0.92 kg per day, respectively). Throughout the trial, no two animals consistently chose the same ingredients, and none selected a diet similar to the nutritionally balanced mixed ration, yet each animal ate a diet adequate to meet its needs. No difference in the ratios of protein to energy ingested (43 vs. 43 g CP $Mcal^{-1}$ ME) was found, but a preference for foods high in energy or protein varied markedly for animals fed free-choice. On day 2 the ratios of protein:energy intakes were equal, on day 21 the ratios were higher than those of animals fed the mixed diet, and on day 40 the ratios were lower than those of animals fed the mixed diet. On the basis of these findings the researchers suggested that: (i) animals can more efficiently meet their individual needs for **macronutrient**s when offered a choice among dietary ingredients than when fed a single diet, even though it is nutritionally balanced; (ii) transient food aversions compound the inefficiency of a single mixed diet by depressing intake even among animals suited to that nutritional profile; and (iii) alternative feeding practices may allow producers to capitalize efficiently on the agency of animals, thus reducing illness and improving performance. The researchers concluded that while research findings and management recommendations typically emphasize responses of the 'average' individual, more than half of the animals in a group may differ significantly from the mean regarding food

preference and intake. The productivity of a herd may be adversely affected if animals differing from the mean are fed a uniform diet formulated to meet the needs of the 'average' individual, emphasizing the beneficial effects of an appropriate choice feeding system.

Grazing

ruminants have also been shown to demonstrate choice **feeding behaviour** (e.g. Soder *et al*., 2009). It is generally accepted that sheep and cattle have evolved behaviours that enabled them to select a diet that met their individual nutrient requirements whilst minimizing the risk of death from predation or by the ingestion of toxins. Grazing on **grass** monocultures or feeding total mixed diets restrict the ability of the animals to select their own diet. Research has shown that grazing sheep and cattle have a partial preference for clover (when offered as a monoculture sward alongside grass), with a consistent diurnal pattern of preference. Factors related to choice appear to include: (i) maintenance of a diverse **rumen** microflora; (ii) maintenance of some optimal carbon/**nitrogen balance** or ratio of rewards with type of foodstuff in the diet; (iii) avoidance of toxic consequences of ingestion of one dietary component to excess; (iv) avoidance of grazing at night due to a perceived risk of predation; (v) constant sampling and evaluation of familiar foods in familiar environments, since nutrient content and toxicity may vary with time; and (vi) resource depletion, which results in a trade-off between remaining at a patch and consuming less desirable species or plant parts, or moving on to a fresh patch of more preferred

species or plant parts. The consistent preference of cows and sheep for a diet containing approximately 50–70% white clover (*Trifolium repens*) has been shown to follow a distinct diurnal pattern, with clover being preferred in the morning and an increasing preference for grass such as perennial ryegrass (*Lolium perenne*) in the afternoon. The explanations suggested for this selection pattern were that: (i) grazing ruminants may increase consumption of grasses in the evening due to the higher fibre content to maintain ruminal fill overnight; (ii) the increasing sugar content of grasses throughout the day makes them more palatable in the afternoon than in the morning; and (iii) **legumes** are easier to masticate and digest, thereby clearing the rumen faster. It was also concluded that selective grazing behaviour not only depends on sward heterogeneity, but also on changes in the sward as it is defoliated, and on the nutritional status of the animal. Daily herbage and nutrient intake results from multiple grazing bouts; therefore, animals may integrate nutritional information from past, present and expected future bouts in order to optimize daily nutrient intake.

According to Ginane *et al*. (2011), **taste** is one of the five senses that provide ruminants and other animals an awareness of their environment, especially for food selection. The sense of taste, which recognizes sweet, bitter, salty, sour and umami basic tastes, is often considered of paramount importance as it is the last sense in use before foods are swallowed. It thus plays a fundamental biological role in assisting animals to regulate intake of suitable food and reject unsuitable food. Studies of the organization and

functioning of the anatomical and neurological structures responsible for the perception of taste in ruminants have shown that sheep, cattle and goats have lingual receptors for all five basic tastes. However, these studies have mainly focused on the sweet and bitter tastes. They have shown in particular that cows have fewer genes coding for the bitter receptors than other mammals, making them more tolerant to this taste. This pattern has been linked to the differences in the range of toxins and in the occurrence of bitterness encountered by different species in their environment. Studies of **ruminant feeding** behaviour have shown that the taste factor inducing the greatest consensus in preferences is the umami taste, with a high positive hedonic value. The bitter taste seems to have a rather negative hedonic value, the salty taste either a positive or a negative one depending on body needs, while the sweet taste seems to have a positive value in cattle and goats but not in sheep. Finally, the hedonic value of the sour taste is uncertain. Besides the hedonic value, the animal may assign a signal value to the tastes. In ruminants, the distinct preference for the umami taste, the need-dependent preference for the salty taste, and the reluctance of sheep to associate a positive reward with the bitter taste suggest that these tastes appear to be related to the dietary presence of proteins, minerals and toxins, respectively. Salt (NaCl) is generally not found in feedstuffs at levels sufficient to meet the needs of cattle and a supplement is necessary. Cattle like salt and will seek it out if it is not readily available. The preferred method of feeding salt is to include it in concentrate mixtures or complete feeds at about 0.5% of the total dietary dry matter for

lactating cows and at 0.25% for dry cows and other non-lactating cattle. Allowing free access to salt lick blocks is a practical way of meeting the requirement of cattle not receiving concentrates. It is common to include all required minerals in the block to prevent deficiencies in the **forage** grazed, and to include an attractant such as **molasses** to mask the undesirable taste/flavour of certain mineral components. Overconsumption of the lick can be prevented by increasing the level of salt in the mixture.

Physical factors related to intake control in ruminants have been shown to be rumen fill, **dietary fibre** concentration and fibre **digestibility**. NDF intake is regarded as a reliable predictor of DM intake and **milk** production in dairy cows.

Humans

Humans possess the same five senses relating to food selection as livestock, to the extent that the dairy cow has been proposed as a model of the human. Therefore, it might be expected that a highly evolved and intelligent species such as humans with access to an extensive range of foods would consume optimal diets. However, that is not the case in many countries, the opposite being more likely. For instance, **obesity** has reached epidemic proportions in several countries. According to the World Health Organization (Kopp, 2020), overweight and obesity remain the leading causes for premature death worldwide. The explanation appears to be that factors other than the basic biological control mechanisms relating to food choice are more important in some humans, to the detriment of their diet. The Pan-European Survey of Consumer Attitudes to Food, Nutrition and Health (EUFIC, 2006) found that

the top five influences on food choice in 15 European member states were 'quality/freshness' (74%), 'price' (43%), 'taste' (38%), 'trying to eat healthy' (32%) and 'what my family wants to eat' (29%). These were average figures obtained by grouping 15 European member states results, which differed significantly from country to country. In the USA the following order of factors affecting food choices has been reported as: taste, cost, nutrition, convenience and weight concerns. The challenge facing many countries in the 21st century is how to alter consumer food choice in a positive way and reduce the incidence of obesity and other food-related diseases, such as type-2 diabetes. (RB; JSav; JMF)

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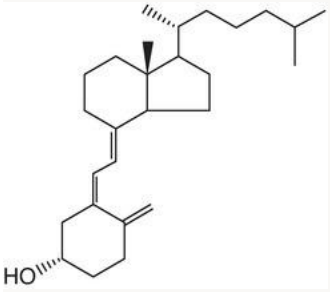
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Cholecalciferol

A specific form of **vitamin D**, namely vitamin D_3. This form of vitamin D possesses the **cholesterol** side-chain, hence the prefix 'chole' on **calciferol**. It has the structure shown here:



It is the form of vitamin D manufactured in skin by ultraviolet irradiation and is thus considered the natural form of vitamin D. Cholecalciferol is biologically inactive until it is hydroxylated in the liver to 25-hydroxyvitamin D_3, producing the blood form of vitamin D_3. This compound must then be further hydroxylated in the 1α-position in the kidney to produce the final vitamin D **hormone**, 1α,25-dihydroxycholecalciferol (trivial name: **calcitriol**). This hormone derived from vitamin D stimulates the **enterocyte**s of the **small intestine** to absorb **calcium** and **phosphorus** into the plasma from the intestine. Together with **parathyroid** hormone it causes the mobilization of calcium from bone and causes renal reabsorption of calcium in the distal tubules of the kidney, resulting in a rise in serum calcium in the blood to normal levels. Cholecalciferol, therefore, is the building block from which the vitamin D endocrine system is constructed. Production of the 1α,25-dihydroxycholecalciferol in the kidney is dictated by either a drop in serum calcium or a drop in serum phosphorus. The drop in serum calcium triggers the parathyroid gland to secrete parathyroid hormone that turns on the **enzyme** in the kidney to

produce the active hormone from vitamin D, i.e. 1α,25-dihydroxycholecalciferol. This major hormone causes the elevation of plasma calcium and phosphorus to normal levels that then suppress further production of parathyroid hormone.

The daily requirement of cholecalciferol for humans is 10 μg or 400 IU. This amount can be produced by 10 min of ultraviolet irradiation of hands and face by summer sunlight in northern hemispheres. A similar production of vitamin D_3 in farm animals can be expected. However, in modern production methods, exposure to sunlight is limited and **supplementation** is recommended. It is necessary to supplement the diets of poultry with 10–20 μg kg^{-1} of diet to prevent a deficiency of vitamin D; and supplementation of diets for cattle, pigs and sheep is also recommended.

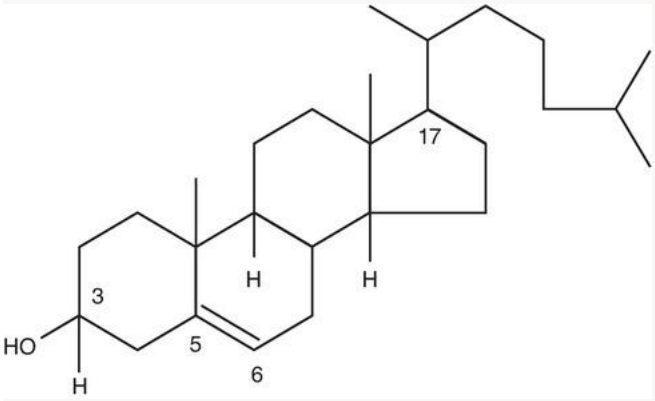
Through its active hormonal form, vitamin D has many functions beyond the elevation of plasma calcium and phosphorus. It is believed to function in the immune system, in the islet cells of the **pancreas**, in the parathyroid glands to suppress the parathyroid gene, and parathyroid gland proliferation. It also is believed to function in the keratinocytes of skin and should, therefore, be considered more broadly than simply a substance that prevents rickets in children and osteomalacia in the adult. A deficiency of vitamin D results in low plasma calcium and low plasma phosphorus. In children it causes the disease rickets, which is characterized by failure of calcification of the organic matrix of bone, resulting in deformities characteristic of the disease. In adults, the deficiency disease is called osteomalacia. (HFDeL)

Cholecalciferol derivatives
Compounds that possess the basic structure of vitamin D_3 but have chemical modifications such as an **acetate** on carbon 3 (cholecalciferol 3-acetate) or a hydroxyl group on the 25-carbon (25-hydroxycholecalciferol) or a hydroxyl on carbon 1 and a hydroxyl on carbon 25 (1α,25-dihydroxycholecalciferol). The acetate increases **lipid** solubility and stability. The hydroxyl groups increase biological activity. (HFDeL)

Cholecystokinin (CCK)
A polypeptide hormone that stimulates **enzyme** secretion from the **pancreas**. CCK is produced in endocrine cells in the **small intestine**, mainly in the **duodenum**, where arriving peptides and lipids stimulate its secretion into the blood, which in turn stimulates the pancreatic secretion of proteases and **lipases**. (SB)

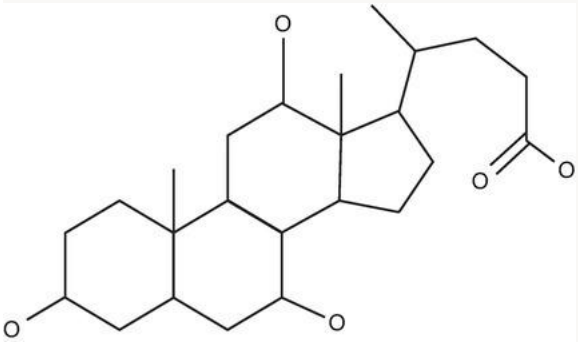
Cholesterol
A neutral **lipid**, $C_{27}H_{45}OH$, and the principal **sterol** of higher animals. It is found in all body tissues, associated with lipids and membranes, in the plasma membrane as well as in intracellular membranes such as those of the Golgi and mitochondria of cells. It is synthesized in the body entirely from acetyl-CoA and is the precursor of all other steroids in the body, e.g. corticosteroids, sex **hormone**s, **bile** acids and **vitamin D**. In the **liver**, cholesterol synthesis is responsive to dietary cholesterol such that synthesis is decreased when dietary levels are elevated. Cholesterol is in low-density (LDL), intermediate-density, high-density (HDL) and **very low-density lipoprotein** particles. It is delivered to tissues by

LDL and removed from tissues by HDL. Cholesterol is excreted from the liver in bile as cholesterol and as the bile salts taurocholic acid and **glycocholic acid**. (NJB)



Cholic acid

A primary **bile** acid, $C_{24}H_{40}O_5$, usually conjugated with **glycine** or **taurine**. It is synthesized in the **liver** from **cholesterol** in a **vitamin C**-dependent step. Because bile is usually alkaline, the carboxyl carbon is negatively charged and cholate is found in bile as the **sodium** or **potassium** salt. (NJB)



Choline

An organic base, $(CH_3)_3{\cdot}N^+{\cdot}CH_2{\cdot}COH$. A major source of choline is the **phospholipid** fraction of seed **oils**, **eggs** and **animal fat**. In **metabolism** it can be directly incorporated into diacylglycerol to form **phosphatidylcholine** (**lecithin**) as cytidine diphosphate

choline. Phosphatidylcholine can also be formed by **methylation** of **phosphatidylethanolamine**, three methyl groups being added by ***S*-adenosylmethionine**. Phosphatidylcholine is a critical constituent of cellular and subcellular membranes. When both **fatty acid**s of phosphatidylcholine are **palmitic acid**, it is a surfactant and plays an important role in the development of neonatal lung function. As **acetylcholine**, it is involved in nerve transmission. Choline can be oxidized to **betaine aldehyde** and then to betaine and is thus a source of the methyl group used in the methylation of L-**homocysteine** to form L-**methionine**. The other two methyl carbons of betaine become one-carbon sources (potential methyl sources) via the **folate** system. (NJB)

Cholinergic mechanisms
The actions of one portion of the autonomic nervous system. Cholinergic neurons innervate **sweat** glands, blood vessels and **skeletal muscles**. Stimulation of these nerves results in vasodilation. In general, cholinergic mechanisms are counteracted by the noradrenergic system which releases **catecholamines**. (NJB)

Chondrocyte
A mature, differentiated chondroblast cell embedded in a cartilaginous matrix, similar to the osteocyte (mature **osteoblast** cell). In the epiphyseal **cartilage** of growth plates, chondroblasts hypertrophy and calcify the matrix before apoptosis, reabsorption and replacement by trabecular bone as a normal sequence of longitudinal bone growth by endochondral ossification. In articular

cartilage, cartilage matrix is not calcified, and chondrocytes maintain the extracellular matrix. (TDC)

Chopping

Forage ensiled in clamps, towers or 'sausages' is generally chopped prior to packing.



Chopping allows greater compaction of cut grass in the stack, excluding oxygen and promoting an anaerobic rather than aerobic fermentation. Photo courtesy of CIAT (International Center for Tropical Agriculture). Licensed under CC BY-SA 2.0.

A range of forage harvesters have been developed that chop forage to varying degrees. Flails harvest a standing crop or previously mown material with limited chopping; forage is ensiled in long lengths. Machines that harvest previously mown forage include: (i) the forage wagon, which has either no chopping or a limited cutting action (forage is ensiled in long lengths); (ii) the double chop, which cuts each forage plant in two places (the forage is still ensiled in relatively long lengths but this method is an improvement on the flail and the forage wagon); and (iii) the 'precision' chop or metered-feed, which can chop forage to lengths of 25 mm or less, offering the optimum chop length for ensilage.

Traditionally balers did not carry out any chopping of the

forage. More modern balers have double-cut or 'opticut' actions which enable limited chopping action for baled silage. Immediately prior to feeding, baled silage can be chopped in **bale** choppers which reduce the particle length to *c.* 50 mm. Such post-ensiling forage processing has shown benefits in terms of forage **digestibility** and intake and overall animal performance. (RJ)

Chromatography

A very powerful method used in the separation of complex, multicomponent samples and for the separation of an analyte from potential interferences. It includes a diverse and important group of methods that permit the physical separation of closely related components of complex mixtures. The components to be separated are selectively distributed between two immiscible phases, a mobile and a stationary phase. All separations involve the **sample** being transported in a mobile phase that may be a gas, liquid or supercritical fluid, through an immiscible stationary phase that is fixed in place in a column or on a solid surface. The phases are selected so that components of the sample distribute themselves with repeated sorption/desorption steps during the movement of the analyte along the stationary phase. Those components that are retained strongly by the stationary phase move slowly with the flow of the mobile phase, whereas weakly held components travel rapidly. Due to these differences in mobility and distribution coefficients of the individual analytes in the sample, components separate into discrete bands or zones that can be qualitatively or quantitatively analysed.

Chromatographic methods can be categorized either by the

physical means by which the phases come into contact, i.e. column chromatography in which the stationary phase is held in a narrow tube, or by the types of phases and kinds of equilibria involved in the transfer of solutes between the phases. Three general categories of chromatography are liquid chromatography (LC), gas chromatography (GC) and supercritical-fluid chromatography (SFC), in which the mobile phases in the techniques are liquids, gases and supercritical fluids, respectively. A detector placed at the end of the column can respond to an eluting analyte, and plotting of its signal as a function of time produces a series of peaks. The plot, known as a chromatogram, can be used to identify components of the sample based upon the position of the peak or, from the area under the peak, give a quantitative measure of the amount of each component.

In LC separations, normal-phase (NP) chromatography involves a polar stationary phase, such as silica gel or alumina, and a non-polar mobile phase, such as hexane, chloroform or dichloromethane. It is used for the analysis of relatively non-polar compounds; however, retention characteristics of silica gel are strongly influenced by trace amounts of water. In reversed-phase (RP) chromatography, there is a non-polar stationary phase and polar mobile phase. It is ideal for the analysis of polar analytes. HPLC (high-pressure liquid chromatography) is a variation of LC in which the mobile phase is forced along under high pressure to allow for a greater efficiency of separation. If an LC mobile phase consists of only one solvent used for the analysis, the chromatography is called isocratic. Alternatively, if the

chromatography starts with one solvent or a mixture of solvents and gradually changes to a different mix of solvents as the analysis proceeds, it is said to be a gradient elution. Common LC applications include the analyses of substances such as drugs, drug metabolites, antibiotics, steroids, food additives, antioxidants, amino acids, proteins, carbohydrates, lipids, pesticides, herbicides, PCBs etc.

GC is used for the separation of volatile components. For GC, the mobile phase (a gas) is usually helium or nitrogen but can also be hydrogen. Components of a mixture have a different affinity for the stationary phase and thus can be separated. Common GC applications include the analysis of hydrocarbons, PCBs, steroids, drugs, pesticides, fatty acids, amino acids, alcohols, ethers, chlorinated aromatics, glycols, etc. (JEM)
See also: Gas–liquid chromatography

Chromic oxide
An inorganic compound, Cr_2O_3, which is not absorbed in the digestive tract and is the **marker** most commonly used in **digestibility** studies. However, its passage does not correspond well to that of either the solid or liquid phase of the **digesta** and it is therefore not a perfect marker. It may be used to mordant **straw** or **cellulose**: in this form it follows more closely the movement of solid digesta. (SB)

Chromium (Cr)
A transition **metal** with an atomic mass of 51.996. It exists in nature in three **oxidation** states as +2, +3, or +6, with +3 being the

most stable. Chromium is purported to be involved in **glucose** metabolism in animals and humans through its influence on **insulin** action. A Cr-containing **oligopeptide** that activates insulin receptor **tyrosine** kinase activity has been isolated from bovine **liver**. A covalent complex of Cr and picolinic acid has been reported to enhance **glucose tolerance** and insulin sensitivity in Type II diabetics. This complex also has been shown to cause chromosomal damage in Chinese hamster ovary cells. Although the US National Research Council does not list recommended amounts of Cr for any of the major farm species, the recommended intake for small **laboratory animal**s is between 1 and 2 mg kg^{-1} diet. However, trivalent Cr is an essential nutrient for humans, whereas hexavalent Cr is toxic when ingested or, more commonly, inhaled. Hexavalent Cr is transported in the erythrocytes, trivalent in plasma. (PGR; CJCP)

Further reading

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Stoecker, B. (1996) Chromium. In: Ziegler, E.E. and Filer, L.J. Jr (eds) *Present Knowledge in Nutrition*. ILSI Press, Washington, DC, pp. 344–352.

Chromium picolinate

The chromium (Cr) salt of picolinic acid. Chromium picolinate is one of many dietary Cr **supplement**s. Chromium appears to have a positive effect on **insulin** action and **glucose** metabolism. Although positive effects have been reported in diabetics, there do not seem to be anabolic responses in animals. (NJB)

Key reference

Lukaski, H.C. (1999) Chromium as a supplement. *Annual Review of Nutrition* 19, 279–302.

Chylomicron

A **lipoprotein** particle found in lymph and blood. It is made in the intestinal cells from the **hydrolysis** products of dietary **triacylglycerol**s (fat), monoacylglycerols and **fatty acid**s, which are combined with a **protein**. These particles are secreted into the lymphatic system. The particles ultimately enter the general circulation as chylomicrons. Specific **apolipoprotein**s bind to the chylomicron. **Lipoprotein lipase** in the inner wall of blood capillaries releases the fatty acids for tissue uptake. (NJB)

Chyme

Intestinal contents, i.e. **digesta**, consisting of undigested food, endogenous secretions, desquamated **mucosa**l cells and microbes. (SB)

Chymotrypsin

The active form of chymotrypsin (α-chymotrypsin; EC 3.4.21.1) is an **endopeptidase** that hydrolyses primarily those **peptide** bonds whose carbonyl groups are contributed by aromatic **amino acid**s, i.e. **tryptophan**, **phenylalanine** or **tyrosine** and, to a lesser extent, by **leucine** and **methionine**. It is secreted from the **pancreas** into the **duodenum** as its inactive precursor, chymotrypsinogen, which is activated in the duodenum after excision of two internal dipeptides by **trypsin**. (SB)

See also: Pancreatic juice

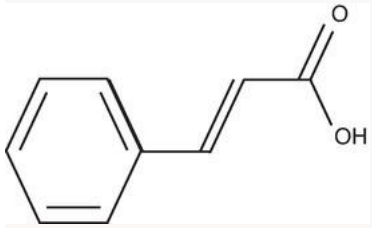
Cimaterol

A phenethanolamine β_2-adrenergic agonist ($C_{12}H_{18}N_3O$, molecular weight 220). These compounds lack the catechol nucleus of the catecholamines whose action they mimic and are therefore not susceptible to degradation by the enzyme, catechol-*o*-methyltransferase, thus exhibiting prolonged action. Originally developed for use as a bronchodilator in humans, but employed as a leanness-enhancing repartitioning agent in livestock, cimaterol acts by redirecting nutrients from **adipose tissue** to **skeletal muscle**. It is closely related to **clenbuterol**. (MMit)

See also: Beta agonists

Cinnamic acid

$C_9H_8O_2$, molecular weight 148. A phenylpropane derivative and the basic building block for many phenolic acids.



Cinnamic acid derivatives (phenolic acids) occur in the cell walls of many forages and are involved in cross-linking fibre. The phenolic acids are antimicrobials and hence may inhibit **digestibility** of cell wall materials. The **phenolic compound**s are metabolized by **rumen** microbes and are conjugated with **glycine** as a mechanism of **detoxification**. Phenolic compounds

form complexes with proteins and other nutrients and therefore have antinutritional activity, especially in animals on low-protein diets. (DING)

Circadian rhythm

A circadian (*circa*, about; *dies*, a day) rhythm is a biological cycle whose period length under constant conditions (continuous illumination or total darkness, constant temperature and random servicing and noise levels) is still close to, though not necessarily equal to, 24 h. In poultry, deep body temperature, locomotor activity and pre-ovulatory **luteinizing hormone** release are examples of biological functions that operate with a circadian rhythm. Under 24 h conditions, most rhythms are principally regulated by dawn, dusk or both signals, and oscillate at 24 h intervals. However, not every rhythm that oscillates every 24 h under a 24 h **light**/dark cycle is a circadian oscillator – only those that tend to persist under constant conditions. It is likely that the activity of **serotonin** *N*-acetyltransferase, the main hormone involved in the control of **melatonin** synthesis in the pineal gland, is responsible for the regulation of circadian rhythms in birds, whilst a circadian pacemaker in the suprachiasmatic nucleus has been identified in mammals. (PDL; CLA)

Cirrhosis

A disease in which functional liver tissue is replaced by scar tissue (fibrosis). Causes include alcoholism, infections (hepatitis), nutritional deficiencies (e.g. **vitamin E**, **selenium**) and dietary hepatotoxins (e.g. pyrrolizidine **alkaloid**s). In advanced stages,

liver cirrhosis is irreversible. (PC)

***cis*-Fatty acids** **Unsaturated fatty acid**s in which the double bonds are in the *cis* configuration, making the carbon chain twist and lowering the melting point. In the *cis* configuration, the single hydrogens on the carbons of the double bond are on the same side of the chain, whereas in the *trans* configuration they are on opposite sides. (NJB)

Citric acid
A six-carbon **tricarboxylic acid**, molecular structure $HOOC{\cdot}CH_2{\cdot}C(OH)(COOH){\cdot}CH_2{\cdot}COOH$. It is produced in the mitochondrion by the combination of oxaloacetic acid and acetyl-CoA produced in the **catabolism** of carbohydrates, fatty acids and some amino acids. This reaction forms part of the tricarboxylic acid cycle or Krebs cycle. With the exception of erythrocytes, citric acid is thought to be produced in all cells. Citric acid can also leave the mitochondrion and provide the two-carbon acetyl-CoA units required for fatty acid biosynthesis. (NJB)

Citrulline
An **amino acid** ($C_6H_{13}N_3O_3$, molecular weight 175.19) found in animals, plants and **microorganism**s. It is an intermediate in the **urea cycle** that is formed in mitochondria from carbamoyl phosphate and **ornithine**. There is no net synthesis of citrulline by the **liver**. In most mammals, citrulline is formed from **glutamine**, **glutamate** and **prolactin** in their **enterocyte**s. Orally ingested or intravenously administered citrulline is effectively converted

into **arginine** in animals. Citrulline in the blood has a longer half-life than arginine. In all animals, a quantitatively very small amount of citrulline is formed from arginine by **nitric oxide** synthase. Of note, in rheumatoid arthritis, some arginine residues in certain proteins can be enzymatically deiminated to form citrulline residues. (GW)
See also: Non-protein amino acids

Citrus products
Citrus pulp is the solid residue remaining after the extraction of juice or segments from citrus fruit. It typically represents 50–70% of the original fresh weight. It comprises peel, rag (internal tissue) and seed in proportions of approximately 60–65, 30–35 and 0–10%, respectively. The pulp, predominantly from **oranges**, is usually dried. **Calcium** oxide, added to reduce the hydrophilic effect of the pectins, ensures that citrus pulp is a good source of calcium (2.2%); however, it is low in **phosphorus** (0.2%). In composition and **nutritive value**, citrus pulp is similar to **sugarbeet** pulp. Although the pectin and neutral detergent fibre contents comprise 50% of the pulp, both are highly degradable. **Protein** and **ash** contents are low. Fresh pulp has a pH of 4.0 but the buffering capacity is only one-fifth that of grass **silage**. The pulp stores well in the absence of air and produces a high-quality silage when combined with grass, the low pH and residual sugars having an immediate impact on the ensiling process. The pulp also has an absorptive action, restricting the loss of effluent and associated nutrients. To some extent the high fibre content limits its use in non-ruminants and if large quantities of seeds are present

their limonin content could render the pulp toxic to non-ruminants.

Citrus **molasses** is the syrup produced by concentration of the juice released from citrus peel. It has a typical **dry matter** content of 70%, of which 60–65% is **sugar**, but is low in protein. The material is highly viscous and requires to be stirred regularly. It is highly acceptable to cattle but pigs require a few days to become accustomed to the flavour. In both cases it can replace up to 50% of the starchy concentrate in the diet of **fattening** animals. (FLM)

Claws

Present in some animals and all birds, claws are formed from the terminal phalanges and are composed of closely packed, renewable layers of keratinized cells producing horny pointed nails. In birds, claws are adapted for grasping, perching and preening. In very young birds, claws can be clipped to obtain blood samples. (MMax)

Clenbuterol

A phenethanolamine β_2-adrenergic agonist ($C_{12}H_{18}Cl_2N_2O$, molecular weight 277). These compounds lack the catechol nucleus of the **catecholamines** whose action they mimic, and are therefore not susceptible to degradation by the enzyme, catechol-ortho-methyltransferase, thus exhibiting prolonged action. Originally developed for use as a bronchodilator in humans but employed as a leanness-enhancing repartitioning agent in livestock, clenbuterol acts by redirecting nutrients from **adipose tissue** to **skeletal muscle**. It is shown to promote growth and leanness in

broiler chickens, an effect that is markedly influenced by dietary protein content. Clenbuterol is closely related to **cimaterol**. (MMit)
See also: Beta agonists

Climate
Climate describes the usual weather conditions of a location, whereas weather refers to the actual conditions (**temperature**, humidity, wind, precipitation and barometric pressure) at a given time. Both affect the performance and productivity of animals in a variety of ways. Heat produced by **metabolism** has to be dissipated to the environment as it is produced, requiring a balance between **heat production** and heat loss. Heat losses to the environment can be influenced either reflexly or voluntarily by the animal, but only within limits set by the physical laws that govern conductive, convective, radiative and evaporative exchanges, each of which is determined by climatic factors. Thus Newton's Law of Cooling (a physical law) states that the rate of convective and radiative heat loss from a surface is proportional to the temperature difference between it and its surroundings; nothing the animal does can alter this truism, but the slope of the relationship (temperature difference per unit heat loss, i.e. insulation) can be altered by the animal. Dilation and contraction of peripheral blood vessels and erection of the hair or ruffling of the feathers are short-term reflex actions that alter insulation; huddling and seeking shelter are voluntary short-term actions. Long-term adaptations to climate include laying down of **body fat** and growth of the coat, both of which increase insulation.

Evaporation from the body surface is proportional to the vapour-pressure difference between the surface and the surrounding air (a physical law), the rate constant being dependent on the rate of air movement over the surface. The animal can adjust the availability of moisture at the skin surface by sweating and so increase the surface vapour-pressure; and it can increase air movement over the respiratory passages by panting; but no amount of reflex action by the animal can overcome the final limit set by air humidity. If the absolute humidity of environmental air exceeds the saturation vapour pressure corresponding to deep body temperature, **evaporative heat loss** is impossible.

Solar radiation can impose a large additional heat load on an animal, even exceeding its normal rate of heat production. This is beneficial in **cold environment**s, but in hot climates shade is essential to avoid it.

At air temperatures below a certain level (the lower critical temperature), **heat balance** can only be maintained if the animal increases its heat production. This can be done reflexly by shivering or voluntarily by exercise or by increasing food consumption. Increased heat production of stall-fed animals is wasteful if it involves extra feeding. As long as windbreaks are available, the lower critical temperature is unlikely to be reached by grazing mature sheep or cattle even in the very cold winter conditions of North America, but their young require maternal warmth and protection. Deep snow is not of itself a serious cold hazard for sheep, but proves fatal if it prevents them from finding food. Heavy rain reduces the coat insulation of many species, but does not

penetrate the fleece of sheep.

At high air temperatures, an upper critical temperature is reached when an animal's productivity falls. This is usually due to a reduction in food intake, either because herbage is sparse in hot climates or because the animal becomes unwilling to make the necessary effort to find and eat enough food. This is particularly true of high-producing cows. (JAMcL)
See also: Environmental temperature

Cloaca
In birds and reptiles, the most posterior section of the alimentary canal, also receiving the terminal portions of the urinary and reproductive ducts. In birds the cloaca is divided by folds of mucous membrane into three compartments: proctodeum, urodeum and coprodeum. (MMax)

Clover silage
Two types of clover are commonly used in silage production: white (*Trifolium repens*) and red (*Trifolium pratense*). Clover is usually ensiled as part of a mixture with grasses. Clover contains low concentrations of water-soluble **carbohydrates** but high concentrations of **protein**. The protein is of good feed value but its buffering capacity makes the crop more difficult to ensile. This problem is exacerbated by the low concentrations of water-soluble carbohydrate available for **lactic acid** production during **fermentation**, thus an additive is essential. (DD)
See also: Silage

Coat licking

A behavioural problem in stressed or anxious cats, which leads to fur balls, and also in cattle, in which case consumption of the **salt** in the **sweat** may be the origin of this **stereotyped behaviour**. In intensively raised calves it can cause accumulation of large quantities of **hair** in the rumen, whose apertures become blocked. The condition is most common in cats, as a result of excessive grooming. Accumulated hair blocks the exit to the **stomach**, the pyloric sphincter, and consumed food and the hair are vomited up the oesophagus. Treatment is by administering laxatives, which help the hair to pass through the digestive tract, feeding high-fibre diets, which bind the hair and help it pass through the digestive tract, and encouraging cat owners to brush their cat's coat more regularly. However, it should also be seen as a sign that the cat is anxious or stressed and management changes are needed. Hair consumption, or trichophagia, is less well known in humans, usually occurring in teenage girls, and, in the form of trichobezoar, usually has less serious consequences. **Wool biting** or nibbling occurs in sheep, in which sheep eat their own wool or that of conspecifics. Starting with the hindquarters, it resembles grooming seen in horses and other animals. However, it soon progresses until large areas of the fleece are removed, to the discomfort of the target animal. Affected animals suffer from accumulation of the wool in the **rumen**, **colic**, loss of **appetite** and may die from digestive disorders. Cold exposure of the affected animal is an associated problem. Target animals are usually low in the dominance hierarchy. Conditions that are conducive to the

development of the disorder include intensive housing, overcrowding, deficiencies of fibre or certain minerals in the diet, in particular **zinc**, **sulphur** and **sodium**, and the presence of ectoparasites, such as ticks and keds. (CJCP)

Coating

Some feed materials may be coated to protect their chemical structure and hence nutritional value in extreme environmental situations. For example, **vitamin premix**es are normally coated with **gelatin**, which minimizes the risk of the inherently unstable vitamins becoming denatured by heat during feed manufacture.

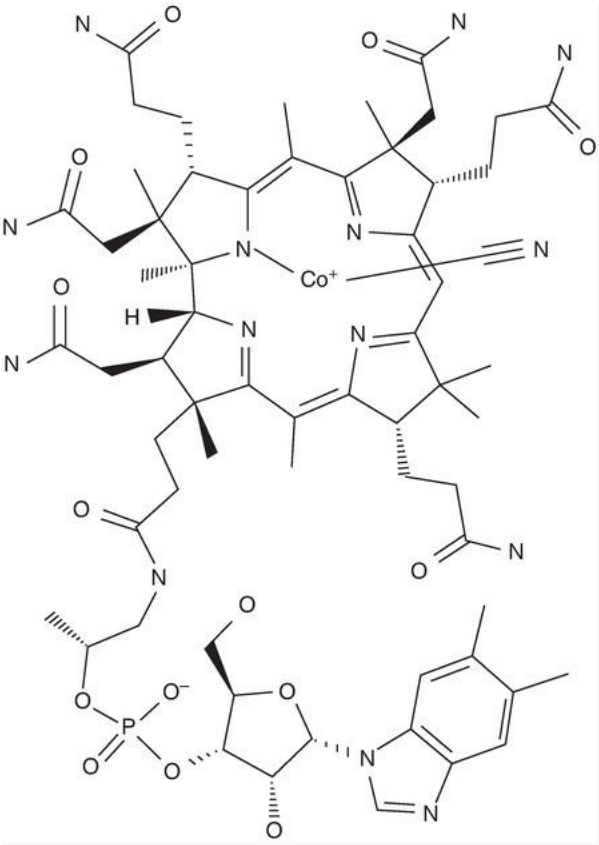
Some feed ingredients may be protected to ensure maximum absorption in specific parts of the **gastrointestinal tract**. This is particularly pertinent for **ruminant animal**s, as many materials are digested in the rumen and utilized by the resident microflora, the direct benefits to the host animal being lost. **Proteins**, specific **amino acid**s and **fats** may be treated in order to protect them from **rumen** degradation so that they are absorbed in the **abomasum** or **small intestine**. It may be of benefit to coat specific mineral elements with either a protein or a polypeptide to maximize absorption. This is not only nutritionally valuable but also reduces environmental pollution from the excretion of elements such as **copper**.

Pelleted **compound feed**s may be coated with flavours, medications or fats to improve **palatability** or for particular veterinary or nutritional reasons. (MG)

Cobalamin

Vitamin B_{12}, $C_{63}H_{88}CoN_{14}O_{14}P$, containing a corrin ring (similar to a porphyrin ring) with a **cobalt** ion at its centre. It is exclusively synthesized by microorganisms and is not found in plants unless they are contaminated by bacteria. In liver it is found as methylcobalamin, adenosylcobalamin and hydroxycobalamin. It can be provided as a **vitamin** as cyanocobalamin. In ruminants, B_{12} analogues are synthesized by **rumen microorganism**s and a dietary supply is generally unnecessary. Cobalamin is absorbed from the intestine by a complex system involving specific **binding protein** (intrinsic factor), acid and proteolytic enzymes and is taken up in the lower **small intestine** by specific transporters. In the **blood** it is transported by transcobalamin II. Once in the cell it can be converted to methylcobalamin in the cytoplasm. In this form, cobalamin participates in a reaction in which L-**homocysteine** is methylated by *N*-**5-methyltetrahydrofolate** to form L-**methionine** and **tetrahydrofolate**. This is a critical metabolic role for vitamin B_{12} in methyl group and **one-carbon metabolism**. A deficiency of vitamin B_{12} results in a deficiency of **folate** and elevated blood **homocysteine**. Animals deficient in vitamin B_{12} have elevated blood levels of homocysteine and ultimately will show signs of a folic acid deficiency. The reason for a folic acid involvement is that the release of tetrahydrofolate in the transmethylation reaction provides tetrahydrofolate to be used in other folate-dependent reactions. Without the transmethylation reaction, folate one-carbon units are 'trapped' as *N*-5-methyltetrahydrofolate. As the *N*-5-methyltetrahydrofolate pool builds up, the tissue becomes deficient in tetrahydrofolate and

metabolic reactions requiring tetrahydrofolate as a co-factor slow or cease. This limits the flow of one-carbon units from **serine**, **glycine**, **betaine**, **histidine**, formate and **formaldehyde** into the folate system. One product excreted in the **urine** and representative of a folate deficiency is an intermediate in histidine **catabolism**, *N*-formiminoglutamate (FIGlu). This limitation in one-carbon units decreases the ability of cells to produce **purines**, because fewer one-carbon units as *N*-10-formyltetrahydrofolate and *N*-5,*N*-10-methenyltetrahydrofolate are available for the **nucleic acid** (purine) synthesis. The result is a megaloblastic **anaemia** due to the impaired DNA synthesis limiting cell division in the developing erythrocytes. B_{12} is transported by transcobalamin II and once in a cell it can be converted in the mitochondrion to adenosylcobalamin, which is required as a vitamin co-factor in **propionate** metabolism. Propionate can be produced from the catabolism of threonine and **methionine** and from anaerobic intestinal **fermentation**. Propionate, as propionyl-CoA, must be carboxylated by a **biotin**-dependent step to produce methylmalonyl-CoA which, with the aid of the vitamin B_{12} co-factor adenosylcobalamin, is ultimately converted to succinyl-CoA, which can be used in **metabolism**. A decrease in the participation of B_{12} in this reaction leads to the urinary excretion of methylmalonate. Elevated excretion of **homocysteine** and methylmalonate, while being signs of a deficiency of vitamin B_{12}, can also be apparent in response to a series of inherited disorders. (NJB)



Key reference

Seetharam, B. (1999) Receptor-mediated endocytosis of cobalamin (vitamin B_{12}). *Annual Review of Nutrition* 19, 173–195.

Cobalt (Co)

A mineral element with an atomic mass of 58.93. It is an essential **trace element** for most animal species but, unlike most other minerals, not in ionic form but as a vital part of vitamin B_{12}, or **cobalamin**, which is involved in methyl group transfer reactions. A deficiency of the vitamin leads to **anaemia**. The minimal requirement of Co for **ruminant animal**s is about 0.1 mg kg^{-1} diet for sufficient microbial synthesis of vitamin B_{12} for the animal to utilize. Cobalt itself is non-toxic but 4–10 mg kg^{-1} body weight could cause loss of **appetite** and reduced weight gain. Ionic Co is readily absorbed from the gut and shares a common pathway with

iron. Co is excreted primarily in the **urine**. (PGR)

Further reading

Smith, R.M. (1987) Cobalt. In: Mertz, W. (ed.) *Trace Elements in Human and Animal Nutrition*, 5th edn. Academic Press, Harcourt Brace Jovanovich, New York, pp. 143–183.

Stabler, S.P. (2001) Vitamin B-12. In: Bowman, B.A. and Russell, R.M. (eds) *Present Knowledge in Nutrition*. ILSI Press, Washington, DC, pp. 230–240.

Coccidiosis

Parasitism by **protozoa** of the genera *Eimeria*, *Isospora*, *Cystoisospora* or *Cryptosporidu*. Nearly all animals are susceptible. Infection generally results in the invasion and destruction of the **intestinal mucosa** with subsequent **diarrhoea** and productive losses. Severity of the disease is directly related to the dose (number of oocysts ingested) and the immune and nutritional status of the host. Both improved management to prevent oral exposure to infective oocysts and treatment with coccidiostats are effective in control. (BLS)

Cockerel

A young male **domestic fowl**. Mature birds are described as cocks or roosters. (KJMcC)

Cocoa bean (*Theobroma cacao* L.)

The cocoa tree is indigenous to South America, but the main centre for cocoa bean production is tropical West Africa. Cocoa beans are found in large yellow or orange pods which grow directly on the stems or branches of the tree. Beans are removed from the pod and

fermented with its encasing white mucilage, and dried for processing into cocoa powder and cocoa oil. Pods contain a high concentration of **potassium**. Cocoa shells, the main residue from processing, contain a toxic **alkaloid**, **theobromine**, which is poisonous to animals, but only traces of this are found in cocoa pods.



Cacao beans in Ghana. Photo courtesy of Charlotte Warren. Licensed under CC BY-ND 2.0.

Although cocoa bean shells have a high **protein** level (16%; see table), the **digestibility** of the protein is low (6.6%). Cocoa pods can be used in a **maintenance** ration for small ruminants, comprising up to 25% of the **diet**. Up to 7 kg per day has been fed to dairy cattle without adverse effects. Dried and ground pods can be included in concentrate mixtures at up to 20% without deleterious effects on production levels. (LR)

Nutrient composition of cocoa bean (% dry matter).

	CP	CF	Ash	EE	NFE

	CP	CF	Ash	EE	NFE
Cocoa pods	7.8	35.1	10.4	2.3	47.6
Cocoa bean shells	16.0	17.4	10.8	3.2	

CF, crude fibre; CP, crude protein; EE, ether extract; NFE, nitrogen-free extract.

Further reading

Devendra, C. (1988) *Non-conventional Feed Resources and Fibrous Agricultural Resources*. IDRC/Indian Council for Agricultural Research, Ottawa, Canada.

Gohl, B. (1981) *Tropical Feeds*. FAO Animal Production and Health Series, No. 12. FAO, Rome.

INRAE, CIRAD, AFZ and FAO (2012–2020) Feedipedia. Animal Feed Resources Information System. Available at https://www.feedipedia.org (accessed 17 August, 2022)

Coconut (*Cocos nucifera* L.)

Nuts are produced on the coconut palm tree, which can grow in poor sandy conditions. The **nut** consists of a hard shell covered by a fibrous outer layer, with an edible kernel inside. The nut must be split and the kernel dried for storage. Coconut water contained inside the nut is usually discarded. The fibrous outer layer has no feed value but can be used for coir matting or as a fuel.



Malayan yellow dwarf coconuts. Photo courtesy of Jason Thien. Licensed under CC BY 2.0.

Apart from their use in human food, coconuts are harvested for their **oil**. This is obtained by expeller or solvent extraction of the dried coconut kernel. The residue after oil extraction is called copra meal (or copra cake) or, less commonly, coconut meal. Copra meal is used in feeds for poultry, pigs, ruminants and horses.

The oil content of copra meal varies widely according to the efficiency of the extraction method, with solvent extraction removing more than 90% of **oil** and expeller extraction removing about 80%. Copra meal is rich in **energy** and **protein** (Table 1) and can be used for lactating animals. Copra may become rancid as it ages, especially if it has been stored under high temperatures, as a result of **oxidation** of residual oil; and this can cause **diarrhoea**. The meal is low in **lysine**, **isoleucine** and **methionine** but has a high fibre content (Table 2). These characteristics limit its use in poultry and pig rations. The maximum safe amount in dairy cow rations is < 2 kg per day because its **saturated fatty acid** content leads to a harder **butterfat**. Beef cattle can consume higher levels without greatly

affecting **carcass** fat. Coconut meal should be introduced gradually into livestock rations.

Table 1. Typical composition of expeller extracted copra meal (% dry matter).

	DM (%)	**CP**	**ADF**	**Ash**	**EE**	**Lys**	**Ca**	**P**
Copra meal	91.5	22.4	28.7	6.8	9.8	0.6	0.12	0.58

ADF, acid detergent fibre; CP, crude protein; EE, ether extract; Lys, lysine; Ca, calcium; P, phosphorus.

Table 2. Available nutrients in expeller extracted copra meal.

	CP degradability (%)	**CP digestibility** (%)	**ME** (MJ kg^{-1} DM)		
			ME	MEn	AMEn
Ruminants	49		12.8		
Pigs		71		10.4	
Poultry					8.7

Ruminants can graze coconut orchards once the trees have reached 5–6 years old. Because livestock can eat young coconut

leaves, which damages tree development, grazing in coconut plantations is restricted until trees are too high for the animals to reach the leaves. (LR; GMcLD)

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Heuzé V., Tran G., Sauvant D. and Bastianelli, D. (2015) Copra meal and coconut by-products. Feedipedia (INRAE, CIRAD, AFZ and FAO). Available at https://www.feedipedia.org/node/496 (accessed 18 August 2022)

Cod

Atlantic cod (*Gadus morhua*, L.) occurs naturally on both sides of the North Atlantic from Iceland and Spitsbergen to the Baltic Sea and Bay of Biscay in the eastern Atlantic, and from Greenland to Cape Hatteras, North Carolina, in the western Atlantic. Cod, haddock and pollock belong to the Gadidae, a family of physoclistous, soft-rayed **fish** featuring thoracic pelvic fins and, frequently, a barbel on the lower jaw. The **aquaculture** production cost of cod is relatively high, due to slow growth and early sexual maturation problems, which may be reduced by **photoperiod** manipulation.

There is small-scale cod hatchery production and grow-out in Newfoundland and, more recently, the New England states have initiated a successful early rearing programme. Atlantic cod eggs

are buoyant, 1.2–1.6 mm in diameter and have no oil globule. Hatching occurs in 14–40 days at 6°C and 0°C, respectively. Newly hatched larvae are 4.0–4.5 mm long and are pelagic until a length of 25–50 mm. Larvae can be successfully reared to metamorphosis on a sequential diet of microalgae, live food organisms such as **rotifers** and artemia, and microparticulate **weaning** feeds.

Murray cod (*Maccullochella peelii peelii*) can be grown as fingerlings and used to restock private and public waters. The first aquaculture farm was established in 1977. (RHP; CJCP)

Cod liver oil

Oil obtained from the **livers** of cod and other fish from the Gadidae family. It is used as a source of **unsaturated fatty acid**s (oleic, docosahexaenoic and eicosapentanoic) and **fat-soluble vitamins**. The nutrient composition is 38 MJ energy kg^{-1}, 1,000,000 IU **vitamin A** and 100,000 IU **vitamin D** kg^{-1}, with 226 g saturated, 467 g monounsaturated and 225 g **polyunsaturated fatty acid**s kg^{-1} and 5700 mg **cholesterol** kg^{-1}. (JKM)

Coenzymes

Metabolically essential compounds derived from B **vitamins**. The vitamins themselves are not able to participate as enzyme co-factors in **metabolism**. For example, **thiamine** is metabolically converted to its mono-, di- and triphosphate forms. It functions as a vitamin co-factor only as thiamine diphosphate. (NJB)

Coffee

Coffee production for human consumption gives rise to a number of **by-product**s that may be used as ruminant feeds. These include leaves, pulp from the bean, coffee residues, coffee meal and spent coffee grounds. The fresh fruit consists of 45% pulp, 10% mucilage, 5% skin and 40% bean. To produce coffee the fruit is processed to free the bean from the pulp, which accumulates in large quantities and is used in some areas as **roughage** for cattle. The fruit can be processed by either a dry method or by a wet soaking method. The pulp from the dry method is fibrous and rather poor roughage (see table), whereas that from wet processing has much greater feed value. Coffee pulp from the wet method can be fed to lactating dairy cattle at levels below 20% of the diet without affecting milk production. **Digestibility** of pulp (dry method) in sheep is **crude protein** 10.3%, **crude fibre** 27.9%, **ether extract** 53.2% and NFE 50.2%, with ME 1.33 MJ kg^{-1}.



Coffee plant in Colombia. Photo courtesy of Brian Smith/American Bird Conservancy. Licensed under Public Domain 1.0

Typical composition of coffee products (g kg^{-1} dry matter).

	Dry matter (g kg^{-1})	**Crude protein**	**Crude fibre**	**Ash**	**EE**	**NFE**
Dried leaves	936	99	187	130	59	525
Residue/meal	910	120	440	17	25	398
Pulp, wet method	230	128	241	95	28	508
Pulp, dry method	900	97	326	73	18	486
Skins, Columbia	900	24	952	4	6	214
Coffee ground	197	133	624	5	196	42
Coffee oil meal	898	174	270	55	18	483

EE, ether extract; NFE, nitrogen-free extract.

Coffee meal is a dark brown to black residue produced when coffee seeds are removed from the outer **coating**, dried and then roasted. Coffee meal is high in fibre and has a very low **energy value**. It is a bitter product that inhibits food intake and will reduce overall **feed intake** if fed at levels greater than 2–4% of the total diet. It has a strong diuretic effect, which encourages urinary **nitrogen** and **sodium** losses, making it unsuitable for feeding to horses. Coffee meal can contain high **oil** levels which interfere with fibre **digestion** in ruminants at high inclusion levels. In addition, the oil content may cause the product to become rancid in storage. Coffee meal can be fed to dairy cows, beef cows and ewes, but not at an inclusion level greater than 4%.

Dried coffee leaves have a relatively low nutritional quality but they can be included in concentrates. The high **tannin** content of the coffee leaves reduces the digestibility of proteins and possibly of other dietary components. Spent coffee grounds, or cherko, are the waste product from instant coffee production. These are unpalatable and contain diuretics including caffeine, and tannins that reduce **protein digestibility**; inclusion rates should not exceed 2.5%. The nutritional composition of spent coffee grounds can be improved by solid fermentation (*see* Solid-state fermentation). (JKM)

Cold environment

In a cold environment an animal is forced to raise its **metabolism** above the normal level in order to keep warm. This occurs at the

so-called lower critical **temperature**, which in still air can be as low as –40°C for a fully fleeced sheep and as high as 34°C for a newly hatched chicken. Wind causes a decrease and solar radiation an increase in the critical temperature. (JAMcL)
See also: Climate; Environmental temperature

Cold-water species
Generally, aquatic animals' survival **water temperature** range is 0–20°C and the best temperature is 12–18°C. The maximum water temperature that they can tolerate is 22–24°C. The **growth** rate will be reduced greatly if the water temperature is higher than 20°C, with a **heat stress** situation that may even cause death. Cold-water species are mainly distributed at latitudes higher than 45 degrees or at high-altitude localities. The cultured cold-water species of fish are mainly salmon, **trout**, **cod** and **sturgeon**. (QS)

Reference

Zhang, J. (1990) Coldwater fishes and their prospects for exploitation and utilization in China. *Salmon Fishery* 3, 1–20 [in Chinese].

Colestyramine
A synthetic strong basic anion-exchange resin. It has quaternary ammonium functional groups attached to a polystyrene polymer. It can bind **bile** salts and if consumed in sufficient amounts may alter the excretion of **cholesterol**-based substances. (NJB)

Colic
Severe and sudden attack of abdominal pain, often caused by indigestion. Caused in horses by the presence of gas, impaction of

the **colon**, or a variety of other gastrointestinal disorders. It may also be caused by large numbers of parasitic worms, urinary calculi or nephritis. (JMF)

Colitis

Inflammation of the **colon**, often accompanied by haemorrhage and ulceration. Symptoms are abdominal pain, fever, watery **diarrhoea**, **dehydration**, hypovolaemia, toxaemia, leucopenia, decreased serum Cl, Na and K levels and metabolic acidosis. The disturbances of **mineral** balance arise from damage to the epithelial tissue of the colon. The aetiological agents are many and include ***Escherichia coli***, *Salmonella* spp., *Clostridium* spp., *Ehrlichia risticii*, cyathostomes, fungi, various antibiotics, drugs and toxins. All farm animal species are potentially affected and can transmit the infection to humans. (CJCP)

Collagen

A fibrous **protein** that makes up the major portion of white fibres in **connective tissue**s. It is found in skin, tendons and bones and contributes approximately 25% of body protein in mammals. Collagen is converted to **gelatin** by boiling in water. At least 19 types of collagen, at least 35 mammalian collagen genes and at least 30 separate polypeptide chains have been identified. The characteristic molecular structure of collagen can be described as a three-stranded rope with strands winding around each other with a 1.5 nm right-handed twist. The polypeptide chains that make each strand have a left-handed twist composed of 18 **amino acid** residues for each turn in the helix. The three polypeptide chains of

mature collagen type 1 are made of approximately 1000 amino acids. The three polypeptide chains have a unique amino acid sequence. A structural requirement for the triple helix assembly is a **glycine** residue in every third amino acid position. Two other amino acids found in high frequency are **prolactin** and **hydroxyproline**. Hydroxyproline is formed by post-translational modification of prolactin during collagen synthesis. Hydroxyproline accounts for 13–14% of the total amino acid content of collagen. These two amino acids make the structure more rigid. Another structurally important amino acid found in collagen fibrils is **lysine**. A post-translational modification of the ε-amino group of lysine involves conversion to a hydroxyl group to form **hydroxylysine**. Hydroxylysine can bind covalently to hydroxylysine in adjoining polypeptide chains to form cross-links, making a more rigid structure. The enzymes involved in forming hydroxyproline (prolyl hydroxylase) and hydroxylysine (lysyl hydroxylase) both require **ascorbic acid** (**vitamin C**) as a co-factor. This requirement may explain the bleeding gums and poor wound healing seen in scurvy (vitamin C deficiency) in humans, other primates and some birds.

As a nutrient source, collagen is an incomplete protein with regard to the amino acid pattern required by simple-stomached animals, as it is devoid of the indispensable amino acid **tryptophan**. Collagen has less than one-half the required concentrations (1 g amino acid 16 g^{-1} **nitrogen**) of eight of the nine indispensable amino acids; it also has excessive concentrations of the dispensable amino acids glycine, prolactin

and hydroxyproline, which make up 47% of the total amino acids. Hydroxyproline cannot be used as an amino acid in **protein synthesis**, as it is only produced from prolactin during collagen synthesis. (TDC)

Colon
That part of the digestive tract that lies between the **caecum** and the **rectum** (or, in those species lacking a caecum, between the **ileum** and the rectum). The colon is the main site for the **resorption** of water and **sodium**. It is also important for microbial activity and production of **short-chain fatty acids** (SCFA), particularly in non-ruminant **herbivore**s, such as the horse, in which up to 70% of absorbed energy is from SCFA produced in the colon. (SB)

Colonization:
see Gastrointestinal microflora; Rumen microorganisms

Colour and pigmentation agentsFish and **shrimp** pigment their bodies with oxygenated **carotenoid**s (xanthophylls). They cannot be synthesized and function as precursors to **vitamin A**, **antioxidant**s, in communication and growth. In salmonids, two carotenoids, **astaxanthin** and canthaxanthin, produce the red/orange coloration of the skin and flesh desired by consumers. In wild salmonids they are derived from **phytoplankton** but in **aquaculture** synthetic astaxanthin or that in a red **yeast** (*Phaffia rhodozyma*) or *Haematococcus* **algae** is added to the diet. Plants usually do not contain suitable pigments for this purpose, but have

lutein (3R,3′R,6′R-β,ε-carotene-3,3′-diole) and zeaxanthin (3R,3′R-β,β-carotene-3,3′-diol), for example in **alfalfa**, yellow **corn** and algae. These produce yellow and yellow-orange colours, rather than the desired red. Appropriate coloration is also sought in **yellowtail**, sea bream and red porgy, and in the wild the colours are obtained from crustaceans. Goldfish and other ornamental fish metabolize carotenoids to impart colour to their skin. (QS)

Reference

NRC (2011) *Nutrient Requirements of Fish and Shrimp*. National Academic Press, Washington, DC.

Colostomy

Surgical removal of the **large intestine** with the creation of a fistula for the outlet of **digesta** from the distal **ileum**. (SB)

See also: Cannula

Colostral immunity

This passive immunity is of potentially enormous benefit to the young animal. It can provide protection against species-specific and environmental pathogens to which the dam, or colostrum provider, was exposed before parturition. This passive protection may be systemic, from colostral **antibodies** absorbed in the first 24–48 h of life, or by local action in the gut subsequent to this. (EM)

See also: Immunity

Colostrum

The **milk** formed before and around the time of parturition. It may differ in consistency (thicker) and colour (cream/beige/yellow)

from subsequent milk production.

Colostrum is the major source of passive **immunity** for most domestic animals (in contrast to humans, rabbits and guinea pigs) and is also a rich source of nutrients. **Lipids** and proteins (primarily **casein**s and **albumin**s) are present in relatively high concentration, around 20%, but **lactose** levels are lower than in subsequent milk production. Vitamin content is high, particularly **vitamin A**, which is important in pigs and calves as placental transfer is limited. Colostrum acts as a natural laxative in the neonate, aiding passage of the meconium, the accumulated fetal faecal material.

Immunoglobulins in colostrum protect the neonates in two ways. Immunoglobulin A (IgA) acts locally in the gut lumen and immunoglobulin G (IgG) is absorbed into the neonate's circulation, providing short- to medium-term protection against specific diseases. In many mammals IgG is the major immunoglobulin in colostrum, though IgA is present in milk for longer.

IgA is produced in the **mammary gland** by plasma cells that have migrated from gut-associated lymphoid tissue of the dam, where they are stimulated by the gut flora. This IgA is not absorbed into the **blood** of the neonate but remains in the gut to act to protect the gut wall against infection.

IgG is transported and concentrated from the dam's sera into colostrum by mammary acinar cells. Thus if circulating IgG is present at a high concentration in response to a specific **antigen** in the dam's sera, it should also be at a high concentration in the colostrum. This type of antibody is specifically transported across

the neonate's intestinal epithelium (optimally in the lower **jejunum** in the calf) and into the circulation, provided that the neonate is less than 36 h old. **Absorption** of antibody is reduced after the neonate is 12 h old. Unless infected as a fetus, neonates of most farm species are born without gamma globulins in their circulation. Measurement of serum IgG in the neonate can thus indicate whether a satisfactory amount of colostrum has been consumed and antibody absorbed. Calves with less than 10 mg IgG_1 ml^{-1} are considered hypogammaglobulinaemic.

It is generally accepted that the neonate should consume 10% of its body weight in colostrum in the first 24 h and, if possible, half of that in the first 6 h of life. Colostrum contains **trypsin inhibitor**s to help to prevent breakdown of the antibody proteins. Antimicrobial factors such as lysosomes, lactoperoxidases and **lactoferrin**s are also present.

Antibody levels in colostrum drop rapidly over the first few days of **lactation**. By day 3, **globulin** levels are less than 10% of those in the first colostrums to be produced. If the dam has no colostrum, donor colostrum or frozen stored colostrum can be used. Commercial colostrum substitutes are also available. (EM)

Comfort eating

In humans it is recognized that eating may fulfil an emotional deficiency, often associated with stress, anxiety, depression, anger, apathy and alienation. Consumption of foods high in **sugar** and **fat** provide temporary alleviation of these conditions, and these are actively sought out when the animal is experiencing these negative emotions. The widespread availability of snack food, often

providing for rapid **absorption** of nutrients, and to a lesser extent a lack of exercise, are partly responsible. The presence of situational cues, such as regular attendance at social functions, is also believed to trigger comfort eating. It is commonly associated with **obesity** in both companion animals and humans, but although most animals respond to stress by varying their intake, approximately half undereat and half overeat. **Laboratory animal**s, in particular rats, also suffer from the same compulsion to eat during times of negative emotions. It is likely that this response evolved as a security for the animal in negative situations, for example when **feed** becomes in short supply. In many companion animals, especially dogs and cats, the permanent availability of a highly palatable diet is responsible for overeating. There is evidence that stress is associated with overeating in both dogs and cats, resulting in obesity. There are breed differences in susceptibility to **obesity** in companion animals, being more prevalent in Labrador retriever, Cavalier King Charles and cocker spaniels, cairn and fox terriers; in cats, domestic shorthairs are more at risk. Physiologically, comfort eating is associated with the generation of endogenous opioids, such as **endorphin**. Elevated corticosteroids during stress induce such behaviour, but consumption of high fat or sugar food suppresses corticotropin-releasing **hormone** and adrenocorticotropic hormone, suggesting that the chronic stress response has been diminished. (CJCP)

Common carp (*Cyprinus carpio*)

A **freshwater fish** of the family Cyprinidae, probably the most

abundant domesticated fish species. It has four subspecies: *C. c. carpio* of the European–Transcaucasian area; *C. c. aralensis* of the mid-Asian region; *C. c. haematopterus* of the Amur–Chinese or Far Eastern region; and *C. c. viridivio-laceus* of North Vietnam; and a large number of strains are known. The original natural distribution of common carp was probably restricted to a narrow belt in central Asia but it has been introduced into so many parts of the world that it now enjoys the status of a virtually global fish and its culture is very widespread. Common carp are omnivorous fish and can be polycultured with other freshwater species. Carp dig and burrow into pond embankments and sides in search of **organic matter**. They gulp in mud, from which digestible matter is sieved and the rest rejected – a habit that often makes pondwater turbid. In the wild, adult common carp thrive on decayed vegetable matter containing bottom-dwelling organisms, notably tubificids, **mollusc**s, chironomids, etc. In some countries the common carp is considered a nuisance species.

Although common carp have been farmed since ancient times, scientific studies of their **nutrition** is of relatively recent origin (mid-1960s) and most of the work is conducted on small fish under laboratory conditions and on post-juvenile stages in net-cage culture with practical diets. The protein requirement is 30–38% **crude protein** in the diet. Common carp can effectively utilize both **carbohydrate** and **lipid** as dietary **energy source**s. For growth of carp, the optimum ratio of digestible protein (mg) to energy (kcal) is 97:116. Common carp have no **stomach**, and it is better to feed them frequently, about four times a day. In 2020 the

total production of common carp in the world was 4.24 million tonnes. (RMG)

Comparative slaughter research
The sacrifice of research animals for the purpose of measuring changes in the composition of the whole body or in the mass or composition of a tissue. The whole animal or the part of interest may be analysed for some biochemical or chemical analyte. Animals in an initial control group are slaughtered at the beginning of the experiment to provide a baseline against which changes can be assessed. (JSA)

Compensatory growth
The accelerated growth that occurs when previously undernourished animals are well fed. They then appear to grow faster and more efficiently than similar animals that have been continuously fed. Compensatory growth occurs in ruminants and non-ruminants. It is sometimes referred to as 'catch-up growth', particularly in humans where it can be observed after a period of prolonged infection and poor food intake. In the agricultural context, it is characteristically associated with the spurt of growth that occurs when ruminants fed on low-quality conserved **roughage** are turned out to fresh grass in the spring or when the poor **forage** of a **dry season** is replaced by more nutritious growth when the rains return.

Undernutrition
may be either quantitative, with less feed consumed per unit of

time, or qualitative, with reduced concentrations of usable energy or specific nutrients in the diet. In ruminants, deficiencies of **ruminally available nitrogen** (RAN) and minerals such as **phosphorus** will reduce **feed intake**. The extent to which compensatory growth occurs depends on the severity of the undernutrition, the stage of growth during which it is imposed and the length of time for which undernutrition continues.

The precise scientific explanation of compensatory growth is fraught with many difficulties. Experiments purporting to demonstrate compensatory growth require great clarity of thought for proper elucidation. The growth rates of all animals slow down as they approach **maturity**, so when they are compared with ones that are physiologically younger, the latter will appear to be growing more rapidly. Compensatory growth in some circumstances may merely be a reflection of a rehabilitated animal rejoining its normal growth curve at a younger physiological age than its contemporaries. For this reason it is helpful to compare animals of similar physiological age (or weight range) rather than those of similar chronological age.

Many publications refer only to an acceleration of observed **liveweight** gain. This does not allow a distinction to be made between the growth of bone and muscle and the relatively simple changes resulting from a sudden increase in gut-fill (very significant in ruminants) or the rapid responses of the accessory organs of **digestion** such as the intestines and **liver**. Only in experiments where there has been a degree of **carcass** evaluation or measurement of chemical changes can tissue differences be

confidently affirmed.

Apparent changes in efficiency have been variously explained as a carry-over of adaptive responses to undernutrition, including a reduced **maintenance** requirement and reduced **energy cost**s of tissue deposition. Early feed restriction in broilers has been shown to reduce abdominal **fat** but not overall body weight, leading to an improvement in efficiency. This has been attributed to impaired hyperplasia of **adipocyte**s in the restricted groups.

Many experiments show an enhanced daily intake per kilogram body weight in the compensating group, as for example in pigs (Ratcliffe and Fowler, 1980). Another key feature of the apparent improvement in efficiency is due to tissues with a relatively low energy density being deposited in the gain of the compensating group. This is due to a preferential growth of muscles and organs rather than the growth of **adipose tissue**s (Blaxter, 1989; Lawrence and Fowler, 2002). In many agricultural situations, compensatory growth is a corollary of circumstances in which the growth curve is necessarily interrupted by a seasonal food shortage. Examples of deliberate exploitation of the phenomenon are rare, although Auckland *et al*. (1969) claimed that a 'low–high' pattern of protein concentration in the diet gave a greater efficiency of **protein utilization** in turkeys than did feeding them continuously with a high concentration. Deliberately slowing growth may be of benefit in the context of metabolic diseases such as **ascites** and bone disorders in poultry and this may be more acceptable if the period of retardation is followed by a period of compensatory growth. (VRF)

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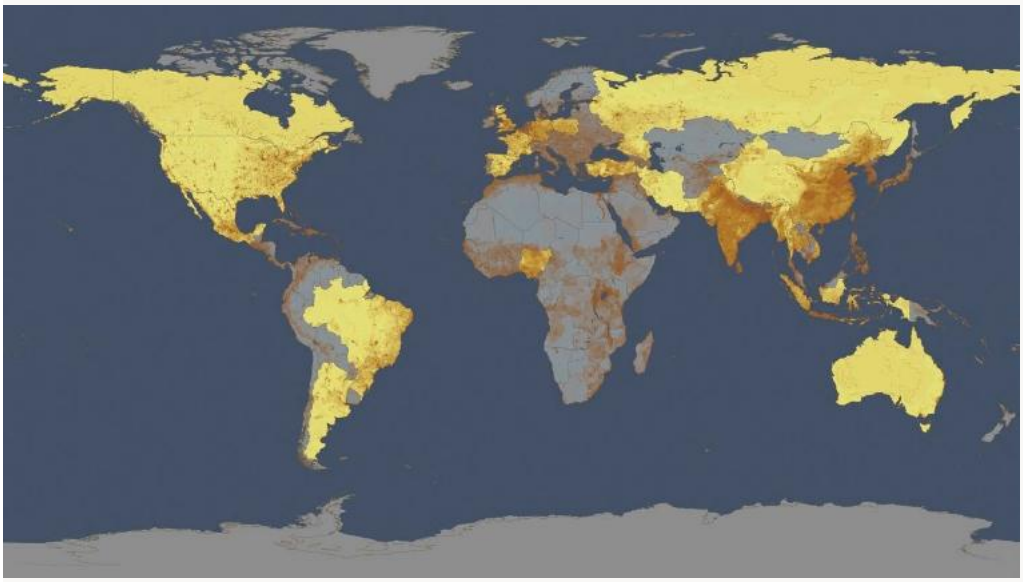
Competition

Animals in a group may compete with each other for access to food or water when availability of these resources is limiting relative to demand. This can occur if there is insufficient space at feeders or **drinker**s (especially nipples), or if the food or water supply is intermittent. Demand for food is greatest when animals are subjected to restricted feeding programmes, and demand for water increases when ambient temperature rises. Animals in a group tend to feed and drink synchronously, due to social facilitation, and competition at feeders and drinkers can lead to aggression, fights and injury, as dominant animals displace subordinate ones.
(JSav)

Competition for grain between humans and animals

Feed–food competition is one of the most contentious aspects of livestock production and modern threats to food security demand a disruptive shift in resourcing animal feeding. The ethical issue

presents as the trade-offs between using edible crops and other resources to either feed humans directly or feed livestock. **Grain**s are mostly grown in parts of the world with high populations, but some countries, such as Australia and Ukraine, are net exporters, whereas most countries in Africa are net importers.



Countries that produce most (82%) of the world's cereals (grain, oats, wheat, rice, maize, millet, sorghum) in 2008 are shown in yellow and the world population is shown in brown. Some countries, such as Australia, have low populations but are major grain producers; others, such as those in Africa, have large populations but grow little of the grain required for human consumption. Photo courtesy of NASA Goddard Photo and Video. Licensed under CC BY 2.0.



Should cattle be fed grain or forages? This dilemma will increase as world human population grows and there is not enough grain for human consumption. Photo courtesy of United Soybean Board. Licensed under CC BY 2.0.

Using food that could contribute to human food security to feed to livestock reduces the efficiency of utilization of land and other resources, first because the passage through any animal, including humans, involves a loss of nutrients, which are required to maintain the animal, and secondly because the ruminant livestock to which many grains are fed are inherently inefficient because of their use of microorganisms in digestive processes, again involving a loss of nutrients. However, **feed grain**s are nutrient rich, and these may enable inefficient livestock production to be made more efficient by increasing the animals' production rate. Decreasing the volume of grains used for livestock is most likely through the adoption of other alternative feeding options – such as agro-industrial **by-product**s, including the use of dried distillers' grains, **gluten** meal, **cassava** residue, castor meal, palm kernel meal, **algae** residue, biofuel co-products, animal offal and **faeces** – which could contribute to a reduction in the total part of grain in

the ruminant diet. The opportunity exists to improve the nutrient availability in low-quality agroindustrial by-products by pre-treatment with alkali, such as sodium hydroxide or **ammonia**. Another possibility to reduce reliance on grain is to use high-output green **fodder**, such as **leucaena**, **mulberry** or **glyricidium**. It has been contended that, in future, taxes may need to be introduced on the use of grains for livestock in order to protect their availability for human consumption (Phillips, 2015), particularly if world grain supplies are limited by trade disputes, wars, global climate change, plant diseases or fertilizer restrictions. Grains play an important role in the diet of humans living to 100 years or more, as shown in a study (Bernstein *et al*., 2004) of centenarians living on the Japanese island of Okinawa, who enjoy one of the longest life expectancies in the world. (DB; CJCP)

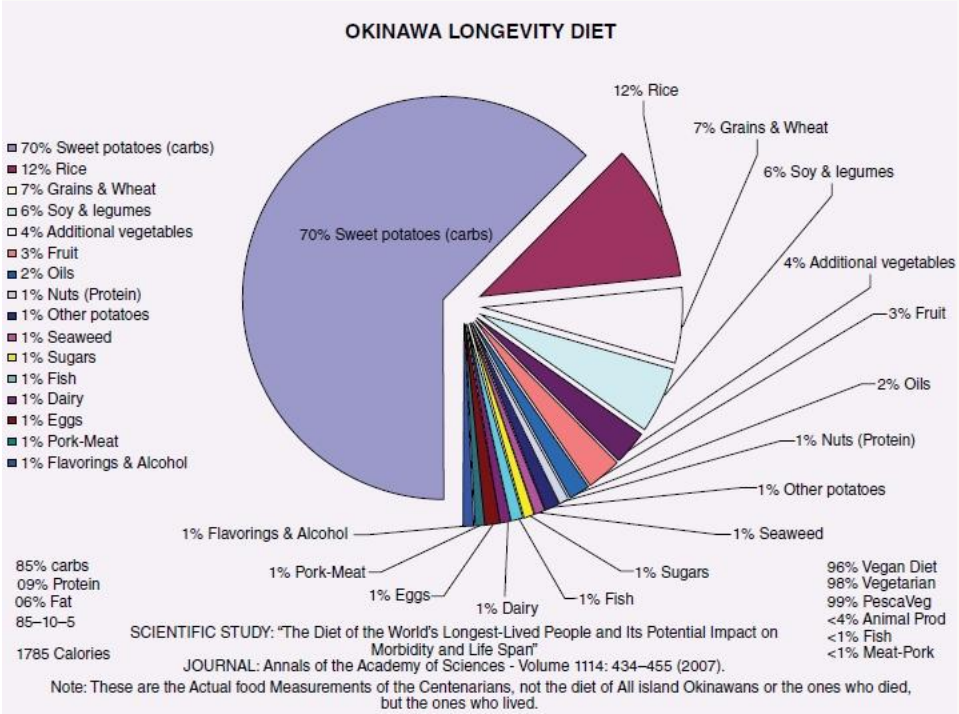


Chart of Foods eaten by the longest-lived Okinawan Japanese centenarians – 98% vegetarian, 96% vegan diet, only 1% pork, grain-based, anti-Paleo, anti-lowcarb diet. Courtesy of Centenarian Diet

Research. Licensed under CC BY 2.0.

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Complementation

The positive result of mixing one or more proteins to achieve a more favourable dietary **amino acid** pattern. When the amino acid pattern of one **protein** or mixture of proteins provides amino acids that are limiting in the pattern of another protein, the process of mixing the proteins in a specified ratio yields a mixture of amino

acids that meet the animal's needs for a specific process (e.g. **growth**, **milk** production) at a lower total **nitrogen** intake. Thus, the amino acid pattern of one protein complements that of another. (NJB)

Complete feed

A mixture of dietary ingredients designed to meet all the **nutrient requirement**s of an animal. The mixture is normally mixed to a uniform blend so that the animal cannot select individual ingredients.

For pigs and poultry, complete feeds are usually blended from **cereal**s and **protein source**s, with added **oil**, **minerals** and **vitamins** to meet requirements. For ruminants, complete feeds (often referred to as total mixed rations) contain a mixture of forages, **by-product**s, cereals, protein sources, **fats**, minerals and vitamins.

Complete feeds are normally designed to be fed *ad libitum*, which requires an estimation of potential voluntary **feed intake**. Where less productive stock are offered complete feeds (e.g. **sows** in early pregnancy), the **metabolizable energy** content of the complete **feed** is normally reduced, by inclusion of high-fibre sources, so as to limit **energy intake** and prevent excessive deposition of **body fat**. In ruminants, voluntary feed intake is usually greater when forages and concentrates are mixed as a complete feed than when offered separately. This is because the microbial population of the **rumen** reaches a stable equilibrium that enhances the **digestibility** of the **forage** components. Complete feeds also allow utilization of less-palatable feed

ingredients that would otherwise be rejected when fed separately. (PCG)
See also: Total mixed ration

Composition:
see Body composition; Botanical composition; Chemical composition; Feed composition; Meat composition

Compound feed
A mixture of different dietary ingredients blended together to form a complete **feed** for non-ruminants, or a supplementary feed to complement **forage** for ruminants. Compound feeds contain **carbohydrate** sources, such as **cereal**s, and **protein source**s, such as **oilseed**s or fish meal, with **mineral and vitamin supplement**s. The ingredients are usually milled to reduce **particle size** and aid mixing. Most compound feeds are pelleted for ease of handling and use on farms. The energy content of pelleted compound feeds is often increased by spraying oil onto the pellets during the final phase of manufacture. Compound feeds are colloquially referred to as **concentrates**. (PCG)

Computed tomography (CT)
Also called computed axial tomography (CAT), a specialized form of X-ray technique that acquires cross-sectional images of the body. The X-ray source and scanner rotate around the body measuring the transmission of the X-ray beam from which cross-sectional images are generated by computer. The image has dark and light areas corresponding to specific tissues. Computed tomography is

used in animal nutrition studies to detect and measure **adipose tissue**, **muscle** and bone. CAT scanning is widely used in clinical practice. (SPL)



Computed tomography image of nautile seashell (*Nautilius pompilius*). Photo courtesy of Royonx. Licensed under CC BY-SA 3.0

Computer software

Programs, or series of instructions, performed by a computer to fulfil a task or application. For example, a word processor, database, spreadsheet or **feed formulation** utility. (RG)

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Concentrate

A generic term to describe any non-forage dietary ingredient, usually for **herbivore**s. A commonly used definition is 'a feed which contains less than 18% **crude fibre**' (about 24% **acid detergent fibre**). Concentrates are usually classed as protein or energy concentrates, depending on whether they have more or less than 20% protein. Concentrates include **compound feed**s, **protein concentrate**s, single raw materials (also called straights) and **supplement**s. The concentrate:forage ratio of a ration is the sum of these ingredients divided by the total forage content of the ration, though some classes of stock may be fed on 100% concentrates, with no forage component.

Concentrates are generally more readily digested, and may contain greater concentrations of **metabolizable energy** and protein than forages, although immature temperate **grasses** can have 25% or more protein. Because of their lower fibre content, concentrates are also fermented more rapidly in the **rumen**. Production responses in growing stock to concentrate **supplementation** normally arise through alterations in the molar proportions of the principal **volatile fatty acid**s within the rumen, high-**grain** diets resulting in increased **propionate** production from the rumen. With the possible exception of protected sources of **starch**, older and more slowly growing cattle seldom benefit from 'rumen-protected' supplements, the products of rumen **fermentation** normally being sufficient to meet their requirements for **maintenance** and growth. Further exceptions to this rule arise when young cattle (particularly non-castrated males) undergo **compensatory growth** or have an abnormally high

potential for lean tissue growth, e.g. the doubled-muscled breeds.

Rapid consumption of starchy concentrates in large quantities can upset rumen fermentation. Starch is rapidly fermented in the rumen, leading to a build-up of **lactic acid** and drop in rumen pH. Fibre **digestion** and rumen movements are both adversely affected when the rumen pH falls to about 5.5. As well, when ruminants are fed diets with little fibre they chew less and produce less **saliva**. Consequently, the buffering action of saliva is reduced, exacerbating the drop in rumen pH. Acute cases of acidosis arise when animals accidentally gorge themselves on concentrates, often resulting in death within hours. Mild acidosis (sub-acute acidosis, SARA) occurs in dairy cows or beef cattle given a high-concentrate diet and may be associated with reduced **forage** digestion, low **milk** fat content and **laminitis**

Cattle fed on an all-forage diet normally have volatile fatty acid concentrations in the rumen of approximately 70% **acetate**, 20% **propionate**, 8% **butyrate** and 2% others. Feeding starch-rich concentrates increases the proportion of propionate in **rumen fluid**, since this volatile fatty acid is an end-product of starch digestion. Propionate is a major precursor of **glucose** and so increased propionate production from concentrates results in increased circulating levels of **insulin** and greater **body fat** deposition. Concentrates are therefore useful for **fattening** animals and for lactating animals in early **lactation** that would otherwise be unable to consume sufficient energy to meet the requirements of milk production. Concentrates are also the major source of undegradable protein in ruminant diets which, for high-

producing animals, is an essential supplement to **microbial protein** produced in the rumen. They are also used to provide **mineral and vitamin supplement**s.

Concentrates are usually fed at a restricted rate in order to avoid disrupting rumen function and also because they are more expensive than forages. Large allowances of concentrates should be divided into two or more separate meals.

Lot-fed beef cattle are typically given diets that contain 70–90% cereal grain and other concentrates. These diets are introduced gradually, and lot-fed cattle may be given an introductory diet that has only 20% or 30% concentrate to start with, gradually increasing to the growing diet composition over 2–3 weeks. (PCG; GMcLD)

Further reading

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Conception rate

Strictly defined as the number of animals conceiving, expressed as a percentage of the total number mated or inseminated. It is not normally possible to detect that an animal has conceived until some time after the event so that, in practice, conception rate is often synonymous with pregnancy rate. It may be expressed as the non-return rate, which is the percentage of animals not seen to return to oestrus within a defined period after mating or insemination.

Conception rate depends on the proportion of females that ovulate close to the time of insemination and on the proportion of ovulating females whose ova are fertilized. This in turn depends on the viability of the ova, the uterine environment and the number

and viability of available spermatozoa.

Provided that females are not malnourished, nutritional levels tend to affect the number of ovulations, rather than the occurrence of ovulation. Severe underfeeding is likely to suppress cycling and oestrous behaviour. The female is thus less likely to be mated, and there will be no effect on conception rate per se.

Specific nutritional imbalances may affect the reproductive tract environment. High levels of dietary protein have been associated with low pregnancy rates in cows, for example. (PJHB)

Conditioning

The mechanical treatment of crops at the time of mowing. The aim is to provide a rapid rate of moisture loss from the crop with minimal loss of **dry matter**. Conditioners are an integral part of the mower and can range from a simple mechanical tine that lacerates the crop, to a more complex mechanism with rubber or metal rollers. (RJ)

Connective tissue

A tough sheet of fibrous tissue found as the outer membrane of organs (**liver**, kidney, **muscle** or skin), or the tough cord-like tissue that connects muscles to bones (tendons), or the tough fibrous tissue that connects bones to **cartilage**, muscle or other bones (ligaments). Connective tissues comprise primarily extracellular **collagen** fibres that appear white. Another abundant protein in some connective tissue is elastin, which is yellow. (TDC)

Contamination
The presence of substances not intentionally added and usually of an undesirable nature. Common examples include: toxic elements occurring naturally or picked up during transport next to inappropriate substances or in dirty containers; **pesticide** residues from incorrect use; fruits or seeds of poisonous plants; or toxic fungal bodies such as **ergot**. **Aflatoxin**s may develop in poor storage conditions and microbial pathogens such as salmonella may contaminate feeds. Lack of care in the feedmill may lead to one feed being contaminated by another. It is particularly important to avoid contaminating a non-medicated feed with one containing a medicine. (CRL)

ConvulsionsElectrolyte
imbalances, especially **magnesium** deficiency, can upset the electrical potential of brain neurones, causing them to be hyperexcitable. This can cause uncontrolled motor neurone excitation, leading to irregular and spastic muscle contraction due to excessive excitation of neurones within the brain. (JPG)
See also: Hypomagnesaemia

Cooking:
see Heat treatment

Copper (Cu)
A mineral element with an atomic mass of 63.546. Copper is an essential dietary component for all farm animals. Copper is a transition element and has two redox states, Cu^{+} and Cu^{2+}. It is one

of the most biologically active mineral elements and is an indispensable part of many enzyme systems involved in electron transfer and **oxidation**–reduction reactions in mammalian systems. Some of these Cu enzymes have **antioxidant** activity and are involved in the **metabolism** of reactive **oxygen** species such as **superoxide** and **hydrogen peroxide**. Others have ferroxidase activity, oxidizing Fe^{2+} to Fe^{3+}.

In most non-ruminant mammals, ingested Cu is absorbed primarily from the **duodenum**. The mechanisms of **absorption** involve transport proteins that are located in the plasma membranes of the **enterocyte**s. These include CTR1 for Cu influx and ATP7a for Cu efflux. A genetic aberration in the gene for ATP7a produces a dysfunctional transporter allowing Cu to accumulate in the enterocyte, with little transferred to the blood. Although the mechanisms of Cu absorption in farm animals have not been studied to this extent, they are probably similar. After Cu is transferred to the blood, it is transported to the **liver** and other organs bound to serum **albumin**. Similar transport proteins as found in the intestine probably affect Cu uptake into the liver and other tissues; however, the efflux transporter in liver is ATP7b. Aberrations in this gene cause Cu accumulation in the liver.

In cattle, copper concentrations below 20 mg kg^{-1} DM in the liver or 0.5 μg ml^{-1} in the plasma indicate deficiency (NRC, 1996). During low intakes of dietary Cu in young animals, the Cu concentration in plasma can decrease to one-half the normal value within a few weeks. Adult animals are more resistant to Cu deprivation than the young. If the deficiency is allowed to progress,

the animals can die of an aortic dissecting aneurysm, caused by the reduction of the Cu-dependent enzyme lysyl oxidase that cross-links **collagen** and elastin fibres.

The outward signs of Cu deficiency in mammals are less evident than with other **mineral deficiencies**. Food intake and weight gain are not affected to a great extent but the animals will develop **anaemia**. Copper-containing enzymes will be reduced in activity and can result in increased susceptibility to oxygen stress. Large blood vessels can weaken and lead to aneurysms. Copper deficiency *in utero* can lead to neurological damage in the offspring that is irreversible. An example is 'swayback' (**enzootic ataxia**) in sheep, where the **myelin** sheath of the spinal cord does not form correctly. High **zinc** concentrations in the diet can interfere with Cu absorption and lead to signs of Cu deficiency. **Ruminant animal**s that consume diets modestly high in **molybdenum** and **sulphur** are susceptible to Cu deficiency because of the *in vivo* formation of thiomolybdate that binds Cu and renders it unavailable for absorption.

According to the US National Research Council, the Cu requirement of most farm species, including dairy and beef cattle, and horses is approximately 10 mg kg^{-1} diet for all age groups. The requirement for pigs can range from 3 to 6 mg kg^{-1} diet, with the young animal requiring more than the adult. The Cu requirement for poultry ranges from 4 to 5 mg kg^{-1}; the young chick requires more than the adult.

Ruminants are rather susceptible to Cu toxicity. Hepatic necrosis has been observed in calves fed 45 mg Cu kg^{-1} diet for 13

weeks; however, adult cattle seem to show no adverse effects after consuming 200 mg daily for up to 15 weeks. Sheep, on the other hand, develop toxicity signs when exposed to as little as 30–80 mg Cu kg^{-1} diet for 20 weeks, but when dietary sulphur and molybdenum are low, Cu toxicity signs can develop with as little as 11 mg dietary Cu kg^{-1}. Young swine can show toxicity signs when fed Cu in excess of 250 mg kg^{-1} diet but Cu fed at levels of 100–250 mg kg^{-1} can promote growth in weanling pigs. Toxicity signs manifest themselves mostly as reductions in growth rates and/or haemolytic responses. (PGR; GMcLD)

See also: Availability; Iron; Thiomolybdates

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Copra:

see Coconut

Coprophagy
The consumption of **faeces**, generally implying the animal's own faeces. Nutritional benefits include the consumption of **B-complex vitamins** and bacterial proteins synthesized by microbes in the hindgut. In some animals, such as the rabbit, the process is more correctly referred to as caecotrophy and the ingested material referred to as caecotropes. Small herbivores such as rabbits and guinea pigs selectively excrete fibre and retain non-fibre components in the **caecum**, where they are fermented. At intervals, the caecotropes (night faeces, soft faeces) are consumed. Coprophagy and caecotrophy increase the **digestibility** of feeds, because of enhanced caecal **fermentation** and a second transit of ingesta through the digestive tract. (PC)

Cori cycle
A metabolic cycle in which **lactate** produced from **glucose** by anaerobic **metabolism** in **muscle** is recycled to the **liver** and converted back into glucose. Anaerobic **glycolysis** in muscle produces **pyruvate**, which is reduced to lactate by the NADH produced in glycolysis. The Cori cycle also occurs in animals with an adequate supply of molecular **oxygen**. (NJB; GW)

Corn
Any growing **cereal** crop or harvested **grain** may be referred to as 'corn', especially the predominant crop of a particular area (such as **wheat** in England, **oats** in Scotland or **maize** in the USA). (ED)

Corrinoids

Compounds containing the basic octadehydrocorrin ring structure of vitamin B_{12} and related compounds. Similar structures are the **iron** porphyrin ring of haem in **haemoglobin** and the **magnesium**-containing porphyrin of **chlorophyll**. (NJB)

Corticoids:
see Adrenal

Corticosterone:
see Adrenal

Cortisol:
see Adrenal

Cottonseed
The seed of cotton (*Gossypium* spp.) is obtained as a **by-product** of cotton fibre production, about 2 t of seed for each tonne of fibre. The seeds contain about 200 g of **oil** kg^{-1}, which contains a high proportion of **unsaturated fatty acid**s. The oil is often extracted by compression and the fibrous husk is pressed with the seed kernel. The resultant cake is known as undecorticated cake and has a **crude fibre** content of around 300 g kg^{-1}; the decorticated cake has about 90 g kg^{-1}. This difference in fibre considerably affects the **nutritive value** of cottonseed, especially for non-ruminants. Decorticated meal has a **protein** content of 400–500 g kg^{-1}, the undecorticated meal 200–250 g kg^{-1}. The protein is first limiting in **lysine**. Undecorticated cottonseed meal has an apparent **metabolizable energy** for poultry of about 8 MJ kg^{-1} while for

ruminants it is about 12 MJ kg^{-1}. Cottonseed meal is rarely included in the diets of poultry or at levels of more than about 100 g kg^{-1} for mature ruminants, because it may cause digestive problems. Cottonseed and the meal contain condensed **tannins**, a **polyphenol**ic **aldehyde**, **gossypol** and two cyclopropenoid **fatty acid**s (malvalic and sterculic acids). The tannins are present in small quantities (less than about 30 g kg^{-1}) and may reduce nutrient utilization slightly. The older varieties of cotton can contain up to about 20 g kg^{-1} but the newer cultivars have much lower concentrations in the seed.

Like tannins, gossypol chelates mineral elements and may reduce their **absorption**. **Iron** salts are sometimes added to **chelate** the gossypol and thus reduce the effects in animals. Processing the seed may cause reaction of gossypol with lysine, reducing its **availability**. Gossypol has an adverse effect on rumen microbes and is also associated with reduced reproductive capacity in animals. Feeding cottonseed to sheep has been shown to reduce **protozoa**l numbers but it is uncertain if this was due to the effects of the gossypol or of the oil. Other adverse effects of gossypol include coloration of **egg** yolks in hens' eggs due to chelation of minerals. The cyclopropenoid **fatty acid**s disturb **lipid metabolism** in animals and reduce performance. (TA)

Coumarin:
see Dicoumarol

Cow
The mature female of any species of Bovidae (cattle). The term is

usually applied after the animal has delivered her first calf. Before that, she is called a heifer. (PJHB)

Cow pregnancy

Pregnancy in the cow lasts from the time of fertilization of an **ovum** or ova in the oviduct until the resulting conceptus leaves the uterus. In a successful pregnancy a live **calf**, with its associated placenta, is born approximately 9 months after fertilization. The average length of gestation is typically 280–285 days but depends to some extent on the breed, particularly of the sire. For example, when used to inseminate Friesian cows, bulls of large breeds such as the Charolais, Simmental or Chianina tend to produce longer **gestation period**s than Friesian or Hereford bulls.

A cow normally ovulates one ovum at each oestrous period. Occasionally two or more are ovulated (*see* Twinning). More rarely, a fertilized embryo may divide to form identical twins.



Charolais cow with twins. Photo courtesy of Elisa Antognini. Licensed under CC BY 2.0.

Immediately after fertilization, the ovum begins to divide,

forming a solid cluster of cells or blastomeres known as a morula (mulberry shape). This process takes 5 or 6 days, during which the embryo continues its passage down the oviduct and enters the uterus. From about day 6 after fertilization, the ovum hollows out to become a blastocyst, which consists of a single spherical layer of cells, the trophoblast, with a hollow centre and an inner cell mass at one edge. The inner cell mass is destined to form the embryo, whilst the trophoblast provides it with nutrients and will form the fetal component of the placenta. At about day 8 the blastocyst 'hatches' from its shell (the zona pellucida) and begins to elongate rapidly. From about day 14 the development of the so-called germ layers begins within the inner cell mass. These are termed the ectoderm, mesoderm and endoderm. The ectoderm gives rise to the external structures such as skin, **hair**, **hooves** and **mammary gland**s and also the nervous system. The heart, muscles and bones are eventually formed from the mesoderm whereas the other internal organs are derived from the endoderm layer. By day 45, formation of the primitive organs is complete.

The embryo is able to exist for a short time by absorbing nutrients from its own tissues and from the uterine fluids, but it ultimately becomes attached to the endometrium by means of its membranes through which nutrients and **metabolite**s are transferred from mother to fetus and vice versa. In the cow, **antibodies** cannot pass the placental barrier and the calf is thus dependent on the first **milk** (colostrum) produced by its mother at parturition to acquire **immunity** from her. The attachment process is known as implantation and may begin as early as day 20,

although definitive placentation does not occur until days 40–45. If the cow is carrying twins, the placentae and their blood supplies tend to grow together. Thus, sex **hormone**s from a male which is co-twin to a female are likely to interfere with the development of her sexual organs, resulting in a sterile female called a freemartin. The male may be affected to a lesser extent by hormones from the female. Twin calves are somewhat less likely to survive than singles, especially if they are developing in the same uterine horn.

Fetal growth is exponential throughout gestation, the rate increasing as pregnancy progresses. Thus, fetal requirements for **energy**, **protein** and **minerals** increase rapidly, especially during the last third of gestation (see table).

Deposition of nutrients and energy in the uterus of the cow. (Source: McDonald *et al.*, 1995.)

	Deposited in uterus (per day)			
Days after conception	**Energy** (kcal)	**Protein** (g)	**Calcium** (g)	**Phosphorus** (g)
100	40	5	–	–
150	100	14	0.1	–
200	235	34	0.7	7
250	560	83	3.2	22
280	940	144	8.0	44

Days after conception	Deposited in uterus (per day)			
	Energy (kcal)	**Protein** (g)	**Calcium** (g)	**Phosphorus** (g)
Maintenance[(a)]	7000	300	8.0	12

[(a)] Approximate net daily maintenance requirement of a 450 kg cow.

Uptake of nutrients by the uterus and its contents is less efficient than for the cow's body in general, so that nutritional requirements to meet the demands of pregnancy in the cow are actually higher than the amounts deposited in the uterus. Furthermore, **fasting metabolism** during pregnancy is higher than that in non-pregnancy, because of a higher **basal metabolism** in the mother herself rather than the heat produced by the fetus. This may be a response to changes in hormone levels during pregnancy and it increases throughout pregnancy. This, together with the **liveweight** increase that should occur, leads to a gradual rise in the maintenance **energy requirement**. Thus, the requirement for energy in pregnancy is increased by far more than would be deduced from the storage of energy in the fetus. Nevertheless, in early pregnancy, nutritional requirements for pregnancy per se are small, especially in relation to the requirements for **maintenance** and for **milk** production in the mid-**lactation** cow. It is only in the last 3 months of pregnancy that special dietary provision has to be made for the growth of the

fetus. At this stage, net requirements for protein and minerals such as **calcium** and **phosphorus** are quite substantial. Additionally, in the last 2 weeks, when mammary growth is fastest, a relatively modest 45 g protein per day is deposited in the udder. **Metabolizable energy** requirements for **fetal growth** are still quite small in relation to maintenance requirements. Furthermore, in the dairy cow, there will be no energy demands for lactation in the last 2 months or so of pregnancy. Dry pregnant dairy cattle normally have a dry-matter **appetite** in excess of their requirements. It is thus relatively easy for a cow to gain weight during this period, and it is usually necessary to restrict **energy intake** at this time to avoid the cow calving at too high a condition. The latter can lead to calving difficulties and subsequent **metabolic disorder**s, such as fatty liver syndrome, which can seriously affect production and reproductive performance. Intake can be restricted by feeding a single **forage**, such as grazed **grass** or **silage**, or by including chopped cereal **straw** in the diet to raise its cell wall content. (PJHB)

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Cowpea (*Vigna unguiculata*)
A leguminous plant grown in the semi-arid and sub-humid tropics, primarily for its seeds. These contain 200–300 g **crude protein** kg^{-1} and have an apparent **metabolizable energy** of about 14 MJ kg^{-1} for both sheep and poultry. The proteins are relatively low in **sulphur** amino acids. The seeds contain **protease inhibitor**s: this limits the usefulness of raw seeds. The protease inhibitors can be inactivated by **heat treatment**. Cowpeas may be used as a green or dried **fodder** with a **protein** content of about 120 g kg^{-1}. (TA)



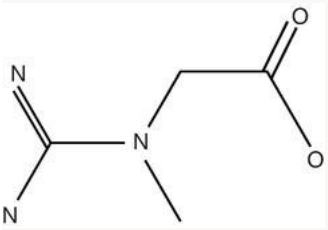
Cowpeas. Photo courtesy of Greenhouse 17. Licensed under CC BY 2.0.

Crambe
An annual of the *Brassica* group, native to the Mediterranean area and cultivated in North and Central America. *Crambe abyssinica* is grown for its **oil**, which is used in industry and contains 50–60% **erucic acid**. The residual crambe seed meal has value as a **supplement** in livestock and poultry feeds because of its high **protein** content (300–400 g kg^{-1}) and well-balanced **amino acid** content. However, the seeds contain anti-**metabolite**s, including **goitrogen**s, and unprocessed meal is limited to 5% inclusion in diets for adult ruminants and is unsuitable for inclusion in non-

ruminant feeds. (JKM)

Crazy chick disease (encephalomalacia):
see Vitamin E

Creatine
$HN{=}C(NH_2){\cdot}N{\cdot}(CH_3){\cdot}CH_2{\cdot}COOH$. Creatine is produced in a number of steps, first in the kidney and then in the liver, from **arginine**, **glycine** and **methionine**. It is converted to creatine phosphate in muscle (ATP + creatine ⇌ creatine phosphate + ADP), where it serves as an energy reserve to convert ADP to ATP during times of high ATP use. Creatine is oxidized and then excreted in the **urine** as **creatinine**. (NJB)



See also: Adenosine triphosphate

Creatinine
The anhydride of **creatine** and the end-product of creatine breakdown (by loss of H_2O and P_i) in muscle followed by total excretion by the kidney. Creatinine excretion is related to muscle mass and thought to be constant over 24 h. For this reason it is used in clinical settings as a basis to calculate total 24 h **urine** excretion from a single urine **sample**. (NJB)

Creep feeding

The feeding of supplementary diet to **suckling** animals, most commonly applied to piglets. This practice allows piglets to compensate for any deficiencies in sow **milk** production and become gradually accustomed to eating solid food; it also induces development of the digestive **enzymes** necessary for breakdown of complex **carbohydrates** on which they will be dependent for energy after **weaning**. Because of the high nutritional quality of sow milk, piglets generally consume very little solid food before 3 weeks of age. However, if weaned later than this, creep feed will be consumed increasingly as milk supply declines and becomes inadequate. Thus, whilst creep feeding of piglets weaned at 3 weeks of age or younger is generally of little benefit, piglets weaned at later ages will show increased growth rate both before and after weaning.

There are large and unexplained differences, both within and between litters, in the quantity of creep feed consumed. To achieve good intake, it is necessary to feed a highly digestible and palatable diet containing a high proportion of milk products. Intake is further encouraged by freshness of feed, achieved by feeding little and often, and by presentation in a feeder in which the diet is easily visible and accessible. (SAE)

See also: Piglets

Crib biting

A form of oral dyskinesia associated with stress in horses, in which the horse grasps a horizontal part of its wooden enclosure and aspirates repeatedly. It then flexes its neck and aspirates into the pharynx. It can be avoided if there is adequate environmental

enrichment and exercise. It occurs in 2–5% of horses and will devalue a horse, which is normally identified as a 'cribber' to the seller. The behaviour may redirect to **wind sucking.** There are various methods to stop the behaviour, but none adequately address the cause of the problem. Cribbing straps may be fitted, creosote or other noxious substances painted on the horizontal surfaces of the stable, and collars may be fitted to stop the aspiration process. (CJCP)

Crop

The crop (ingluvies) is a thin-walled diverticulum of the oesophagus and has the same basic structural pattern as the remainder of the digestive tract. The presence and function of the crop varies among avian species and, in poultry, major functional differences exist between altricial species like pigeons and precocial species like chickens and turkeys. In breeding pigeons, physiological changes induce epithelial hyperplasia and the production of rice-shaped pellets composed of parakeratinized cells ('crop milk') which are regurgitated to feed young squabs. In chickens and turkeys, the crop serves as a site for storage and moistening of ingested feed, initiation of **digestion** by bacterial and **feed enzymes**, and a first line of defence against poultry pathogens and zoonotic organisms. The latter function relates to crop adaptive and innate immune function as well as reduced pH caused by **lactic acid** derived from content **fermentation** by the lactobacilli-dominated microbiota. Regular and extended feed storage (crop utilization) is required for efficient crop function and

factors affecting storage include diet, frequency of feeding and the use of extended dark periods in lighting programmes. Healthy and functional crops benefit bird well-being and performance. (HLC)

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Crop fractionation:

see Fractionation, green-crop

Crop residues:

see Stover; Straw; Winemaking residues. *See also:* individual crop

Cross-sucking

Calves naturally have a motivation to **suckle** from their mother, which lasts for many months after they are born, or even a year. Because they are normally weaned off their mother's **milk** at an early age in dairy herds, and fed milk replacer, the motivation to suckle persists and may only be satiated when the calf sucks at other objects: the bars of their pen, parts of neighbouring calves (e.g. ears, prepuce, mouths), the bucket from which they are fed and any other suitable appendage. This is particularly the case if milk is fed from a bucket rather than via a teat connected to a vat of milk. Milk in a bucket is imbibed solely by **sucking**, whereas it is extracted from a teat by both sucking and squeezing the teat with

the lips. These redirected behaviours mostly occur immediately after imbibing milk and may be reduced by provision of an empty teat at this time. **Lactose** in milk provides a sweet reward for suckling and, as calves are usually fed less milk replacer than they would naturally obtain from their mothers, they naturally seek more when milk consumption is ended. This redirection of a motivation suggests that the calves' **welfare** is impaired. Furthermore, cross-sucking in calves may lead to the taking of milk from other cows in adulthood (milk stealing). This encourages farmers to put a plate in the nose of the suckling cow with spikes in it to create pain in the suckled **cow**, who then refuses to allow this behaviour. Cross-sucking can be prevented by providing access to the calves' mothers (or other cows) for two short periods per day (*see* Intersuckling). Cross-sucking usually terminates when the calf begins to ruminate after consuming solid feed. (CJCP)

Crucian carp (*Carassius auratus*)

A common omnivorous **freshwater fish** in Eurasia and an important economic **aquaculture** fish, with very fine bones and desirable **meat quality**. By hybridization, some new 'breeds' of aquaculture carp have been obtained, such as gibel carp (*Carassius auratus gibelio*♀ × *Cyprinus carpio*♂), allotriploid crucian carp (*Carassius auratus red var*♀ × *allotetraploid Carassiusauratus*♂), and hefang crucian carp (*Carassius auratus* cuvieri *Tem-minck et Schlegel*♀ × *Carassius auratus red var*♂). *C. a. gibelio* (Bloch) has been becoming one of the most important freshwater aquaculture species in China since its special **reproduction** mode of gynogenesis was applied in the early 1980s (Gui and Zhou, 2010).

Successive artificial breeding of several improved varieties with excellent growth performance, such as the allogynogenetic gibel carp 'CAS III', have further improved its suitability for aquaculture. Annual global output was approximately 3.0 million tonnes in 2019. (QS)

Reference

Gui, J.F. and Zhou, L. (2010) Genetic basis and breeding application of clonal diversity and dual reproduction modes in polyploid *Carassius auratus gibelio*. *Science China. Life Sciences* 53, 400–415. doi: 10.1007/s11427-010-0092-6

Cruciferae

Cabbage (*Brassica*) family, consisting of some 300 genera and 3000 species, including **cabbage**, sea cabbage, **kale**, Brussels sprouts, **cauliflower**, broccoli, **kohlrabi**, **oilseed rape**, **mustard**, radish, **crambe** and related weeds and herbs. (JKM)

Crude fibre

A collective term for complex **carbohydrates**, mainly **cellulose**s and **lignin**, that are insoluble in water, dilute acid and dilute alkali. There are various ways of estimating fibre, each of which defines a somewhat different fraction. In the **proximate analysis** of foods (the **Weende** system) crude fibre is measured by digesting a feed sample successively with dilute acid (1.25% **sulphuric acid**) and dilute alkali (1.25% sodium hydroxide). Soluble components such as **sugars**, **starch**, **fat** and **protein** are thereby removed, leaving an insoluble residue. The weight loss on ignition of this dried residue represents crude fibre. Other methods for examining

complex, insoluble carbohydrate in feeds have involved the use of a neutral detergent that removes soluble material and leaves behind cellulose, **hemicellulose** and lignin (neutral detergent fibre). Subsequent boiling with an acid detergent hydrolyses the hemicellulose, leaving behind cellulose and lignin (**acid detergent fibre**). **Oxidation** of lignin with **potassium** permanganate leaves cellulose and **ash**. Ignition of this residue gives a value for cellulose. (CBC)

Crude protein

The crude protein content of a feed, or other biological material, is defined as its N content multiplied by the factor 6.25. The value of this factor is based on the observation that N occurs in different proteins in a fairly constant proportion, 16% on average. In determining the crude protein content of a material its N content is measured, usually by a **Kjeldahl** procedure. Crude protein is not an exact measure of the protein content of a material, because different proteins have different proportions of **amino acid**s and their N content may thus vary a little from 16%, and also because not all the N present in biological materials is in the form of protein. Compounds, other than protein, that contain N are generally classed as non-protein N. These compounds are diverse in structure and function; they include free amino acids, **amine**s, **amide**s, **purines**, **pyrimidine**s and nitrogenous **lipids**. The level of non-protein N in most animal feeds and tissues is very small compared with the level of protein N. In addition, much of the non-protein N in feeds may be utilized by animals for the synthesis of non-essential amino acids or, in the case of ruminants especially,

for the synthesis of **microbial protein**. Although the use of an average conversion factor of 6.25 does not lead to an exact value, the protein content of feeds and the protein requirements of farm animals are invariably expressed in this way. (CBC)
See also: True protein

Crushing
Usually refers to the pressing of **oilseed**s in order to extract their **oil**. Oil-rich vegetable seeds, such as **soybean** (20% oil), oilseed **rape** (46%) and **linseed** (39%), are first dehulled and then crushed between rollers or in a screw press. The resultant oil is collected, further purified and used for other purposes. The remaining meal is known as expeller or cake and still contains approximately 10% oil. This can either be used as an animal feed or, more commonly, it undergoes further chemical treatment to extract the remaining oil.

Crushing can also refer to rolling, especially of cereals such as **oats** and **barley**, to prepare them for feeding. This is also known as 'bruising'. (MG)

Crustacean feeding
Fisheries biologists have always had some interest in the type of food needed by large crustaceans such as **lobster**, **shrimp** or prawn. These animals were known to thrive on a variety of **mollusc**s, worms and other invertebrates found in **aquatic environment**s. Aquaculturists interested in culturing crustaceans used this knowledge to maintain crustaceans in the laboratory and, in the case of shrimp and the prawn, to produce limited numbers in

ponds where abundant supplies of natural feeds were present. However, in the 1970s as culturists became interested in intensifying the production of crustaceans, natural feeds quickly became a limiting factor. The lack of suitable formulated feeds and, more importantly, the paucity of information on what was needed to make formulated diets for crustaceans, stimulated research interests in **aquaculture** centres throughout the world.

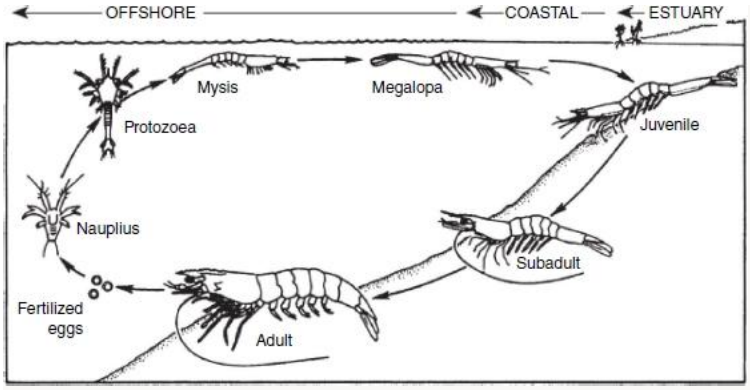


Shrimp netting in Bangladesh. Photo courtesy of Josey Shawaa. Licensed under CC BY-SA 2.0.

The initial flurry of nutritional research encompassed a fairly diverse group of crustaceans, including lobster, shrimp, the freshwater prawn and crayfish, but today this has narrowed to focus primarily on marine shrimp. Commercial pond production of marine shrimp grew exponentially during the 1980s to become a significant industry in a number of tropical countries. Early culturists almost always used an extensive approach that depended on enriching the natural productivity of the pond ecosystems to

provide food for the shrimp. However, intensification in response to continuing market demand necessitated the direct addition of feeds to increase production per pond area. As a consequence, crustacean nutritional studies became centred on providing information applicable to marine shrimp and the need to formulate artificial feeds for their culture.

Culturing of marine shrimp and many other crustaceans is made more difficult by the fact that they have complicated life cycles, with each stage requiring a distinct type of feed. Such a life cycle is not unusual for crustaceans of aquacultural interest. The nauplius sustains itself on stored yolk but the rest of the hatchery (sub-juvenile) stages have distinctive requirements. Protozoea feed exclusively on **algae** or other similar-sized microscopic feedstuffs. Increasingly, specific species of algae are cultured to provide an optimum feed for the protozoea stage. After a few days the protozoea stage moults into a mysis stage that requires **zooplankton** rather than **phytoplankton** for continuing growth. The shrimp industry is heavily dependent on feeding brine-shrimp nauplii that have been freshly hatched from cysts to support mysis production. Finally, as the mysis stage moults into the megalopa (or post-larva, as the industry describes it) larger types of zooplankton are needed. It is only at this last stage that formulated rations are exclusively used.



Life cycle of a typical marine shrimp species.

Most crustaceans require ten essential **amino acid**s, **essential fatty acid**s (EFA), **vitamins** and **minerals** for their growth, survival, **reproduction** and health. Unlike **fish** and terrestrial animals, they require **sterols** and **phospholipid**s, particularly phosphatidyl **choline**, as indispensable nutrients. **Cholesterol** is more effective in promoting growth and development of crustaceans, including lobster and penaeid shrimps. Juvenile *Penaeus japonicus* require 1% **eicosapentaenoic acid** (20:5 n-3) and **docosahexaenoic acid** (22:6 n-3) in their diet. Several crustaceans (*P. japonicus*, *Penaeus orientalis*, *Macrobrachium rosenbergii* and *Palemon paucidence*) have limited ability to convert **linolenic acid** (18:3 n-3) to 20:5 n-3 and 22:6 n-3. The recommended dietary phospholipid concentration for various penaeids ranges from 0.84% for *Penaeus chinensis* to 1.25% for *Penaeus penicillatus* and *Penaeus monodon*. Recommended **lipid** levels for commercial shrimp feeds range from 6% to 7.5% and the level should not exceed 10% of the diet.

Protein is an important component of crustacean diets. The optimum protein level for growth of penaeid shrimps ranges from 28% to 57%. Wide variations in these values among and within

species in various studies have been due to the differences in species, size, **protein quality**, utilization of **non-protein nitrogen** for energy, stability of pellet, feeding rate, **water quality** and the contribution of natural food organisms in the pond system. Quantitative dietary requirements for **arginine**, **histidine**, **isoleucine**, **leucine**, **lysine**, **methionine**, **phenylalanine**, threonine, **tryptophan** and **valine** have been determined for *P. japonicus*. Information on **carbohydrate** utilization by crustaceans is limited. Generally, simple **sugars** are poorly utilized by shrimp. **Starch** is commonly used as a carbohydrate source in shrimp diets and its **protein-sparing effect** on **energy utilization** has been demonstrated in *P. monodon*. **Chitin** is the major structural component of the exoskeleton of crustaceans, and some benefit of supplemented chitin (0.5%) but not glucosamine has been reported in *P. japonicus*.

Most vitamins that have been established as essential nutrients for fish and terrestrial animals are also considered to be essential for various crustacean species. The optimum levels reported for penaeid shrimp include the following (IU or mg kg^{-1}): **vitamin D**, 4000 IU; **vitamin E**, 100 mg; **vitamin K**, 30 mg; **thiamine**, 15–100 mg; **riboflavin**, 20 mg; **pyridoxine**, 80 mg; **niacin**, 400 mg; **biotin**, 2 mg; vitamin B_{12}, 0.2 mg; **inositol**, 2000–4000 mg; **choline chloride**, 600 mg; **vitamin C**, 20–215 mg. Dietary deficiencies of these vitamins have been shown to cause reduced growth of penaeid shrimp but specific deficiency signs have not been reported, except vitamin C. Black death syndrome,

characterized by blackened lesions of the digestive tract and other tissues, is a typical sign of vitamin C deficiency.

Dietary deficiencies of most minerals have been difficult to produce in crustaceans because of the presence of these minerals in **fresh water** and **sea water**. Marine shrimp *P. japonicus* do not require **calcium**, **magnesium**, **iron** or **manganese**, but do require **phosphorus**, **potassium** and **trace element**s in the diet. Although calcium is not an essential element, a calcium:phosphorus ratio of 1:1 to 1:2 has been recommended. Phosphorus requirement increases with the increase in dietary calcium concentration. Most crustaceans moult to grow and certain minerals lost during this process must be replaced from their diet.

Marine and freshwater shrimp farmed in conventional ponds or tank-based systems are generally fed high quality, nutritionally complete, compounded diets for the duration of the production cycle. These feeds are usually formulated to satisfy all of the known **nutrient requirement**s of the cultured species. However, shrimp can also derive a substantial portion of their nutrient requirements from **aquatic organisms** produced within the culture system. Sinking pellets or crumbles of various sizes, produced by **extrusion** or steam-**pelleting** processes, are widely used for feeding shrimp at various stages of development. Water stability of feed is important, because they are slow eaters and must break the feed into smaller particles before ingestion. Feed **attractants** such as **amino acid**s, fish extracts, shrimp **by-product**s, squid, clam and mussel stimulate the feeding response.

The amount of feed offered to shrimp is determined by the size

of shrimps, stocking density, availability of natural foods, dietary energy content and **water quality**. Daily feed allowances may range from approximately 25% of the body weight for larvae to less than 3% of body weight per day at market size. Under laboratory conditions, feeding frequency is reduced from six times per day for larvae to two or three times per day for juveniles to produce optimum growth and feed utilization. It is important to maintain the water quality at an acceptable level to produce a high standing crop of shrimp; therefore, the amount of feed offered should not exceed the capacity of the system to accumulate the waste products and to maintain sufficient levels of dissolved **oxygen**. (DEC; SPL)
See also: Prawn

Crypts of Lieberkühn
Hollows between the **villi** with groups of undifferentiated cells. These are the only cells of the villi that undergo division. Renewal of the villi is provided by the migration of new cells from the crypts towards the tip of the villi. These cells are among the most rapidly regenerating cells of the body. (SB)

Cubes
Pellets of **compound feed** with a diameter > 15 mm. Very large pellets, normally called rolls or cobs, tend to be used for feeding directly onto the ground; the larger size minimizes wastage and theft by birds. (MG)
See also: Feed blocks; Pelleted feed; Pelleting

Cultured meatMeat grown in a laboratory from isolated cells or a biopsy of a small number of animal stem cells taken from a living

adult animal. Also known as cellular agriculture, clean meat, lab meat, *in vitro* meat. The physiological function of the cells is to participate in muscle cells regeneration. The cells are cultured under controlled condition in a special nutrient-dense medium and, under the influence of hormones (made from the blood of dead calves), multiply into masses of cells. Then the stem cells are placed into sterile enclosed bioreactor tanks containing liquid nutrients to expose them to the equivalent environment replicating the environment in the real animal. They are stimulated with growth factors to induce rapid proliferation. Through the use of tissue engineering the cells are transformed into muscle cells and mechanically assembled into muscle tissue and then into a consumable artificial meat product. But the technology is still far from being able to replicate complex meat cuts, which are made up of organized fibres, blood vessels, nerves, connective tissue and fat cells. Initial products will include burgers (patties), reconstituted meat products and chicken nuggets. A potential benefit of cultured meat is that producing foods in laboratories can potentially improve the nutritional value of meat products, by excluding, for example, growth promoters, antibiotic residues and saturated fatty acids, and increasing the concentration of nutrients such as selenium or fluorine that may be limited in the human diet. This would thereby guarantee improved quality of meat for human nutrition. This could be achieved when scientists genetically modify the products. Scientists may also be able to improve the taste of cell-based products. Cultured meat also has the potential to disconnect the reliance of humans on animals to produce food,

which is ethically attractive to many, particularly as the welfare of animals in intensive farming system is generally acknowledged to be poor. Cultured meat also potentially releases land that could be used for wildlife and preservation of native habitats. It is potentially more efficient in use of resources, with no animal to maintain, though the creation of abiotic facilities to produce the meat on a large scale may be expensive. Public acceptability of the product is likely to be good, based on surveys conducted so far, although vegetarians appear unlikely to accept the product as part of their diet. Cultured meat as an emerging food sector is believed to disrupt conventional ways of producing animal products, with the goal of reducing animal farming, as well as creating a more sustainable and ethical global food system. (DB; CJCP)

References and further reading

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Curled-toe paralysis

A condition of chickens caused by **riboflavin** deficiency. Deficiency of this vitamin affects several tissues, mainly the epithelium and the **myelin** sheaths of some of the main nerves. Degenerative changes to the sciatic nerves results in the curled-toe

paralysis observed in growing chickens, causing them to walk on their hocks and with the toes curling under and inward. (RB)



Curled toe due to **vitamin** B2 deficiency in chickens. Photo courtesy of L. Mahin. Licensed under CC BY-SA 3.0.

See also: Foot diseases; Vitamin deficiencies

Cutting herbage for livestock

Cutting strategy determines herbage quality and quantity, particularly the date of first cut, cutting frequency and cutting height. The date of first cut of the season will depend on the start of **grass** growth. The term includes cutting for conservation or **green feed**ing and **grazing**. In intensive systems the use of fertilizers and irrigation can hasten the start of growth, but extensive systems are reliant on adequate rainfall. Ambient **temperature** must be adequate for growth.

The frequency with which **forage** is cut for conservation or 'green feeding' throughout the growing season will affect both yield (longer intervals give higher yields) and quality (shorter intervals give higher **protein** and lower fibre concentrations). In intensive systems, with adequate rainfall or irrigation, the cutting cycle may be interspersed with grazing.

Cutting height depends on the grass species and the cutting frequency. Longer intervals between cuts increase height, indicating greater **maturity** and, unless this is associated with extra leaf material, there could be a reduction in quality (less protein, more fibre). The chosen cutting height will reflect the need for high bulk versus high-quality material. (TS)
See also: Seasonal variation

Cyanide
An anion containing carbon and **nitrogen**, which very readily complexes with ligands. A common form in nature is **hydrogen** cyanide, which dissolves in water to form hydrocyanic acid. This smells like bitter almonds and can be detected in the breath of affected subjects. It is extremely toxic, causing pulmonary failure as a result of the capacity of the cyanide ion to bind with **cytochrome** oxidase and reduce the **oxygen**-carrying capacity of the cells. Cyanide also stimulates the chemoreceptors of the carotid and aortic bodies, causing hyperpnoea. Death is usually caused by respiratory arrest, however, rather than cardiac irregularities. Following ingestion of cyanogenic compounds, toxic symptoms appear within 1 h and so urgent treatment is essential. Treatment is by intravenous injection of sodium **nitrite**, which is converted to a tolerable amount of **methaemoglobin** that has a stronger affinity than cytochrome for the cyanide. To prevent the cyanmethaemoglobin complex releasing cyanide, a second injection of **sodium** thiosulphate is required, which invokes the **enzyme** rhodanese to convert the cyanide to the excretable thiocyanate. (CJCP)

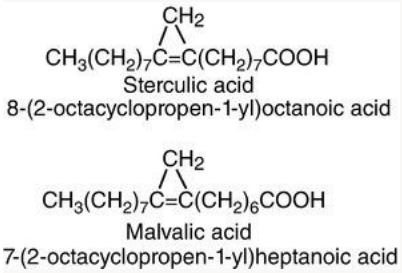
Cyanocobalamin:
see Cobalamin

Cyanogenic glycosides
Cyanogenesis is the process by which plants release **hydrogen** cyanide (HCN) from endogenous **cyanide**-containing compounds. It is thought to play a role in plant defence against generalist herbivores. In ruminants, hydrogen cyanide is formed in the rumen and absorbed into the bloodstream. A **metabolite** of hydrogen cyanide, thiocyanate, can be detected in **urine** after 1–2 days and can be used in diagnosis.

Cyanogenic glycosides are common in tropical **fodder** trees, which may make them unpalatable and can interfere with nutrient utilization. The cyanogenic glycoside, prunasin, is the toxic component in a number of browse species (serviceberry, *Amelanchier alnifolia*, and chokecherry, *Prunus virginiana*) and also in the eucalyptus tree (*Eucalyptus melanophloia*). Drying, soaking, leaching and **fermentation** are simple means of detoxifying these potential feed sources. Although grasses generally contain few intrinsic toxins, **sorghum** does have significant concentrations of cyanogenic glycosides. Cassava (*Manihot esculenta*) roots contain two potent cyanogenic glycosides: **linamarin** and lotaustralin. Cassava can be fed to livestock only after **detoxification** by fermentation, boiling or ensiling. Similarly, **linseed** contains linustatin and neolinustatin, which must be detoxified before feeding. (CJCP)

Cyanogens:
see Cyanogenic glycosides

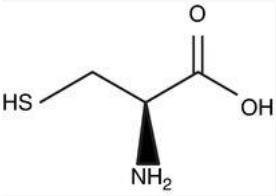
Cyclopropenoic fatty acids
Naturally occurring cyclopropenoic **fatty acid**s, sterculic and malvalic acid, are found in stercula and cotton seeds.



These compounds are potent inhibitors of Δ9 desaturase, which converts stearic to **oleic acid**. Their effect is to alter the permeability of membranes. In **laying hen**s, a diet containing sterculic acid gives rise to a condition known as pink–white disease when pink ferroproteins pass from the yolk into the white. **Cottonseed** oil is the most important edible oil-containing cyclopropene **fatty acid**s (concentration range from 0.6 to 1.2%) but for human consumption the oil is processed to reduce the level to 0.1–0.5%. (JEM)

Cysteine
An **amino acid** ($HS{\cdot}CH_2{\cdot}CH{\cdot}NH_2{\cdot}COOH$, molecular weight 121.2) found in **protein**. It is synthesized from **methionine** (which provides the **sulphur**) and **serine** (which provides the carbon skeleton) in the metabolic process known as trans-sulphuration. Of the cysteine not used in **protein synthesis** or catabolized (to CO_2, SO_4^{2-} and H_2O), some is used for the synthesis of **glutathione**,

some for the synthesis of **taurine** and some for the synthesis of phosphoadenosine phosphosulphate. Many of the sulphydryl groups of cysteine that exist in protein are oxidized, with formation of a disulphide bridge between two cysteine residues, forming the dimeric amino acid, **cystine**. Cysteine (or cystine) is capable of supplying up to 50% of dietary need for sulphur amino acids (methionine + cysteine) of growing animals and an even larger portion (up to 80%) of the sulphur amino acid need of adult animals. (DHB)



See also: Cystine

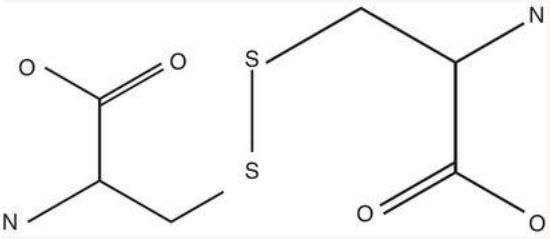
Cysteine dioxygenase

One of two **enzymes** involved in the conversion of L-**cysteine** to **pyruvate**. Cysteine dioxygenase, a cytoplasmic enzyme, converts L-cysteine ($HSCH_2{\cdot}CHNH_3^+{\cdot}COO^-$) to L-cysteine sulphinate using molecular **oxygen**. In this process the **sulphur** atom of L-cysteine is converted to **sulphate** (SO_4^{2-}) and the carbon skeleton becomes **pyruvate**. (NJB)

Cystine

An **amino acid** ($COOH{\cdot}NH_2{\cdot}CH{\cdot}CH_2{\cdot}S{\cdot}S{\cdot}CH_2{\cdot}CH{\cdot}NH_2{\cdot}COOH$) found in protein. A disulphide bridge within or between **peptide** chains can be formed when two **cysteine** groups combine.

Following **digestion** (breaking of peptide bonds), cystine or cystine-containing small peptides are released. Cystine that exists in food proteins, particularly heat-processed proteins, is less digestible (available) than either **methionine** or cysteine. (DHB)



Cystinuria (cysturia)

An inherited disease of **amino acid** transport in the renal tubules. Urinary concentrations of **cystine**, **lysine**, **arginine**, **ornithine** and **cysteine–homocysteine**-mixed disulphide are elevated. Because of its low **solubility**, cystine forms calculi in the tubules leading to obstruction, infection and ultimately renal insufficiency. (NJB)

Key reference

Segal, S. and Their, S.O. (1989) Cystinuria. In: Scriver, C.C., Beaudet, S.L., Sly, W.S. and Valle, D. (eds) *The Metabolic Basis of Inherited Disease*. McGraw-Hill, New York.

Cytochrome

A class of **iron**-porphyrin-containing proteins. Cytochromes are intimately associated with the respiratory chain involved in electron transport and the **oxidation**–reduction reactions of cell respiration. Cytochromes in the mitochondria are a direct link to the use of molecular **oxygen** as a terminal electron acceptor in aerobic **metabolism** leading to the production of ATP. (NJB)

Cytokines

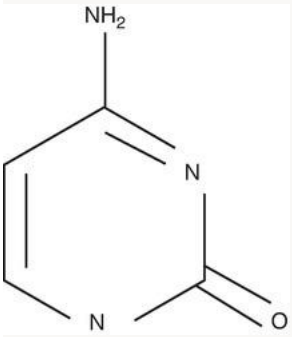
A family of low-molecular-weight (~30,000) proteins secreted by various cells with autocrine and paracrine actions. Cytokines are involved in the coordination of cellular responses in various pathways, including immune responses, haematopoietic cell signalling, calcium **homeostasis**, skeletal modelling and remodelling, wound healing and tissue repair, growth and ordinary replacement of aged cells. Cytokines regulate the intensity and duration of a response by stimulating or inhibiting activation, proliferation or differentiation of cells by regulating the secretion of proteins or other cytokines. Cytokines include interleukins, interferons, colony-stimulating factors and tumour necrosis factors. The specificity of cytokines and cell response is via specific cell surface receptors. For example, white blood cells (macrophages) and other cells (activated T helper cells, T_H) act by secreting cytokines that bind receptors on the surface of specific cells to stimulate proliferation, differentiation or both. Interleukins may induce pro-inflammation responses, killer cell activation and immunoglobulin production while interferons may prevent viral replication. At least 18 interleukins, three interferons and two tumour necrosis factor subclasses have been identified. The two tumour necrosis factors (α and β) have cytotoxic effects on tumour cells. Still other cytokines exist and more will probably be identified. (TDC)

Key reference

Owen, J., Stranford, S. and Jones, P. (2018) *Kuby Immunology*, 8th edn. W.H. Freeman and Co., London.

Cytosine

A **pyrimidine**, $C_4H_5N_3O$, found in both RNA and DNA. In RNA it is cytidine 5′-monophosphate (CMP); when in DNA it is deoxycytidine 5′-monophosphate (dCMP). Cytidine is involved as cytidine diphosphate **choline** (CDP-choline) in **phosphatidylcholine** synthesis and as CDP-diacylglycerol in **phosphatidylinositol** biosynthesis. (NJB)



D

D value

A **digestibility** coefficient, i.e. the proportion of a feed constituent or nutrient that can be digested and absorbed from the digestive tract. Quoted D values are apparent digestibilities (*see* Digestibility measurement). Examples are: **dry matter** digestibility (DMD);

organic matter (OMD); or digestible organic matter contained in the dry matter (DOMD). These terms are most often used in **feed evaluation** for ruminants and their definition needs care, as the terms 'digestibility' and 'digestible content' are not interchangeable. In the UK the 'D' value usually means DOMD in practical publications, while OMD or DMD are used in scientific research.

D values are calculated as follows:

$DMD = (DM_{eaten} - DM_{faeces}) / (DM_{eaten})$

$OMD = (OM_{eaten} - OM_{faeces}) / (OM_{eaten})$

$DOMD = (OM_{eaten} - OM_{faeces}) / (DM_{eaten}) = OMD * \text{feed OM content (on a DM basis)}$

where DM = dry matter = total feed minus moisture; OM = organic matter = DM minus **ash**; DOM = digestible organic matter = OM in feed minus OM in faeces; DM_{eaten} is the difference between DM fed and DM refused; D_{faeces} = amount of DM excreted in the faeces.

These terms can be expressed as digestibility coefficients (e.g. 0.7) or as percentages (e.g. 70%). DOMD can be calculated from OMD and the OM percentage in the food when this is expressed on a DM basis. Digestibility determined *in vivo* is **apparent digestibility**, since excreta contain endogenous matter. Most of these digestibility coefficients can also be applied to the two-stage **rumen-pepsin** *in vitro* technique devised originally by Tilley and Terry (1963) and applied by Alexander and McGowan (1966). Digestibility as D value (DOMD) can be scaled into **metabolizable energy** (ME) using an assumed value for the **gross energy** of the digestible organic matter. If this is taken as 18.4 MJ kg^{-1}, and the

efficiency of converting DOM to ME is 81%, then ME (MJ kg^{-1} DM) = 0.15 DOMD%. (IM; GMcLD)

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Alexander, R.H. and McGowan, M. (1966) The routine determination of *in vitro* digestibility of organic matter in forages – an investigation of the problems associated with continuous large-scale operation. *Journal of the British Grassland Society* 21, 140.

Tilley, J.M.A. and Terry, R.A.A. (1963) A two-stage technique for the *in vitro* digestion of forage crops. *Journal of the British Grassland Society* 18, 104.

Dairy cattle

Bovine animals bred and kept principally for **milk** production. Dairy cattle have been bred to produce large quantities of milk over a **lactation** of about 300 days in length. *Bos taurus* dairy cattle can be classified into European, British and Channel Island breeds. The yield and composition of milk is influenced by the animal's diet, with pasture-fed cows producing less than those given a concentrate **supplement**, and cows given high levels of low-fibre ingredients produce less milk **fat**. Under their usual management, European breeds such as the Holstein, Normande and Brown Swiss produce upwards of 4500 l of milk per lactation with typically 3.6% milk fat. Holstein cows can yield 7500 l or more; Channel Islands breeds such as Guernsey and Jersey have lower yields (about 3000 l per lactation) with higher milk fat contents – about 4–6%. *Bos indicus* breeds such as the Sahiwal, Red Sindhi and Brazilian Gir are used in tropical regions. They typically yield 2000–3500 l per lactation, although in favourable conditions

yields can be greater than this. These foundation breeds have been used to generate other breeds through local selection and crossbreeding. The Australian Illawarra Shorthorn (a cross between the milking Shorthorn, Devon and Ayrshire breeds) and the Australian Milking Zebu (a Sahiwal × Jersey cross) are examples. (PCG; GMcLD)

Further reading

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Dairy cow feeding systems

There are three commonly used systems for feeding lactating dairy cows: (i) year-round **grazing** on permanent or annual pastures based on grasses and possibly supplemented with **fodder** crops or concentrates; (ii) mixed grazing/housing where cows are grazed on pastures during the spring, summer and early autumn, and are housed during the winter; and (iii) lot-feeding, where cows are kept in yards and fed a **total mixed ration** which generally comprises forages (including **silage**) and concentrates.



Cows feeding on a total mixed ration in a barn in the USA. Photo courtesy of US Department of Agriculture. Licensed under Public Domain Mark 1.0.

Feeding lactating dairy cattle on forages

Year-round grazing is commonly used in warm temperate and subtropical regions where pasture grows throughout the whole year, albeit at varying rates; while a grazing/housing system is used where winters are severe and cattle have to be protected from low temperatures. In most regions grass (or other feeds for grazing) does not grow at rates sufficient to meet the cows' requirements all year, and so farmers conserve surpluses from times when growing conditions are good so that they can be fed to the cattle during periods of pasture shortage, such as in the winter months when it is too cold for grass to grow, or in the **dry season** when there is insufficient moisture.

In temperate countries fodder is mainly conserved as silage, which is cut at a younger stage of growth than **hay** and, therefore,

tends to be more nutritious. In the humid tropics, making good-quality silage is more difficult, because tropical grasses have higher fibre contents than temperate species and are thus more difficult to compact in the silage heap, and are fermented more slowly so that the reduction in pH of the silage occurs more slowly, with the possibility of a butyric acid **fermentation** rather than the desired **lactic acid** fermentation. Also, high temperature and humidity make controlling the fermentation more difficult. Silage is usually made from grass or forage **maize**, with maize silage being popular with cattle farmers because of the higher yield of this crop. Silage can be fed either directly from a clamp, so-called self-feeding, or it can be extracted from the clamp by machine and fed along a passageway or in a circular feeder. If the silage is fed in a passageway, cows should be restrained behind a barrier that allows them to put their heads through to feed, but not to walk on the silage or pull their heads back through the barrier while they are still eating silage.

Haymaking relies on preserving grass by removing the moisture that microorganisms require for survival. Energy losses from the grass plant can be very high during haymaking, due to continued plant respiration and the loss of material during raking, baling and storage. However, if the same grass could be used to make either hay or silage, the protein value of the hay would usually be greater than that of silage, because there is less **protein degradation** during the conservation process.

In many parts of the world, **straw** and other crop residues, such as maize **stover**, are important feeds for cattle. However,

their nutritional value is low, as the lignification of **hemicellulose** and other cell wall **polysaccharide**s makes this material relatively indigestible, their protein contents are much less than that required by most cows (e.g. straws often have only 40 g protein kg^{-1} DM), and they may have low concentrations of minerals and vitamins. Cows will not consume much straw, because its rate of breakdown in the rumen is slow. Thus, for high-yielding cows, **roughages** like straw have little nutritional value but they help to maintain rumen function and animal health. Straw can be upgraded by treating it with **sodium** hydroxide or **ammonia**, which reduced the lignification of the structural **carbohydrate**. It can also be harvested together with the cereal grain in the form of 'whole-crop' or arable silage or hay.

Feeding concentrates to lactating dairy cows

A Holstein dairy cow can give milk yields of 7000 l per lactation (23.5 l per day) on high-quality forage alone, but in most situations farmers get an economic response to providing at least a low level of supplementary concentrates. This is because the nutrient requirements of high-yielding dairy cows (for example, animals producing 35 l per day or more) cannot be met from microbial digestion of plant fibre alone. The inability of the high-yielding cow to derive all the nutrients necessary to sustain her metabolic requirements during early lactation means that frequently she will benefit from feed supplements that provide dietary components that resist microbial fermentation in the rumen. These forms of **starch**, **lipid** and **protein** are largely digested and absorbed in the **small intestine**. Young and rapidly growing cattle may also

benefit from such supplements, particularly from protected sources of protein. In these circumstances, the efficiency of absorption of **amino acid**s and the production response will depend on the **biological value** of the rumen-undegradable protein fraction of the supplement.

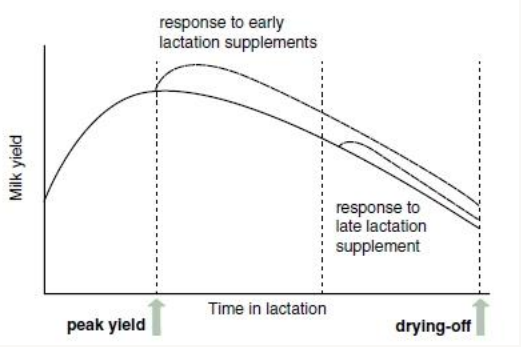
Concentrates fed to dairy cows are based on cereal grains and **oilseed** meals, or other feeds high in energy and protein; they usually also include supplementary minerals and vitamins. They can be fed after **milling** as a loose **mash** (a mixture of milled grain, protein meals and minerals), or made into a pellet. Excessive use of concentrates risks upsetting **rumen digestion** and causing low milk-fat contents and this has led to such diets being based on digestible fibre, e.g. **sugarbeet** pulp (where this is available), rather than starch from cereal grains. Large allowances of concentrates should be divided into two or more separate meals. In tropical countries, concentrate supplements are often grain-processing **by-product**s, because cereal grains are relatively expensive and are reserved mainly for feeding to humans.

Traditionally, concentrates were given to dairy cows during milking but the greater milk yields achieved today require higher concentrate allowances, and faster milking routines mean that it is not possible for cows to consume all of their concentrate allowance in the milking parlour. Electronic concentrate dispensers are available for allocating concentrates to individual cows in small quantities and frequent meals throughout the day. Alternatively, a proportion of the concentrate allocation can be mixed with forage to form a basal ration that is supplemented on an individual cow

basis with the remaining concentrates, or the whole concentrate allowance can be mixed with forage to form a complete feed.

Dairy farmers generally prefer to feed most concentrates to those cows giving the most milk, whatever their forage feeding system, but loose-housed cows fed high-quality forage *ad libitum* respond similarly whatever their milk yield. Feeding all the cows their concentrate supplement at a flat rate has the advantage of simplicity. If concentrates and forage are fed separately, the concentrate allowance may be varied according to individual milk yield (e.g. 0.4 kg l^{-1}), or on a flat rate to all cows. Research results suggest that total milk yield is determined by the total allowance of concentrates throughout the year, rather than pattern of allocation.

The response of pasture-fed lactating cows to grain-based supplements varies according to their stage of **lactation** (see figure). During the mid-lactation we can expect an additional 0.6–1.2 l of milk per day per kg of **supplement**.



Response of a lactating dairy cow grazing pasture to a grain-based supplement.

Feeding total mixed rations (lot feeding)

Dairy cows can be given a complete diet (also called a total mixed ration (TMR)). This is usually a mixture of silage or hay and

concentrates mixed up in a portable feeding wagon. An advantage of complete diets is that inexpensive by-product feeds can be incorporated into a mix, and feeds with low **palatability** can be masked by the strong **taste** of silage. Typical nutrient requirements for lactating cows in early, mid and late lactation, or dry cows, are given in the table.

Diet composition recommendations for early, mid and late lactation cows.

	Early	**Mid**	**Late/dry**
Milk yield level (kg per cow per day)	30–40	20	10
Metabolizable energy (MJ kg^{-1} DM)	11.7	10.6	9.8
Crude protein (g kg^{-1} DM)	17	15	12
Ruminally degradable protein (g kg^{-1} DM)	78	87	99
Acid detergent fibre (g kg^{-1} DM)	21	21	21

	Early	Mid	Late/dry
Calcium (g kg^{-1} DM)	6.1	5.1	4.3
Phosphorus (g kg^{-1} DM)	3.9	3.3	2.8
Magnesium (g kg^{-1} DM)	2.0	2.0	2.3
Sodium (g kg^{-1} DM)	1.8	1.8	1.8

Metabolic and digestive disorders of lactating dairy cows

Metabolic and digestive tract disorders can occur during the lactation, with **metabolic disorder**s more likely in early lactation when demands placed on the animal's **metabolism** are at their greatest, and especially with high-yielding cows. The major risks are **hypocalcaemia** (**milk fever**), **hypomagnesaemia** (lactation **tetany** or grass tetany) and acetonaemia or **ketosis** (**twin lamb disease**).

Hypocalcaemia is most likely to occur soon after calving, when the output of **calcium** in milk is suddenly increased and the animal cannot absorb sufficient dietary calcium or mobilize sufficient reserves of calcium from body stores to meet the increased requirement. Calcium metabolism in mammals is tightly regulated and, whilst total bone calcium levels are high, only the most recently deposited fraction of bone calcium can be mobilized. Factors that predispose cows to milk fever include age (older cows

are more prone than younger cows) and calcium supplementation during the immediate pre-partum period; restricted intake during this time can increase the efficiency of **absorption** following parturition. Immediate treatment with a readily available source of calcium, coupled with supplementary calcium in the diet, usually alleviates the condition. Careful management of the mineral nutrition of the cow during the dry period can reduce the risk and incidence of milk fever.

Hypomagnesaemia can also occur soon after calving and is often associated with the start of the grazing season, when the animal is presented with herbage of lower **magnesium** concentration than the previous winter diet. The condition can also occur following a short period of inappetence, when magnesium intake is suddenly reduced. Hypomagnesaemia is prevented by supplementing the diet with magnesium.

Excessive mobilization of body **lipids** during the early lactation, combined with an inadequate dietary supply of glucogenic precursors, can result in the incomplete **oxidation** of **fatty acid**s, causing an accumulation of **ketone** bodies in the blood (acetonaemia or ketosis) that can ultimately lead to clinical ketosis. In time, the accumulation of fat deposits in the liver can impair **liver function**, resulting in various disorders and culminating in fatty liver syndrome. Acetonaemia may be triggered by a period of inappetence caused by an infectious disease or sudden deprivation of food, or by a chronic deficiency of energy in the diet itself. Prevention of acetonaemia is by ensuring that the animal's appetite is maintained at all times, and that the early-lactation diet is

relatively high in readily digested sources of energy.

Excessive use of starch-rich feeds can cause **subacute ruminal acidosis** (SARS), and this is a common condition in cows fed grain-rich diets (Morgante, 2009). If the rumen pH falls repeatedly to less than about 5.8, **feed intake** is reduced and the cow may become lame or scour. (JMW; PGC; CJCP; GMcLD)

See also: Alkali treatment; Ammonia treatment; Concentrate

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Phillips, C.J.C. (2018) *Principles of Cattle Production*, 3rd edn. CAB International, Wallingford, UK.

Dairy cow milk production and milk composition

The dairy cow's annual production cycle consists of four phases: (i) a dry period of 7–10 weeks leading up to calving and the start of **lactation**; (ii) early lactation, between calving and peak yield at about 100–120 days; (iii) mid-lactation, the period between 100 and 240 days of lactation; and (iv) late lactation, days 240–305 of lactation. Dairy cattle are re-mated during their lactation so that

they calve again 12 or 13 months after their previous calving.

Milk yield and composition

Milk yield is low at first and rapidly rises to a peak between 8 and 16 weeks after calving. The yield then gradually falls through the mid-lactation, and reaches its minimum in the late lactation stage (Fig. 1).

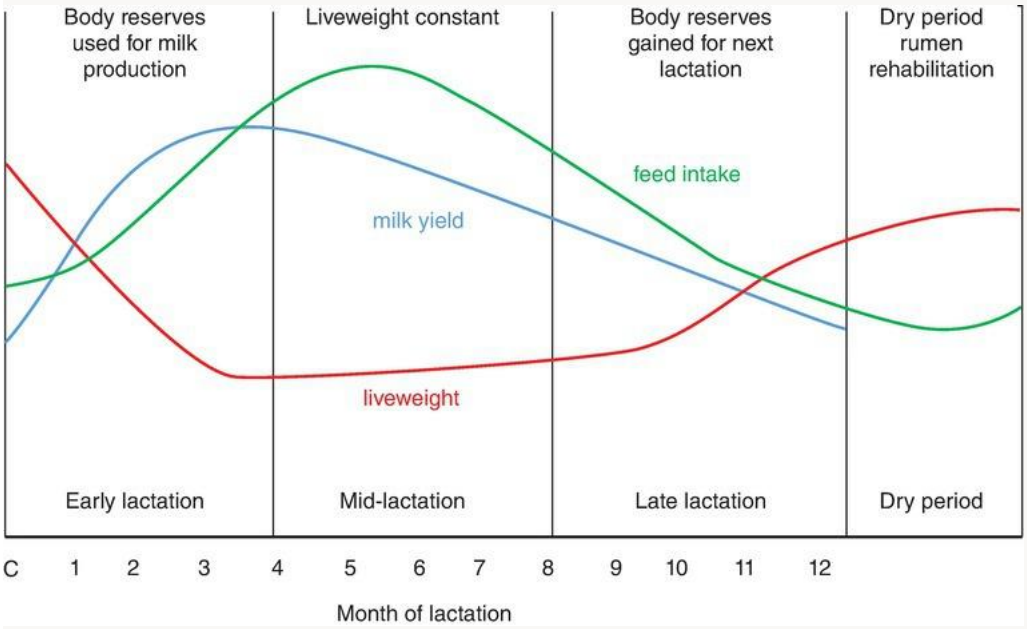


Fig. 1. Changes in milk yield, feed intake and liveweight of a lactating dairy cow during her lactation (after Moran, 2015).

The composition of milk changes during the lactation (Fig. 2). Colostrum, or first milk, is secreted for 2–3 days after calving. After that time, the udder secretions gradually change to produce the liquid we call milk. Colostrum is particularly rich in fat, protein, immunoglobulins, minerals and vitamins. Milk fat (*see* Butterfat) content is low in the first few weeks when the volume of milk produced is at its greatest (Fig. 2). The concentrations of milk fat and protein increase progressively as the volume of milk secreted is reduced later in the lactation; milk fat content averages about 3.7%

of total milk (in Holstein cows) for most of the lactation. The protein content of milk – averaging about 3.4% – follows a similar trajectory.

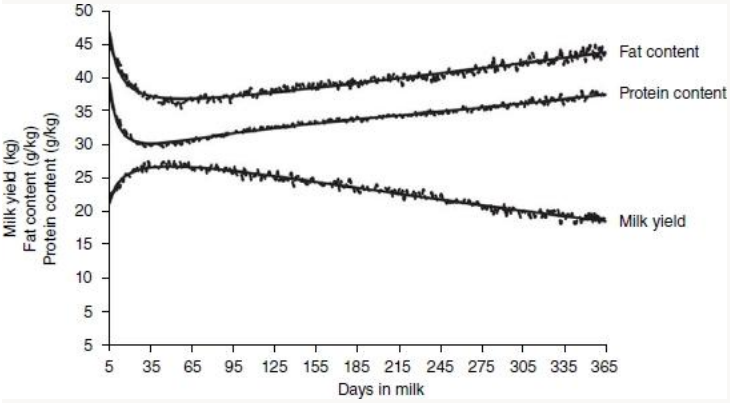


Fig. 2. Changes in milk yield, and fat and protein contents during the lactation (Lainé *et al.*, 2017).

Milk fat is produced both by the synthesis of **fatty acid**s in the **mammary gland** and by the **absorption** and secretion into milk of dietary fatty acids. In microbial **digestion**, the fatty acid profile of the feed is modified. Acetic acid is the main precursor for milk fat synthesis and is an end-product of **cellulose** and **hemicellulose** digestion. This means that the fibre content of the diet is an important determinant of the fat content of the milk. The ratio of lipogenic nutrients (acetic acid, butyric acid and **long-chain fatty acid**s) to glucogenic nutrients (**propionic acid**, **glucose** and some **amino acid**s) therefore determines milk fat content, in particular the ratio of **acetate** to **propionate**. Fibre digestion is impaired if the rumen pH is less than 6.3, and feeding large quantities of concentrates that are rapidly fermented in the rumen to acid end-products should be avoided. In practice this means that the minimum **roughage** content of lactating cow feeds

is about 55%. Rumen pH can be maintained by feeding alkali-treated **forage** or **grain**, or by stimulating the production of **saliva**, which contains carbonate/**bicarbonate** and phosphate buffers. The incorporation of **unsaturated fatty acid**s into milk is possible if fats are protected from rumen fermentation. Normally no more than about 6% of unprotected fat should be included in the diet, as it has adverse effects on the digestion of fibre in the rumen.

Milk protein is mainly **casein** (about 70%), the remaining 30% comprising β-**lactoglobulin**, α-lactalbumin and immunoglobulins. **Solids-not-fat** and milk protein concentrations change in response to the energy supply to the cow. The response of milk protein content is mainly due to the reduced use of amino acids to supply energy. Cows that are catabolizing body tissue to provide for their **energy requirement**s, therefore, tend to have low concentrations of milk protein, as some of the feed protein will be utilized for energy.

Milk may acquire **taints** from feeds. For example, **brassicas** and beets may produce a taint if fed within 3 h of milking and so should preferably be fed after milking.

Feeding throughout the cow's annual production cycle

The dairy cow has been selectively bred to produce considerably more milk than is required by any calf and so high-producing cows, particularly at the beginning of their lactation, will respond to a much greater intake of nutrients than can be supplied by the traditional high-fibre diet of cattle. Very productive herds are often given a concentrate **supplement**.

Cows normally have a 7–9 weeks dry period (i.e. they do not **lactate**) before calving. This period is also called the transition period, as it is when the cow is prepared for her next lactation. Because voluntary **feed intake** is insufficient in early lactation to supply the **nutrient requirement**s for milk production (see below), and because milk production in early lactation determines the size of the peak yield and the productivity and persistence of milk production in the rest of the lactation, it is important that the cow is well prepared during the dry period for her early lactation.

The transition from the dry period to early lactation should be smooth, and the cow is often introduced to a lactation diet in the final 14–21 days of the dry period to allow the rumen microflora to adapt to the change in dietary ingredients from the dry-cow diet to the lactation diet. Farmers usually feed a high-fibre ration for the first 4–7 weeks of the dry period and increase the energy content just for the last 2 weeks. The amount of concentrates fed near calving depends on the condition of the cow and the desired milk output, but would typically be 2–4 kg per day. Feeding a high nutrient-density diet before lactation prepares the cow for milk production by, firstly, supporting growth of the rumen papillae, which takes about 5 weeks of exposure to cereals, and, secondly, allowing the cow to lay down additional body reserves that can be used in early lactation, when voluntary feed intake is insufficient to supply the nutrient requirements for milk production. However, cows that are fat at calving consume less feed post-partum than cows that are thin. They rely more on catabolizing body tissue for their energy and, to some extent, protein requirements. If cows

have a low level of body reserves on entering their lactation, it is less likely that they will be able to endure a period of underfeeding without milk yield being reduced. As well, a large negative **energy balance** in the first 100 days of lactation increases the time to first ovulation and reduces **progesterone** secretion, leading to a longer calving interval.

At the start of the lactation the rise in food intake is slower than the increase in milk yield, particularly in the first 2 months, and maximum food intake is not normally achieved until the fourth month of lactation, i.e. in mid-lactation (see Fig. 1). Voluntary feed intake in ruminants is highly variable and difficult to predict. Intake (per unit **liveweight**) is affected by a number of animal- and feed-related factors. The principal animal-related factors include **genotype** (generally dairy genotypes have a higher intake capacity than beef genotypes; and high-yielding cows eat more than low-yielding cows), **body composition** (thinner cows eat more than fatter cows) and physiological status (lactating cows eat more than non-lactating cows). Principal feed-related factors include the **dry matter** content of the feed, its **particle size**, cell wall content and rate of digestion, and a variety of factors that influence conditions within the rumen. All these factors interact during early lactation to limit nutrient intake and the products of rumen fermentation relative to the metabolic requirements of the cow.

The rapid increase in milk yield during the first 8–16 weeks of lactation normally requires the cow to meet her metabolic requirements through a combination of dietary intake and body

tissue mobilization. The metabolic demands during this period are carefully regulated through the combined effects of a number of homeorhetic and homeostatic **hormone**s that collectively coordinate the processes of lactogenesis, voluntary feed intake and nutrient partitioning in support of **galactopoiesis**. Of these, growth hormone (**somatotrophin**) promotes milk production by diverting the products of digestion and intermediary metabolism away from tissue deposition and towards the mammary gland during periods of negative energy balance, characteristic of early lactation. This is achieved, in part, by inhibiting the **insulin**-mediated uptake of glucose by **skeletal muscle**, and by inhibiting the ability of insulin to stimulate **lipogenesis**. Exogenous bovine somatotrophin (BST) has been shown to result in a 12–35% increase in milk yield in high-yielding dairy cows (Zinn and Bravo-Ureta, 1996).

Because the cow's requirement for energy in early lactation exceeds her intake of energy, she is in negative energy balance and loses body weight. Accordingly, the feeding strategy to meet the high nutrient requirements of the cow in early lactation is to have the cow calve in good body condition (but *see* Cow pregnancy) and to maximize voluntary intake as soon as possible after calving. The energy density of the diet is increased in early lactation in an attempt to facilitate achieving maximum **energy intake** and thus to minimize the deficiency in energy intake at this time. The early lactation diet often comprises a higher proportion of rapidly digested concentrated feeds, including starch and **lipids**, and a lower proportion of slowly digested forages than the mid- and late-

lactation diets. The concentration of **metabolizable protein** is also higher in early lactation diets than in diets formulated for mid and late lactation.

Hypocalcaemia is a serious risk in early lactation and the cow's **calcium** intake requires careful management before and immediately after calving. During early lactation the output of calcium increases considerably, because of milk production, and this may be more than the cow can provide from body stores in the bone tissue. Calcium absorption and excretion are regulated by the production of **parathyroid hormone**. If it is possible to restrict calcium intake before calving to approximately 3 g kg^{-1} dry matter, increased activity of parathyroid hormone increases the absorption of calcium from the **gastrointestinal tract**.
In mid-lactation, the nutritional strategy is aimed at minimizing the rate of decline in milk yield, which can often be as much as 2.5% per week. Ideally, the milk yield of the cow should remain as close to peak yield as possible during the second 100 days of lactation, though the onset of pregnancy, with associated changes in the hormonal balance of the animal, is reflected in a change in the partition of nutrients from lactation to the growth of the placenta and fetus. Thus, if milk yield decreases substantially in mid-lactation and the diet is not reformulated to take account of the reduction in nutrient requirements, the cow is liable to gain weight during this period.

Late lactation is the period when the voluntary intake of nutrients is most likely to exceed requirements for milk production, and as a result the weight lost in the early stages of

lactation is normally replaced in the final 3 months of lactation, when milk yield is relatively lower than in mid and early lactation. The target for feeding the dairy cow should be to achieve a similar body weight and condition score at the end of the lactation as at its start. Slowly digested forages should comprise the majority of the animal's nutrient supply. Supplementary protein may be required if the forage is deficient. The supply of essential mineral elements should be checked and any deficiencies rectified. **Straw** can be used at this stage of lactation as a way of reducing the energy density of the diet.

Cows are usually dried off at least 60 days before the predicted date of calving, to allow the udder to recover from the previous lactation and to condition the cow for the next lactation. Drying-off is achieved by stopping milking abruptly. This can cause problems if the cow is still yielding a relatively large quantity of milk, and for this reason some very high-yielding cows have extended lactations, up to 36 months in total, especially if they are not due to calve for a further 80–100 days after their normal 305-day lactation, because of delayed conception. (JMW; CJCP; GMcLD)

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Dairy cows, feeding strategies to improve milk production and composition

Both pre-partum and post-partum nutrition can significantly influence **milk** yield and milk composition in dairy cows. During late **lactation** and the dry period, most of the **fat** reserves are deposited in the body. These body reserves are used during early lactation (first 10–12 weeks), where the cow's metabolic demand very often cannot be fulfilled solely by the **diet** consumed. The level of nutrition post-partum should optimize milk production while simultaneously maintaining the cow's **basal metabolism** and body **maintenance**. However, it is essential to avoid excess mobilization of **body fat** reserves, to maintain dairy cow health and well-being, future **fertility** and **conception rate**. Therefore, the best feeding strategy is phase feeding. Phase feeding is practised according to the cow's lactation and gestation cycle, as well as production stage, pregnancy, energy partitioning and nutrient density in diets. Feeding from calving to peak lactation is the first phase of phase feeding. It ensures the maximum peak milk yield, increases the voluntary **feed intake** as rapidly as possible,

minimizes the negative **energy balance** and returns a positive balance by 8–10 weeks. In this phase, cows positively respond to special ration formulations, additives and dietary treatments, thus demanding the best feeding management. Maintaining a ratio of forage to concentrates at 55:45 or 50:50 in **total mixed ration** (TMR) and gradual incremental increases of concentrate intake by 0.5–0.7 kg per day within this phase helps cows to reach positive energy balance. **Supplementation** of ruminant bypass proteins, buffers and increases in the energy density of diets are some other recommended practices during phase I.

The lactating cow's feed intake capacity lags behind its milk production, and peak feed intake occurs some 2–4 months after peak milk yield. Phase II is feeding from peak lactation to the time of peak feed intake, aiming for the maximum DM intake as soon as possible. In this phase, ration recommendations are made according to the animal's body weight and milk yield. It is necessary to provide balanced **rumen**-degradable **protein** and **carbohydrates**, and bypass proteins may not be useful at this second phase.

Phase III is the feeding from mid-lactation to late lactation. Nutrient intake during this phase usually exceeds the nutrient demand of cows for milk production. Nutrients are directed more to gains in body weight and condition, and less to milk synthesis. This is the most economical phase to improve the **body condition** of cows, as they can utilize sources of **non-protein nitrogen** more efficiently during this phase. Phase IV includes feeding dry cows, and it ensures the appropriate body reserves at calving. Since

pregnant cows require more proteins, Ca and P, feeding combinations of **legume–grass hay** and corn **silage** supplemented with vitamins, Ca and P is recommended. Excessive **energy intake** should be avoided at this stage. In all of these phases, water should be available *ad libitum*, as water intake directly affects cow performance and body maintenance. High water intake always leads to higher milk yield as well. These phase-feeding practices ensure the optimum utilization of nutrients and maintenance of proper body conditions, thus better milk production at current and the following lactations.

The provision of high-quality **forage** and **supplement**s to dairy cows has a positive influence on their milk yield. Numerous grasses and foliage types are available under different farming systems in tropical regions (see table). Thus, evaluating and comparing the potential of varying kinds of grasses, grains, foliage and **by-product**s on milk yield and composition is crucial for the sustainability of dairy production.

Chemical composition (percentages on dry matter basis) of commonly available feed ingredients for dairy cattle, goats and water buffalo in the tropics

Feed source	DM	OM	CP	NDF	ADF	References
Lentisk	45.90	95.60	08.50	42.10	31.40	Decandia *et al.* (2000)

Feed source	DM	OM	CP	NDF	ADF	References
Alfalfa	87.50	NA	15.00	54.20	36.80	Giorgio *et al.* (2020)
Sulla	19.10	NA	17.20	44.30	26.90	Giorgio *et al.* (2020)
Green maize	12.90	88.94	08.74	52.47	32.80	Shelke *et al.* (2012)
Wheat straw	90.07	91.5	03.12	77.80	50.40	Shelke *et al.* (2012)
Elephant grass silage	51.30	NA	06.60	71.15	42.70	Santiago *et al.* (2019)
Brachiaria briquettes	90.90	NA	05.32	73.32	50.71	Santiago *et al.* (2019)
Sugarcane	32.80	NA	10.50	45.24	32.53	Santiago *et al.* (2019)

Feed source	DM	OM	CP	NDF	ADF	References
Sugarcane bagasse	70.96	96.69	01.85	83.36	57.93	Borges *et al.* (2019)
Sorghum silage	33.20	92.20	06.55	65.02	38.90	Borges *et al.* (2019)
Cactus pear	08.30	95.40	09.20	30.01	19.02	Borges *et al.* (2019)
Corn ground grain	90.15	97.90	09.20	20.40	05.90	Borges *et al.* (2019)
Soybean meal	90.01	94.00	46.90	16.17	11.22	Pimentel *et al.* (2018)
Palm kernel cake	92.25	NA	10.71	65.63	46.40	Dias *et al.* (2018)
Peanut cake	94.8	NA	44.70	11.80	10.9	Costa *et al.* (2015)

Feed source	DM	OM	CP	NDF	ADF	References
Cramb e meal	91.70	93.40	36.30	28.0	16.70	do Carmo Araújo *et al.* (2018)
Banan a peel (sun dried)	87.76	NA	08.28	47.92	29.83	Piment el *et al.* (2018)
Tithoni a diversi folia	29.30	NA	14.50	39.50	20.80	Ribeiro *et al.* (2016)
Cassav a shoots hay	83.51	94.20	05.22	60.10	48.24	Saraiva *et al.* (2015)
Cynod on nlemfu ensis	33.74	NA	07.94	NA	39.17	Penich e-Gonzál ez *et al.* (2014)

Feed source	DM	OM	CP	NDF	ADF	References
Leucaena leucocephala	30.33	NA	25.94	NA	24.84	Penich e-González *et al.* (2014)
Pennisetum purpureum	25.50	NA	03.10	67.7	44.30	Arjona-Alcocer *et al.* (2020)
Citrus pulp	20.00	NA	09.00	31.60	07.80	Arjona-Alcocer *et al.* (2020)
Rice polishings	92.00	NA	08.10	17.80	32.20	Arjona-Alcocer *et al.* (2020)

ADF, acid detergent fibre; CP, crude protein; DM, dry matter; NA, data not available; NDF, neutral detergent fibre; OM, organic matter

The quality of raw milk and processed dairy products are

closely associated with on-farm production factors and feeding management strategies. For example, **grazing** Holstein cows offered corn grain and canola meal demonstrate a positive linear relationship between supplementation level and milk yield, fat and protein content, and a negative linear relationship between supplementation level and milk fat content (Auldist *et al.*, 2016). Some of the differences in milk quality observed between the concentrate supplement levels are due to intake differences in terms of basal pasture diet and supplement. The time of grazing of a ryegrass pasture has been found to impact milk quality, as a result of changes to the herbage nutrient supply.

Milk fat yield may be slightly improved with an isoenergetic ration, which also contains **lucerne,** corn **grain** and silage. When concentrates were supplemented for Italian Brown cows grazing on mountain pasture, higher supplementation levels (4.8 kg **organic matter** per day) resulted in improved milk yield and cheesemaking properties compared with a low level of supplementation (1.6 kg organic matter per day) (Bovolenta *et al.*, 2009). In order to exploit Alpine pastures, summer transhumance (i.e. movement from permanent farms in the valleys to temporary farms in the highland areas) is applied in mountainous areas (Sturaro *et al.*, 2013). However, milk volume is lowered when cows are moved to Alpine pastures during summer, which is probably an effect of the nutrient imbalance of diet (Bergamaschi *et al.*, 2016).

The type and diversity of the forage will also influence the milk **fatty acid** profile. Feeding pasture at the early growth stage increases the content of *trans*-11-18:1 (vaccenic acid) and *cis*-9,

trans-11-18:2 (conjugated **linoleic acid**) fatty acids in milk compared with the concentrate and hay (65:35, respectively) feeding. **Lipolysis** values of milk are lowered as milk yield negatively relates to lipolysis when cows are provided concentrates with hay-based diets or corn–silage compared with the ryegrass–silage diet. Compared with grass silage, corn silag**e** results in higher proportions of *trans*-10 C18:1 and lower proportions of C18:0 (**stearic acid**) and conjugated linoleic acid in milk fat. Incorporation of flaxseed supplementation into dairy cow diets is a viable strategy to provide a higher level of energy and omega-3 fatty acids. It has been observed that supplementing Jersey cows with ground flaxseed did not alter the milk yield and components but increased omega-3 fatty acid concentration in milk (Shingfield *et al*., 2005; Isenberg *et al*., 2019).

Providing a TMR to dairy cows enables more efficient milk production due to optimized **dry matter** intake and daily milk yield; however, the TMR's makeup should be considered. For example, cheese made from cows fed a TMR based on **maize** silage is characterized by an intense smell of sour milk and a firmer texture than milk derived from cows fed only hay and commercially produced feed (Cipolat-Gotet *et al*., 2018). It is due to the lower proportions of vaccenic acid, conjugated linoleic and **linolenic acid**s provided by TMR based on maize silage, which increases the susceptibility of the resulting cheese to **oxidation** and lipolysis.

Feeding various pomace (e.g. **olive** and **grape**) to dairy cattle provides an opportunity to improve the nutritional and sensory

attributes of milk. They are rich sources of biologically active compounds (e.g. **polyphenol**s) and **crude fibre** content derived from a solid by-product of olive oil separation and the wine industry, respectively. Dietary inclusion of dried olive pomace at 10% of dry matter in the feed decreased palmitic, stearic and linoleic concentrations while increasing oleic concentration in milk compared with the cows fed without dietary supplementation (Castellani *et al*., 2017). Similarly, dietary grape pomace supplementation to lactating cows increases the concentration of **polyunsaturated fatty acids** and has been proven to contribute a pleasant aroma and desirable sensory properties in the resulting cheese. Therefore, the inclusion of pomaces in dairy cattle feed can improve the nutritional profile and functionality of milk. (HP; JKV; HTMH; ENP)

See also: Ruminants, effects of nutrition on milk yield and composition

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Dairy cows, milking routines

Lactating cows are normally milked twice daily, though where *Bos indicus* cattle predominate, the calf must be present to stimulate the release of **oxytocin** and **milk** ejaculation by the cow. *Bos indicus* cattle may only be milked once daily, and their milk yield may be reduced if the calf is allowed to **suckle** before the cow is milked. In contrast, herds *of Bos taurus* cows may be milked three times daily. This practice increases milk output by about 15%. In high-yielding herds the additional expense of the extra milking may be offset by the value of the increased milk yield.

A recent innovation is the introduction of automatic milking systems in which the **cow** is allowed to choose when she is milked. Most cows opt to be milked four to five times daily, usually with a reward of a meal of food following each milking. This system of rewarding cows for entering the automatic milking parlour includes recording each cow's entry, so that any cow not presenting itself can be checked for signs of ill-health. (JMW)

Dairy goats, feeding strategies to improve milk production and composition

The ability of goats to utilize plants with higher condensed **tannins** provides a competitive advantage for ingesting a wide array of plant species, as these are generally rich in tannins. However, despite their high tolerance for tannins, goats have the ability to minimize the ingestion of the amount of tannin through altered bite rate, bite number and selection of plant species. Feeding tannin-rich **forage** species (i.e. lentisk (*Pistaciai lentiscusto*)), Damascus dairy goats in confinement and fed vetch

hay) increased milk protein, fat content and curd firmness (Hadaya *et al*., 2020).



One-year-old African Nubian dairy goats. Photo courtesy of US Department of Agriculture. Licensed under Public Domain Mark 1.0.

Sulla is a perennial **legume** that contains a high protein level, readily fermentable structural **carbohydrates**, total phenolic and non-tannic **phenolic compound**s, and a moderate number of condensed tannins. Provision of sulla fresh forages to Girgentana goats resulted in increased milk total protein, **casein**, total **polyphenol**s and free polyphenols compared with feeding hay with ground **barley** grain meal (Di Trana *et al*., 2015). Goats fed with green borage plant (*Borago officinalis* L.) or hawthorn (*Crataegus oxyacantha* L.) exhibit increased levels of flavonoids and terpenoids in milk, which can adversely affect the quality and sensory attributes of milk (De Feo *et al*., 2006). The concentration of **terpenes** in goat milk is increased by grazing on some novel pasture species, such as lady's bedstraw (*Galium verum*), **chicory** (*Cichorium intybus*) and crown daisy (*Chrisantemum coronarium*). These, in turn, can alter milk and cheese sensorial aspects when compared with grazing on conventional forages. (HP; JKV; HTMH; ENP)

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Dairy products

Milk and products manufactured from milk. Liquid **milk** is heated for short periods of time to kill pathogens. Pasteurized milk (72°C for 15 s) can be stored for up to 5 days. UHT (ultra-heat-treated) milk (132°C for 2 s) can be stored for up to 12 months; sterilized milk (115–130°C for 10–30 min) can be stored for several months. **Heat treatment** denatures the **whey protein**s in milk, giving it a boiled **taste** that is particularly noticeable in UHT and sterilized milk.

The **butterfat** contents of liquid milks are 3.9% (whole), 0.1% (skimmed), 1.6% (semi-skimmed) and > 4% (Channel Islands breeds). In homogenized milk the fat globules are broken up and remain distributed throughout the milk so that it does not form a cream layer.

Cream is separated from whole milk mechanically and either

sold with a fat content between 15% and 45% or churned into butter. Butter manufacture produces buttermilk as a **by-product**.

Yoghurt is made by fermenting milk with bacteria that produce **lactic acid** to coagulate the **casein**; sugar and fruit or flavouring may then be added.

Cheese is manufactured from coagulated milk proteins (*see* Casein) and varying proportions of fat, water and salts. A general method is to coagulate the casein to produce curds and whey, cut and scald the curd, drain off the whey, press, salt and ripen the curd. There are hundreds of varieties of cheese, which obtain their individual characteristics by variations in the production process. (PCG)

Dandelion (*Taraxacum officinale*)

A herbaceous plant, with reddish-brown roots about as thick as a finger and a milky sap. The height of the stem to the inflorescence of its silk web is about 2–50 cm. Its leaves are pointed at the end and look like lion's teeth.



Dandelion seed pods. Photo courtesy of Glavind Strachan Photography. Licensed under CC BY-SA 2.0.

The active compounds of this plant vary with season. In summer, the content of root sap is high. In autumn, the amount of **inulin** increases by up to 25%. The bitterness of the leaves and roots are greatest in spring and summer, respectively (Zargari, 1997). The root contains a bitter substance, taraxacine, as well as choline, taraxasterol, taraxerol, taxine, hydroxycinnamique, folic acid, vitamins A, B, and C, **calcium**, **potassium**, **iron**, **magnesium**, **sodium**, **manganese**, **phosphorus**, **silica**, **sulphur**, various **sugars**, **mannitol**, resin material and **fatty acid**s. The leaves contain trexacin, **inositol**, mucilage, various sugars and a resinous substance. About 39% of leaf ash is potassium. The leaves and roots are most commonly used, even though its seeds contain 20% **oil**. Its claimed therapeutic properties include a tonic for the digestive system, a blood purifier, and reducing bile and liver problems (Zargari, 1997; Di Napoli *et al*., 2021). Due to the presence of many terpenoids and **polysaccharide**s in the root, it may be an effective natural, non-toxic anti-cancer treatment in alternative medicinal and therapeutic programs (Li *et al*., 2022). Scientific studies related to the feeding of dandelion leaves and roots to domestic animals are limited, but there is some evidence in poultry for phytobiotic properties of its roots and leaves, which could enhance digestion, stimulate bile production, remove toxins, improve the **electrolyte** balance, increase the activities of **enzymes** in the liver and other tissues, and act as a digestive stimulant, with a positive effect on

intestinal **villi**, and as an immune modulator (Qureshi *et al*., 2017). (AS; BH-G; CJCP)

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Databases

Collections of valuable measurements that pertain to a specific production system. The most common uses of databases in animal production are in tables of nutrient composition of the large range of feedstuffs that may be used in animal feeds. These data are used in **feed formulation** software packages. (SPR)

Date

Fruit of the palm *Phoenix dactylifera*. When mature at 10–15 years old, date trees yield 45–90 kg of dates per tree. The leading date-producing and exporting countries are Saudi Arabia, Egypt, Iran and Iraq. Dates are usually grown for human consumption but may be fed to goats and cattle if they fall from the tree or are of substandard quality. The seeds can be pressed for **oil**, leaving a

residue useful for stock feed. Date trees are **drought** resistant. The young leaf spines are soft and the branches can be browsed or fed to cattle and goats. (JKM)

Date palm nutrient composition.

		Nutrient composition (g kg^{-1} DM)					
	Dry matter (g kg^{-1})	**Crude protein**	**Ether extract**	**Crude fibre**	**Ash**	**Starch and sugar**	**NFE**
Fruit	660–850	11–25	4–17	39–102	81	760	–
Fresh leaves	–	116–275	15–42	14–23	7–13	–	41–58

NFE, nitrogen-free extract.

DDT

Dichloro-diphenyl-trichloro-ethane, with the chemical formula $(ClC_6H_4)2CHCCl_3$, is a chemical synthesized first in 1874. Its **pesticide** properties were discovered in 1939. During World War II, it was found to be also effective against vector-borne diseases, such as malaria and typhus.

The chemical was widely used in agriculture against pests but scientific evidence started to mount in the 1950s that DDT remains stable under most environmental conditions. It is not broken down

completely by the microorganisms present in the soil or in the bodies of other organisms, causing it to accumulate in the natural environment. Biomagnification occurs when humans consume products containing DDT residues, such as dairy and meat. In the human body, DDT is stored in fatty tissues and is released in the bloodstream, carried out by proteins. It has multiple negative impacts on human health, including being carcinogenic and being detrimental to the cardiovascular system, central nervous system and liver, causing tumours and mutations. Beneficial insects, such as bees and other pollinators, are also negatively impacted by DDT and so are birds, frogs, fish and other wildlife.

In 1962, the publication of the book *Silent Spring* by Rachel Carson exposed the dangers of DDT and laid the foundations of the global environmental movement. It stimulated widespread public concern and calls for better control of the chemicals used in agriculture. Many countries started banning the application of DDT as a pesticide: Hungary in 1968, Bulgaria in 1969, Cuba, Norway and Sweden in 1970, USA and Germany in 1972, France and Poland in 1976, Singapore and UK in 1984, Canada, Chile and Romania in 1985, Korea and Switzerland in 1986. The Stockholm Convention on Persistent Organic Pollutants (POPs), which entered into force in 2004, put a worldwide ban on the application of DDT for agricultural purposes. However, the World Health Organization (WHO) supports the use of the chemical for indoor spraying to control malaria in countries where this vector-borne disease remains a major risk citing that direct human health benefits outweigh other concerns. (CJCP)

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Deamination

The process by which the **nitrogen** from **amino acid**s is released as ammonium nitrogen. This can occur by direct production of ammonium nitrogen from the **metabolism** of **cysteine**, **glutamine**, **glycine**, **histidine**, **methionine**, **serine**, threonine and **tryptophan** by specific enzymes. Ammonium nitrogen can be produced directly from glutamic acid by L-glutamic **dehydrogenase**, which links the **transamination** of nitrogen between amino acids to nitrogen excretion. Ammonium nitrogen can be incorporated into **urea** for **detoxification** and excretion. (NJB)

See also: Ammonia; Nitrogen metabolism

Debeaking

Erroneous term for **beak**-trimming, a procedure commonly used in the poultry industry to reduce feather-**pecking** and **cannibalism**. The usual procedure is to remove the tip of the beak by infrared heat on the day of hatching, which results in a shortened beak with minimal stress. The ethics of the practice are

debatable, since the beak is well innervated and the procedure induces some pain and physiological stress in birds. Alternative methods of reducing feather-pecking are being researched. (RB)

Decarboxylation

The removal of a carboxyl carbon from a **substrate** with the ultimate production of CO_2. **Carbon dioxide** production by decarboxylation occurs in the breakdown of **carbohydrate**-related molecules such as **pyruvate**, TCA cycle intermediates such as isocitrate and α-ketoglutarate, **amino acid**s such as glutamic acid (in the production of γ-aminobutyrate) and other amino acids (or related compounds) in the production of **biogenic amine**s. (NJB)

Deer

The cervid family branched from the ruminant stock some 30 million years ago. There are now 17 living genera, some (especially *Cervus*) still rapidly speciating. Deer are native to all regions except Australasia, Oceania and Africa south of the Sahara, ranging from equatorial to arctic regions. They occupy a wide variety of habitats, forest, open scrubland, mountain and tundra, and so their natural diets and dietary adaptations vary greatly (Hofmann, 1985).



Fallow deer suckling. Photo courtesy of Bertie Mabootoo. Licensed under CC BY-NC-SA 2.0.

Important deer species include the *Odocoileus* spp. (white- and black-tailed deer of North America), *Hippocamelus bisulcus* (the huemul of South America), *Cervus elaphus* (red deer, with several subspecies throughout Europe), *Cervus canadensis* (wapiti or elk of Canada), *Cervus nippon*, *Cervus timorensis*, and *Cervus unicolor* (sika deer of Japan, and rusa and sambar of Indonesia), *Axis axis* (chital deer of India), *Rangifer tarandus* (**reindeer** and caribou of Scandinavia and northern Canada) and *Dama* spp. (fallow deer). The genus *Cervus* can be divided into two distinct genetic groups (Emerson and Tate, 1993). Red deer, wapiti and sika are in one group, and sambar and rusa are in the other. There is a close genetic relationship between the genus *Elaphurus* (e.g. the Père David deer) and the red deer, wapiti and sika group; whereas sambar and rusa are more similar to members of the genera *Dama* and *Axis* than to the other members of their own genus (*Cervus*). This information can help us to predict which species may interbreed. Sambar and rusa deer hybrids in Australia resemble the sambar deer, particularly the large rounded ears, bushy tail, brown coloration and fine coat structure. The hybrids are the same size

and body weight as the older rusa stags. Sambar and red deer have been interbred in New Zealand, but the progeny are infertile (Tate *et al*., 1997). Sika and red deer have interbred in Scotland, and red deer and wapiti crosses are common in New Zealand and southern Australian deer farming.

The social behaviour of forest species, such as roe, moose, white-tailed deer, mule deer and muntjac (territoriality, small family groups, browsing habits), makes them unsuited to intensive management or domestication. However, those adapted to more open habitats show herding behaviour and a hierarchical society, mobility and versatile feeding habits, and recently they have been successfully domesticated as farm animals. Farmed species include fallow, red, rusa, chital, wapiti, sika, sambar, rusa and reindeer,

Modern deer farming involves procedures such as pregnancy testing, embryo transfer, disease control, selective culling and supplementary feeding to increase their productive potential. In red deer, one adult stag will mate with 20–40 hinds; hinds remain fertile for more than 12 years; and surplus animals may be removed for sale or slaughter at 15 months of age (Blaxter *et al*., 1988). As a result, a managed herd of deer can be many times more productive than a fully wild herd. Vital statistics of farmed deer are shown in Table 1.

Table 1. Vital statistics of farmed deer.

Parameter	Fallow	Red	Wapiti (elk)	Rusa (Javan)

Parameter	Fallow	Red	Wapiti (elk)	Rusa (Javan)
Reproduction				
Weight at puberty (kg)	30	80	160	40
Mating season	March–May	March–April	March–April	July–August
Gestation length (days)	230	234	255	260
Fawning/calving season	November–January	November–December	November–December	March–May
Target weights (kg)				
Birth weight	5	8	18	5
Weaning: females	20	40	70	20
males	25	50	85	25

Parameter	Fallow	Red	Wapiti (elk)	Rusa (Javan)
15 months: females	37	80	170	80
males	50	110	220	100
	50	110	230	90
Maturity: females				
males	100	250	400	120

Some typical dietary requirements for domesticated red deer are shown in Table 2. Compared with sheep, red deer have a high **metabolic rate**. They also generally show a shorter **retention time** of food in the gut and so digest **roughage** diets a little less well. As a result, their **maintenance** requirements are rather high (Kay and Staines, 1981; Dryden, 2011).

Table 2. Dietary requirements of red deer (from Adam, 1994).

	Dry matter (kg day^{-1})	**Crude protein** (g kg^{-1} DM)
Calves		
6–8 months (winter)	1.3	100
12–15 months (summer)	2.2	120–170

	Dry matter (kg day^{-1})	**Crude protein** (g kg^{-1} DM)
Hinds		
Pregnant (winter)	2.0	100
Lactating (summer)	3.0	170
Stags		
Maintenance (winter)	3.0	100
Increasing liveweight (summer)	4.0	120

In the southern hemisphere red deer calves are born in November to December, and in May or June in the northern hemisphere. In Australia, rusa deer are born in autumn (April–May). They may be weaned from their dam after taking colostrum and reared on a **milk substitute**. This should be similar to that used for rearing lambs, for deer milk is much richer than cow's milk (Table 3). Alternatively they may be left with their dam at pasture until housed for the winter, or weaned at about 8 weeks of age on to a **fattening diet**, concentrates plus some roughage, similar to that used for sheep or cattle. Rapid **growth** and an excellent conversion efficiency (food intake for weight gain) can be achieved (Blaxter *et al.*, 1988; Adam, 1994). Adult red deer will readily take a wide variety of foods, including **forage crop**s and

browse, hay and silage, root and fruit crops, pelleted or loose concentrates, **protein supplement**s and mineral–**urea** blocks. Care should be taken, of course, to introduce new foods gradually.

Table 3. Composition of milk, mid-lactation (g kg^{-1}).

	Crude protein (N × 6.38)	**Lactose**	**Fat**	**Ash**	**Dry matter**	**Energy** (kJ kg^{-1})
Red deer	75	45	100	11	230	6500
Dairy cow	35	48	35	9	130	2900

Deer from temperate or northern regions show a marked seasonality not only in their reproductive cycle but also in growth and fattening, **appetite** and **nutrient requirement**s (Dryden, 2011). They lay down **fat** and they **lactate** during summer; during winter, **calf** growth slackens and adults mobilize their fat. These cycles help to match food requirement to the natural availability of **forage**. Both antler growth and peak milk production occur during the summer and place similar demands on **mineral** intake (Table 4). Since food intake is naturally high at this time, such mineral requirements are readily met.

Table 4. Minerals
(g) deposited in antlers by a 125 kg red deer stag, and secreted in

milk by a 80 kg red deer hind during full lactation (Kay and Staines, 1981) and recommended dietary content (Adam, 1994).

	Ca	P	Mg
Antlers	350	160	5
Milk	370	300	20
Recommended dietary content (g kg^{-1} DM)	3–6	2–4	1–2

The two main products of deer farming are **meat** and immature antler. Deer meat is usually called venison. Some venison producers have introduced trade names in an effort to get some product differentiation, e.g. 'Cervenna', marketed by some New Zealand producers. Deer, compared with sheep and cattle, can produce an attractively lean, high **dressing percentage** (55–63%) **carcass** with heavy and highly priced hindquarters. This, together with the popular image of venison, ensures a good price for **deer meat**, provided that it is hygienically produced and marketed, with due regard for animal **welfare**. As well-fed adults (but not yearlings) lay down substantial fat reserves by the end of summer, this is an unsuitable time for their slaughter. Venison is marketed as a lean meat, and producers should use farming systems that ensure that the carcass has minimum fat. Drew (1992) showed that carcass fatness of red deer varies with animal **liveweight** and season, but is not independently affected by

farming system. This means that it is possible to use intensive farming practices without adversely affecting **meat quality**.

The immature antler is called velvet. Velvet antler is a fairly soft, uncalcified, cartilaginous material. It is covered with a soft skin which bears short, velvety hairs, from which the product gets its name. Note that velvet antler is not just the skin, but is the whole immature antler. Each male deer has two antlers; each of these is called a stick of velvet. The antler is branched and each branch is called a tine. The whole arrangement (i.e. both antlers) may be referred to as a rack. Velvet antler is used in Chinese traditional medicine and modern pharmacology has shown its value in treating a variety of disorders (Li, 2020).

Other products are pizzles, skins and soft dress leather, while the aesthetic appeal of these lean and agile animals serves to promote tourism. (RNBK; GMcLD)

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Deer meat, effect of nutrition

Deer meat is classified as an unconventional meat, although other deer products are in demand internationally.

Carcass features

Studies about the effect of feeding systems on farmed fallow deer

have shown that a higher **energy intake** leads to higher **dressing percentage** values (Volpelli *et al.*, 2002; Wiklund *et al.*, 2006). Similarly, deer fed on pellets show a higher dressing percentage than pasture-fed deer (58.1 vs. 51.8%). So, in general, use of commercial feed mixtures improves deer nutritional status and **carcass** weight, resulting in higher dressing percentages, but, as in horses, there can be an increase in the proportion of the forequarter.

Chemical composition

Deer meat ranges in moisture content from 73% to 78% and these levels will decrease as the energy content of the diet increases and the intramuscular fat (IMF) content increases (Fig. 1). **Protein** content varies between 19.2% and 24.2%, thus this meat is a good source of proteins and the IMF content is low, ranging from the 0.05% in wild red deer to 2.5% in wild fallow deer. This means that meat from deer is a healthy alternative meat source, but increasing energy intake of farmed deer (usually confined and concentrate fed) compared with wild deer will lead to higher levels of IMF.

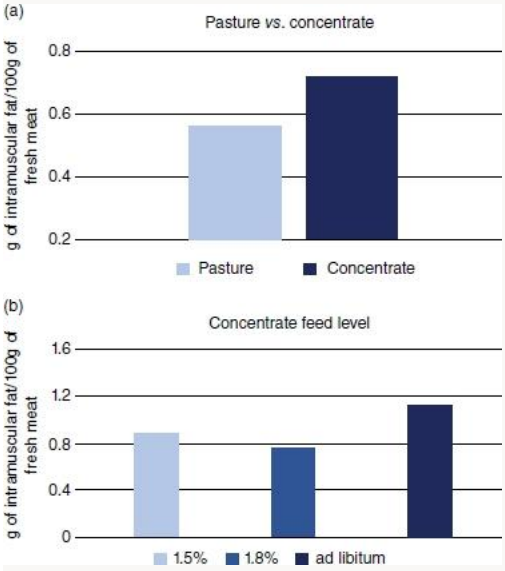


Fig. 1. Effect of different feeding systems/energy intake on deer meat

intramuscular fat concentrations, adapted from (a) Volpelli *et al.*, 2003; and (b) Kim *et al.*, 2017.

Physicochemical properties

Game meat contains more myoglobin than other species because of the need for greater **oxygen** transport capacity, and this explains the darker colour and the greater speed of colour degradation in meat from species like deer. The high content of pro-oxidants leads to low colour stability in deer meat, and for this reason pasture feeding is recommended to improve colour stability, instead of concentrate feeding. The shear force of deer meat exhibits a wide range, from values less than 20 N to greater than 60 N. This reflects high glycolytic capacity of deer muscles and the tendency for high pHs, which consequently increases the pH decline, leading to shortening. There are few studies that have examined the impact of diet on tenderness. There is evidence that concentrate feeding will increase shear force, but the mechanism has not been elucidated (Kim *et al.*, 2017) (Fig. 2).

Fatty acid profile

In general, **saturated fatty acid**s (SFAs) is the most represented category in deer meat, followed by monounsaturated fatty acids (MUFAs) and polyunsaturated fatty acids (PUFAs), but this will be influenced by the type of nutrition (Fig. 3). Indeed, the fatty acid composition in deer muscles can change according to feed composition, despite rumen biohydrogenation of PUFA. α-**Linolenic acid** (ALA, C18:3 n-3), which is contained in grass, and **linoleic acid** (C18:2 n-6), which occurs in concentrated feed, are present primarily in the **phospholipid** fraction of deer IMF

and muscles, as in other species. Pasture-fed deer exhibit favourable SFA levels and n6/n3 ratios and deer meat is also characterized by a low **cholesterol** content, from 55 to 102 mg 100 g^{-1} in wild deer and up to 86 to 98 mg 100 g^{-1} in farmed deer. (AM; PDP)

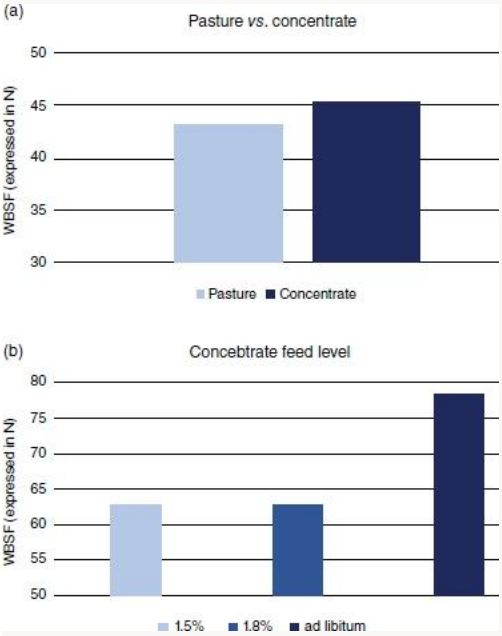


Fig 2. Effect of different feeding systems/energy intake on deer meat Warner Bratzler Shear Force (WBSF) values adapted from (a) Volpelli *et al.*, 2003 and (b) Kim *et al.*, 2017.

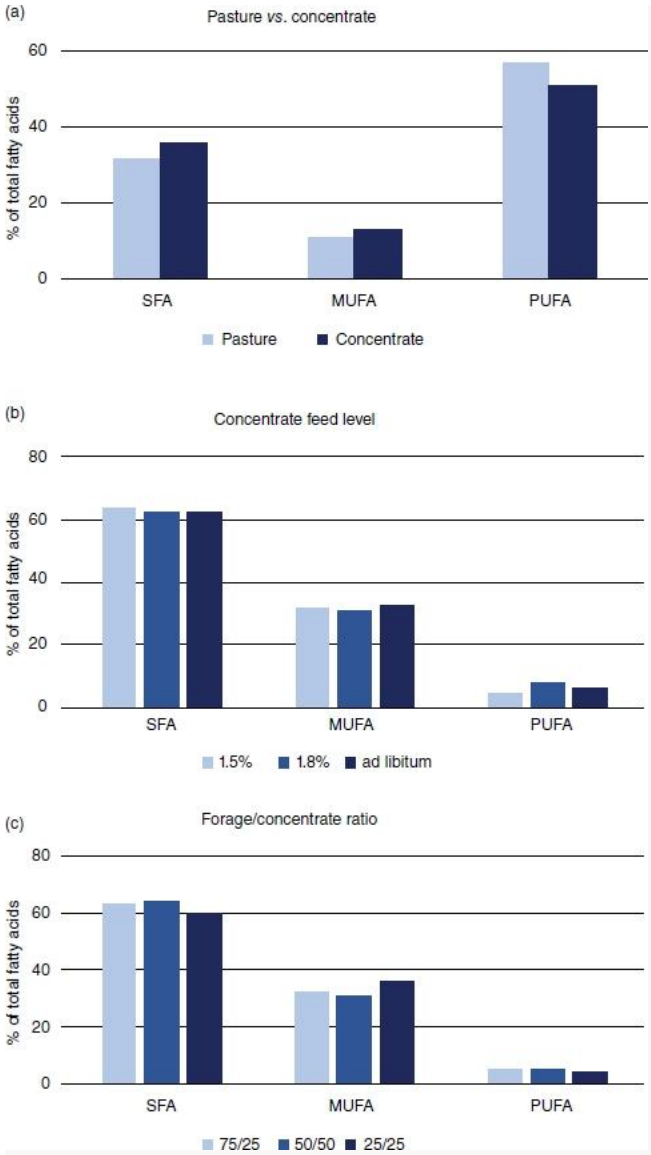


Fig. 3. Effect of different feeding systems/energy intake on deer meat fatty acid groups content, expressed in percentage of total fatty acids, adapted from (a) Volpelli *et al.*, 2003; (b) Kim *et al.*, 2017; and (c) Phillip *et al.*, 2007).

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Defecation

The voiding of **faeces** from the anus. Undigested food is stored in the **rectum** and when sufficient has accumulated stretch receptors are activated and the anal sphincter opens to allow passage of the material to the ground. Stressed animals more regularly void faecal matter, low in **dry matter**, because of **hormone**-induced colonic spasms. Faecal composition can give an indication of **apparent digestibility** of nutrients, such as **phosphorus**, and adequacy of nutrient intake. (CJCP)

Deficiency diseases

A deficiency normally refers to an inadequate supply of one or more specific nutrients, rather than a general restriction of intake or a deficiency in any other aspects of an animal's environment. There are seven major classes of nutrients – **protein**, **carbohydrate**, **minerals**, **vitamins**, **lipids**, fibre and **water** – a deficiency of any of which can cause characteristic disease symptoms, such as **iron** deficiency causing **anaemia**. Some deficiencies cause asymptomatic disorders that reduce vigour, activity and production in farm animals, e.g. restrictions in **energy** or **sodium** intake.

The severity of a **nutrient deficiency** will depend on an animal's requirement, so that a cow in early **lactation** may be deficient in energy when offered a diet with an energy density that would be adequate for a non-lactating cow. A deficiency becomes disease when the **welfare** of the animal is reduced by the nutrient deficit. Thus, depending on how welfare is defined, an animal either fails to cope with the deficiency or feels unwell as a result. In many circumstances the deficiency is temporary, until homeostatic mechanisms are employed that allow the animal to cope. These may be by increasing the **absorption** of the deficient nutrient or by reducing output, e.g. of **milk**. Even if they are only temporary, diseases would normally exist for several days, or regularly for a period of each day, to be classified as such. Theoretically deficiencies can only exist for elements or compounds that are required by the animal, but in recent years an essentiality has been demonstrated for many elements that were not previously believed

to be required by animals, even though it has not so far been possible to quantify the requirement.

The severity of the deficiency is mainly determined by the animal's capacity to store the element and the fluctuation in intake. Fluctuations in intake may arise from a variable food supply in farm animals **foraging** on rough **grazing** or from a deliberate restriction of intake for economic reasons. Towards the end of winter, the availability of **feed** may be deliberately restricted by farmers in anticipation of the growth of **grass** in spring. Food **availability** and intake may also fluctuate with the physiological state of animals; for example, dry sows might be restricted to prevent them from becoming obese. Storage organs, such as the **liver** for **copper** and **zinc**, or the bones for **calcium**, may accumulate toxic elements in place of essential ones, such as **cadmium** being stored in the liver and **lead** in bones, exacerbating or perhaps even triggering a deficiency in the essential element.

If clinical symptoms are evident, the aetiology of a deficiency disease can usually be traced to the nutrient in deficit. However, some farm animals, such as cattle and sheep, having evolved from prey species, do not show overt signs of pain and so diagnosis can be difficult.

The animal's status with regard to many minor or trace nutrients often depends on the intake of other nutrients. Some may have generic effects that influence the availability of several elements, such as the effect of **ascorbic acid** on the availability of many **heavy metals**, particularly **iron**, or the adverse effect on

the immune system of **selenium** or **vitamin E** deficiencies. Others rely on the similarity in the chemical properties of different elements for their interdependency, e.g. cadmium and sodium, or the formation of stable complexes in the digestive tract, e.g. copper thiomolybdates in ruminants.

Samples that can be taken from farm animals to diagnose a deficiency include **blood plasma**, **saliva**, **faeces** or **urine**. Occasionally tissue biopsies (e.g. liver) are performed for diagnostic purposes. Occasionally **hair**, **hoof** and other tissues are sampled to give a historical record of the progression of the deficiency.

Another aid to diagnosis of a deficiency disease is the animal's behaviour. Many animals that are short of specific nutrients develop an opportunistic **appetite** to try to obtain the nutrient in deficit. This has been demonstrated for many species whose members are short of sodium, for chickens that are short of calcium and for cattle that are deficient in **phosphorus**. Sometimes the novel appetite is focused on learnt methods of obtaining the nutrient in deficit; for example, animals with sodium deficiencies lick each other's skin to get **salts**.

As agriculture has developed in recent years, some nutrients have become routinely deficient in farm animals. For example, the milk yields of dairy cows have increased considerably, leading to a significant likelihood that the cow will be deficient in calcium in the first week of lactation. After a few days, it is able to mobilize the necessary calcium from bones and a clinical disorder is usually avoided. Farmers now often prepare cows for the calcium demands

of early lactation by feeding them a calcium-deficient diet for up to 1 month before parturition. This entrains the calcium mobilization pathways in advance of the period of increased requirements. Another example is the deficiency in sodium intake, which arises when large quantities of **potassium** are used on pasture to stimulate grass growth. Potassium in soil is antagonistic to sodium uptake by plants, and potassium in the rumen is antagonistic to **magnesium** absorption. This leads to both sodium deficiency, which is easily rectified by salt supplements or sodium fertilizers, and magnesium deficiency, which is not so easily rectified. Magnesium deficiency, or **hypomagnesaemia**, can sometimes be rectified by adding magnesium salts to the drinking water or feed, or by broadcasting calcined magnesite on the pasture, but none of these mechanisms ensures adequate magnesium intake by cattle. As the onset of the disease is sudden, unlike sodium deficiency, the mortality rate is high. **Herbivore**s have an acute appetite for sodium, unlike magnesium and calcium, which suggests that sodium deficiencies have been common throughout their evolution and indeed they are still observed in wild cattle in Southeast Asia.

Calves reared on milk-based diets for veal production may routinely suffer from iron deficiency, manifested as **anaemia**, because the milk has a low supply of iron. The consequences for the animal – lethargy and fatigue – are not likely to affect the animal's survival adversely and may even increase **feed conversion** efficiency. However, deficiencies that result from an unsuitable farming system are now increasingly believed by the public to be unacceptable, and in the European Union minimum

iron levels in blood are now legally established. Suckling piglets are also prone to iron deficiency and are routinely given an iron injection soon after birth.

Some elements, such as **selenium** and **iodine**, can be given to farm animals so that their products are rich in these elements and human consumers will be more likely to obtain an adequate supply. An increasingly important area of research is the extent to which genetic differences in absorption provoke deficiency diseases. The differences have been identified in the absorption of copper, but a better understanding of mineral absorption is needed before genetic differences can be exploited in practice. (CJCP)

Dehull

To remove the kernel coat or **pericarp** of a seed. (JMW)

Dehydration

A deficit of water in the body. Dehydration may result from a lack of drinking water, excessive evaporative loss or **diarrhoea**. (JMW)

Dehydration, body

A state in which the body is in negative water balance, i.e. when it loses more water than is ingested as liquid and in food. It may arise from either insufficient intake of water or excessive loss, e.g. from **diarrhoea** and vomiting, beyond the ability of the kidneys to compensate. The initial response of the body to negative water balance is the withdrawal of water from the interstitial fluid space in an attempt to maintain normal blood volume. **Connective**

tissue, muscle and skin are most affected, leading to the clinical test of prolonged elevation of a skin fold. More advanced dehydration results in a reduction in blood volume, accompanied by haemoconcentration. Milk yield is depressed in lactating animals. In order to produce more metabolic water, there is an increase in the **oxidation** of **fat**, then of **carbohydrate** and finally of **protein**. Dehydration can contribute to death, especially when combined with another clinical condition, such as an **electrolyte** imbalance.

Racehorses and eventer horses can easily become dehydrated, since they lose large quantities of hypotonic **sweat** when exercised, especially under hot conditions. Because of the conflicting stimuli regulating the secretion of renin and angiotensin II, such horses may refuse to drink to correct the resultant dehydration. (ADC)

Dehydroascorbate

The oxidized form of L-ascorbate (L-ascorbate ⇌ L-dehydroascorbate + 2H). It is produced when ascorbate participates in **oxidation**–reduction reactions in cellular **metabolism**. (NJB)

See also: Ascorbic acid

Dehydrogenase

A class of enzymes involved in metabolic **oxidation**–reduction reactions. They act by removing **hydrogen** from a **substrate** or adding hydrogen to a substrate. These enzymes cannot use **oxygen** as the acceptor but instead use one of three **coenzyme** combinations: NAD/NADH, NADP/NADPH, FAD/FADH. These

coenzymes link metabolic oxidation to the electron transport chain (a series of dehydrogenases involved in oxidation–reduction steps carried out by **cytochrome**s) and link substrate oxidation with molecular oxygen as the terminal electron acceptor, yielding water. (NJB)

Demand feeding
Spontaneous feeding 'on demand', or *ad libitum*, when food availability is unlimited. (JSav)

Deoxynivalenol
A **mycotoxin** of the **trichothecene** class, produced by *Fusarium* **fungi**. Deoxynivalenol (DON), or **vomitoxin**, causes feed refusal and vomiting in pigs, and feed refusal and oesophageal lesions in poultry. Trichothecenes such as DON tend to be produced in moist grain under cool or cold environmental conditions. **Wheat** and **maize** are the grains most commonly contaminated by DON. (PC)
See also: Cold environment

Deoxyribonuclease
An **enzyme**, also called DNase, hydrolysing **deoxyribonucleic acid** (DNA) into **nucleotides**. A DNase (DNase I; deoxyribonucleate 5′-oligonucleotidohydrolase; EC 3.1.21.1) is purified from pancreatic secretions. Another DNase II is purified from the spleen. (SB)

Deoxyribonucleic acid (DNA)
A polymer of deoxyribonucleotides, each consisting of a sugar,

deoxyribose, and a nitrogenous base, which is derived from one of two **purines** (**adenine** or **guanine**) and one of two **pyrimidine**s (thymidine or **cytosine**). DNA can be considered the chemical basis of heredity: the genetic code is the sequence of deoxynucleotides found in the genes that make up chromosomes. DNA is made up of two complementary strands in the form of an α-helix. The genetic code is given by the sequence of deoxynucleotides in DNA, each **amino acid** being represented by a specific set of three. This code is transcribed to messenger RNA, which specifies the complete amino acid sequence of the **protein** being synthesized. (NJB)

Deoxysugar

A **monosaccharide** containing less **oxygen** than the parent **sugar**. Usually, the terminal $-CH_2OH$ group is replaced by a $-CH_3$ group. In bacteria, more than one hydroxyl group may be replaced with **hydrogen**, producing di- and tri-deoxysugars. The most abundant deoxysugar in nature is 2-deoxy-D-ribose, the sugar component of **deoxyribonucleic acid** (DNA). Bacterial **lipopolysaccharide**s can contain L-**rhamnose** (6-deoxy-L-**mannose**) and L-**fucose** (6-deoxy-L-**galactose**). (JAM)

See also: Carbohydrates

Depigmentation

A pigmentation disorder of the skin, mucous membranes, hair, or retina in which melanocytes in these tissues are affected or destroyed. The brown pigment melanin is produced from the

amino acid, **tyrosine**, by specialized pigment cells called melanocytes. **Copper** deficiency causes depigmentation of hair, fur, wool and feathers in animals. Depigmentation may also develop due to hyperthyroidism, adrenocortical insufficiency, alopecia, **anaemia**, certain infectious diseases, excessive sun exposure or albinism in humans and other animals. (SPL)

Desmosine
A unique structure of cross-linked **lysine**, found in mature elastin and collogen. In the biosynthesis of elastin, three lysine residues are oxidized by the **vitamin C**-dependent enzyme, lysyl oxidase; these combine with a fourth lysine to form the cross-linked structure of desmosine. Desmosine stabilizes the structure of elastin and **collagen**, which contributes to **connective tissue**s its properties of extensibility and elastic recoil. (NJB; GW)

Desoxysugar:
see Deoxysugar

Detoxification
A process by which a toxin is changed to a less toxic compound or by which its poisonous effect is reduced. In ruminants, **rumen** microbes are the first line of active defence against some plant toxins, such as **ricin** in **castor bean**, **mimosine** in ***Leucaena***, nitrotoxins in ***Astragalus***, nitrates in many **forage** plants, **oxalates** in *Halogeton*, phyto-oestrogens in clovers, pyrrolizidine **alkaloid**s in *Senecio* and *Heliotropium*, thiaminase in **bracken fern** and many **mycotoxin**s. Once absorbed, some toxins can be

detoxified by enzymes in the gut and intestinal lining, liver, lungs and kidney.

There are antidotes for a few specific plant poisons. Bracken fern **poisoning** can be treated by butyl alcohol in cattle or by **thiamine** in horses, fluoroacetate poisoning by glyceryl monoacetate and pentobarbital, hydrocyanic acid poisoning by **nitrite** or thiosulphate, nitrates and nitrotoxin poisoning by methylene blue or **ascorbic acid**, **oxalate** poisoning by **calcium** hydroxide or calcium gluconate, Jimson weed poisoning by neostigmine and larkspur poisoning by physostigmine. **Potassium** permanganate and tannic acid will bind to many alkaloids.

Compounds that bind toxins may also be given. Activated charcoal binds to many toxins in the gastrointestinal system; clay minerals and aluminosilicates also bind molecules of certain sizes and configurations. Cyclodextrins are oligomers of **glucose** with cylindrical hydrophobic cavities surrounded by hydrophilic margins that encapsulate certain small toxins, such as corynetoxins in annual ryegrass (*Lolium rigidum*).

Vaccines against low-molecular-weight toxins are difficult to create. However, there has been some success in developing a vaccine against phomopsin mycotoxins that cause **lupinosis**, corynetoxins in annual ryegrass and **ergot** alkaloids in tall fescue. Vaccines against other toxins are being developed. (MHR)

Deuterium

A stable isotope of **hydrogen**. It has one neutron and one proton and is twice as heavy as hydrogen (2.014 vs. 1.008). Its physical and chemical properties are very similar to those of hydrogen. It is used

as a non-radioactive tracer in studies of the molecular **metabolism** of **carbohydrates**, **fatty acid**s and **amino acid**s. As a tracer in water (^2H_2O) it is used to measure **total body water** and **body water turnover**. As doubly labelled water ($^2H_2{}^{18}O$) it is used to estimate CO_2 production and (by assuming a **respiratory quotient**) the **heat production** or **energy expenditure** of free-ranging animals. (NJB)

Development:
see Growth; Growth factors

Dextrins
α-Glucosidic chains of varying length, but with a lower average molecular weight than **starch**, soluble in water but insoluble in alcohol and ether. They are intermediate products of starch **hydrolysis**. In aquatic diets dextrin binds the pellets together better and imparts greater water stability than primary starch. (NJB; QS)

Diabetes
A condition characterized by polyuria and polydypsia. There are two separate disorders. Diabetes insipidus is caused either by insufficient production of antidiuretic **hormone** or by failure of its receptor in the renal collecting ducts. Diabetes mellitus is associated with **hyperglycaemia** and the consequent glycosuria as a result of insufficient pancreatic production of **insulin** or impaired response of its tissue receptors to a normal circulating level of insulin. Refined **sugars** in the diet should be replaced by

fibre-rich foods containing unrefined **carbohydrate**; the **protein** content should remain normal but the **fat** content should be reduced, especially if the animal is overweight. (ADC)

Diaminopimelic acid (DAPA)
An amino acid, $H_2N{\cdot}CH{\cdot}(COOH){\cdot}(CH_2)_3{\cdot}CH{\cdot}(COOH){\cdot}NH_2$, in the **peptidoglycan** of all Gram-negative and some Gram-positive bacteria, but not Archaea. DAPA has both D- and L-**isomers**. L-DAPA is an intermediate in the microbial synthesis of L-**lysine** from L-aspartate, **pyruvate**, succinyl-CoA, and L-**glutamate**. In Gram-negative bacteria, the peptidoglycan is 10% of the cell wall, while in Gram-positive bacteria it is 90%. It has been used to estimate bacterial biomass outflow from the **rumen** and the fraction of faecal matter attributed to bacteria. The ratio of DAPA to cell biomass is highly variable. (DMS; GW)

Diammonium phosphate
Dibasic ammonium phosphate, $(NH_4)_2HPO_4$, is typically manufactured by the acidification of rock phosphate to produce phosphoric acid, which is in turn mixed with **ammonia** and heated under pressure. Manipulation of **temperature** and pressure determines whether a mono- or dibasic **salt** is produced. The dibasic salt is extremely unpalatable and is rarely used in animal feeding stuffs. Consequently, most of the material that does come onto the market is unrefined and the level of **contamination** usually prevents it from reaching **feed** grade standard. (CRL)

Diarrhoea

The major cause of diarrhoea is a local irritation of the **intestinal mucosa** by infectious or chemical agents, which often leads to an increased flow of intestinal secretions, distension of the lumen and a consequent increase in **motility**. Dietary diarrhoea occurs in all species and at all ages but is most common in neonatal animals ingesting more **milk** than can be digested, perhaps resulting in secondary colibacillosis and **salmonellosis**. Feeding inferior-quality milk replacer to young calves is also a very common cause of dietary diarrhoea. Heat denaturation during the preparation of milk replacers can result in a decrease in the concentration of non-**casein** proteins, leading to poor clotting in the **abomasum** and thus reduced **digestibility**. The use of excessive amounts of **carbohydrates** and proteins that are not derived from milk also predisposes to diarrhoea in calves, as does the inclusion of too much **protein** from **soybean** or **fish**. The proteases in the digestive tract of pre-ruminant calves and lambs cannot denature the soluble antigenic constituents of soybean protein and so a hypersensitive reaction may develop in the tract of such animals. Similarly, milk replacers made from components of bovine origin may lead to diarrhoea when fed to lambs, piglets or foals.

Dietary diarrhoea can be induced in all species by a sudden change in diet, particularly at the time of weaning. This is particularly important in the early-weaned pig. The cause is probably related to the fact that changes in gut **enzyme activity**, necessary for the **digestion** of a new diet, take some time, so that gradual exposure to the new diet is advisable to maintain proper

digestion.

Treatment of dietary diarrhoea in the neonate involves cessation of milk-feeding for 24 h and its replacement by oral **electrolyte** solutions. Milk of the correct composition is then gradually reintroduced. Treatment with an antibiotic may be necessary if secondary infection is suspected, along with oral **kaolin** or pectin to protect damaged intestinal mucosa. (ADC)

Diastase

An obsolete synonym for **amylase**. (SB)

Dicalcium phosphate

Dibasic calcium phosphate is usually available in anhydrous ($CaHPO_4$) or dihydrate ($CaHPO_4.2H_2O$) forms. The **phosphorus** (P) occurs in the highly available *ortho* (PO_4^{3-}) form. The crystalline product is usually prepared by the treatment of rock phosphate with **hydrochloric acid**. Acid treatment of bones or heat defluorination of rock phosphate are alternative methods of production. Pure anhydrous dicalcium phosphate contains 22.8% P by weight but, depending on the origin and method of production, the actual level is usually between 18% and 20.5%. The corresponding value for the dihydrate is 17% to 18%. (CRL)

See also: Rock phosphate

Dicarboxylic acids

Organic acids containing two ·COOH groups. Examples in metabolism are **oxalate**

($^{-}OOC{\cdot}COO^{-}$), **succinate** ($^{-}OOC{\cdot}CH_2{\cdot}CH_2{\cdot}COO^{-}$), fumarate ($^{-}OOC{\cdot}CH{=}CH{\cdot}COO^{-}$) and **oxaloacetate** ($^{-}OOC{\cdot}CH_2{\cdot}C{=}O{\cdot}COO^{-}$). Aspartate ($^{-}OOC{\cdot}CH_2{\cdot}CHNH_3{\cdot}COO^{-}$) and **glutamate** ($^{-}OOC{\cdot}H_2{\cdot}CH_2{\cdot}CHNH_3{\cdot}COO^{-}$) are dicarboxylic **amino acid**s. (NJB)

Dicoumarol (coumarin)

White and yellow sweet clover (*Melilotus albus* and *M. officinalis*) are biennial **legumes** that grow throughout much of the USA. The plant's pleasant odour is due to coumarin, a non-toxic substance that is converted to the anticoagulant dicoumarol when moulds grow on clover **hay** or **silage**. Dicoumarol is a **vitamin K antagonist** and animals poisoned by it lack the critical proteins needed for blood coagulation. Affected animals bruise easily and bleed excessively. Some may bleed to death from a relatively small injury or surgery such as castration, dehorning, or vaccination. Prevention lies in avoiding mouldy feeds or limiting the dose by intermittently feeding only small amounts of affected clover hay or silage. (LFJ)

Diet

All food consumed over a specified period. The term includes any material that enters the digestive tract, regardless of whether or not it is nutritionally available. It can be applied to a single feed or a combination of feeds, for example **roughage** and concentrate fed to **ruminant animal**s. (SPR)

Diet-induced thermogenesis:

see Heat increment of feeding

Dietary fibre

The name given to the **polysaccharide**s of plants that cannot be hydrolysed by the digestive **enzymes** of higher animals. These are mainly long-chain **carbohydrates** found in plant cell walls and some cereal grains, such as **cellulose**, **hemicellulose**s, **pectic substance**s, **fructans** and β-**glucans**. **Lignin**, a macro-molecule consisting of several **polyphenolic compound**s, is usually also included although this substance is not a carbohydrate. Because it makes a substantial part of plant carbohydrate, the dietary fibre complex is the major source of energy via **fermentation** in ruminants and equids, and can provide an important source of energy in free-range pigs and herbivorous birds.

The rate and extent of fermentation of the polysaccharides that comprise dietary fibre are determined by physical and biochemical characteristics of the plant material. If there is extensive lignification, microbial action is hindered and fermentation of the material is incomplete before it leaves the rumen. The extent of silicification (the presence of **silica** in plant cell walls, e.g. in external walls of epidermal cells) and cutinization (cutin covers the exterior of plant cells exposed to the environment and prevents **water** loss from the cell and the entry of pathogens) also affects microbial fibre degradation, because both of these substances are indigestible. **Tannins**, essential oils and **polyphenol**s, if present, inhibit **cellulase**s and proteases and slow **rumen digestion**. **Solubility** also determines the fermentation rate. Soluble dietary fibre in forages includes unlignified pectic substances, β-glucans

and fructans. Soluble carbohydrates are rapidly and completely fermented both in the rumen and in the **large intestine** of non-ruminants. Structural carbohydrates in plants include cellulose, hemicelluloses and pectins. They may be associated with **lignin**. These components are generally more extensively fermented in the rumen than in the large intestine of non-ruminants. For example, wood and newsprint are not degraded in non-ruminants, whereas in the rumen 0–40% of wood and about a quarter of newsprint is fermented. **Straw**, **cottonseed** hulls and tropical **grasses** are either not fermented or poorly fermented in the large intestine of non-ruminants, but one-third to two-thirds of them is fermented in the rumen. (JAM)

See also: Feed composition and analysis; Gums; Hemicelluloses; Oligosaccharides; Pentosans; Storage polysaccharides; Structural polysaccharides

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Diet selection

Animals can learn about the metabolic consequences of consuming diets with certain physical and sensory properties (e.g. appearance, flavour and texture) and the content of **energy** and nutrients (e.g. **protein**, **fats**, **sugars** and **minerals**), and choose preferentially or avoid diets that they have previously experienced. There are receptors for food flavours in the tongue and the **gastrointestinal tract**, which provides a biochemical basis for animals to reject, adapt to, or maintain food intake. Non-ruminants (e.g. rats, pigs, cats and chickens) have an ability to select a diet that contains adequate **amino acid** levels to meet their requirements. For example, pigs and chicks are able to distinguish among diets differing in the content of **methionine**, threonine or **tryptophan** and to prefer an amino acid-balanced diet over an amino acid-deficient diet. Grazing ruminants can discriminate among forages based on their colour, **taste**, odour, texture and shape to select nutritious foods from a diverse array of plant species to meet their nutritional requirements and avoid foods with low nutrient content and toxins. For example, when sheep are given a choice between a 14.1%- or 17.2%-CP diet and a 23.5%-CP diet, they consume different proportions of the 23.5%-CP diet (17.6% vs. 9% of total **feed intake**), such that the CP content in the mixed feeds is 15.8% and 17.8%, respectively, to minimize the production of **ammonia**. In addition, ruminants choose diets with sufficient fibre content to stabilize rumen **fermentation** (e.g. pH, **short-chain fatty acid**s and **non-protein nitrogen**). The innate ability of animals to select diets for optimal growth and health is orchestrated by changes in the concentrations of **neurotransmitter**s in the

central and peripheral nervous systems. (GW)

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Diffusion

A process of molecular mixing of gases or liquids when pure substances are either poured together or are separated by a semipermeable membrane and allowed to mix. In a cellular setting gases and **substrates** diffuse down electrochemical gradients across membranes by either simple diffusion (no carrier) or facilitated diffusion, where a carrier protein is involved. (NJB)

Digesta

The contents of the digestive tract, synonymous with **chyme**. Digesta consist of undigested feed mixed with secretions, desquamated **mucosa**l cells and **microorganism**s. (SB)

Digestibility

A measure of the degree to which feed constituents are broken down (digested) into small molecules that can be absorbed from the digestive tract. Digestibility values are generally expressed as the percentage of a given nutrient or feed constituent that is digested and absorbed. Digestibility values can be either ‘true’ or

'apparent' (*see* Digestibility measurement).

Digestibility is influenced by a number of factors relating to treatments of the foodstuffs and complete diets, such as **milling** and other forms of processing. Processing can improve digestibility; for example, heat can destroy **antinutritional factor**s such as **protease inhibitor**s in **legume** seeds and thereby reduce endogenous **protein** losses; chemicals such as **sodium** hydroxide can make lignified **cellulose** more available for microbial **enzymes** in ruminants; addition of feed enzymes, such as **glucanase** and arabinoxylase, can reduce **viscosity** in the **small intestine** of poultry and piglets. All these treatments improve digestibility. Food processing may also have a negative influence, in particular on the digestibility of proteins. Heat causes the formation of inter- and intramolecular covalent bonds that are resistant to enzymatic **digestion**. In the presence of **reducing sugars** (e.g. **fructose**) and **amino acid**s, the **Maillard reaction** leads to the formation of complex adducts between the sugar and amino acids, especially **lysine**. The Maillard reaction can also occur during storage of dried foods and make lysine unavailable for **absorption**.

Starch is generally made more available by heat processing (*see* Cereal grain processing) but this can also convert available starch into a form that is unavailable for enzymatic degradation. **Resistant starch** is produced by rearrangements in the molecular structure of **amylose**, which constitutes about 20% of starch and is generally less available than **amylopectin**.

The digestibility of a nutrient is not a constant value. Feeding

conditions (such as method and level of feeding), the particular animal (its species, sex, age and physiological stage) and feed processing influence digestibility. (SB; RB; GMcLD)

Digestibility measurement

The digestibility of a nutrient after passing through the entire digestive tract can be determined by total collection of **faeces** over a suitable period. Digestibility measured directly from the difference between the intake (I) of the nutrient and its output in **digesta** or faeces (O) is called the net or **apparent digestibility** (AD):

$$AD=(I-O)/I$$

However, the excreted matter also includes the endogenous loss of the particular nutrient, which has been digested and absorbed but has then re-entered the gut in the form of endogenous secretions. After correction for this loss (E), the **true digestibility** (TD) of the dietary nutrient can be calculated:

$$TD=(I-O+E)/I$$

The endogenous losses of a nutrient were traditionally estimated by measurements of the losses in animals given diets devoid of that nutrient. However, for some nutrients at least, endogenous secretions may be modified by the diet and these estimates may not represent what occurs under normal circumstances, when the animal eats a complete diet. For this reason, other corrections are used. Undigested food and un-reabsorbed endogenous secretions may, furthermore, be metabolized by the microflora, being either degraded or converted to microbial matter. In non-ruminants, microbial **metabolism**

occurs predominantly in the **large intestine**. The digestibility of protein and **amino acid**s is particularly influenced by microbial metabolism. Most of the protein in faeces is microbial, and because the microflora can synthesize amino acids there may be little relation between the amino acid composition of the undigested food and that of the faeces. This in turn means that digestibility of amino acids measured over the entire digestive tract may be very misleading. **Lipids** are less metabolized by the intestinal microflora but **fatty acid**s can be elongated and **unsaturated fatty acid**s may be partly hydrogenated by the microbial metabolism in the rumen or large intestine. **Carbohydrates** not available for digestion in the **small intestine**, due to either physical inaccessibility (e.g. lignification) or chemical structures not hydrolysed by the mammalian **enzymes** (in **dietary fibre**), are the main **energy source**s for the microflora. The end-products of microbial fermentation, i.e. the **short-chain fatty acid**s, are absorbed by the host animal and contribute to the energy supply.

A complete characterization of nutrient availability in the animal therefore includes measurements of digestibility in the different compartments of the **gastrointestinal tract**, i.e. in non-ruminants, of digesta at both the ileal and faecal level, respectively. In ruminants, measurements of degradation in the rumen are of particular importance, due to a relatively predictable and constant composition of the outflow from the rumen. In animals with a less significant microbial activity, e.g. **carnivore**s such as mink, ileal sampling is of less importance for a proper characterization of

digestibility.

If only a fraction of the whole digesta is collected, an indigestible **marker** must be added to the diet so that the proportion of the whole flow that is collected can be calculated. For a correct measurement of the digestibility of a nutrient, the flow rate of the marker needs to be the same as that of the nutrient. Furthermore, an ideal marker must not be absorbed and affected by the digestive tract or the microbial population in the tract and it should be closely associated with or physically similar to the undigested nutrient in question. No existing marker totally satisfies all these requirements. Markers are either internal (a component of the food itself, such as **lignin**) or external (a substance added to the food, such as **chromic oxide**, one of the most commonly used external markers, and Cr-mordanted neutral detergent fibre). The combined use of internal and external markers can improve the measurements; for example, insoluble **ash** can be used as an internal marker together with chromic oxide as an external marker. Internal markers are used to measure digestibility, while external markers are used to estimate total faecal excretion, or rate of passage of undigested food residues through the digestive tract.

Sampling of digesta for measurements of digestibility in different compartments of the digestive tract requires a **cannula**. To determine the digestibility of nutrients that are modified in the large intestine, especially amino acids, digesta are sampled at the terminal **ileum** to determine 'ileal digestibility'. The simplest method of obtaining samples of digesta from the terminal ileum is to sacrifice the animals, taking the samples under terminal

anaesthesia. For repeated sampling, various kinds of cannula may be used. A simple T-cannula allows only partial sampling and needs the inclusion in the diet of an indigestible marker. The cannula is relatively small and may give unrepresentative samples with coarse or fibre-rich feeds. A more advanced technique, the post-valvular ileocaecal cannula, involves a large cannula placed in the **caecum** opposite the ileocaecal valve. It can be steered with a nylon cord in such a way that, during the collection, digesta are directed into the cannula, so that, during the sampling period, all the digesta leaving the ileum are collected. An alternative surgical approach, which avoids the use of a cannula, is to bypass the large intestine by ileorectal anastomosis.

By the use of marker technique, the determination of digestibility is based on the increase of the marker concentration in relation to the nutrient in the digesta or faeces. AD is calculated from analyses of the concentrations (g kg^{-1}) of nutrient (N) and marker (M) in the experimental diet, and in samples of digesta (or faeces), n and m, respectively.

$$AD = (N - n.(M/m))/N$$

or

$$AD = 1 - [(M \times n) / (m \times n)]$$

Other approaches to determining digestibility are based on: (i) the rate of appearance of the nutrient in the body by measuring the difference in the arteriovenous concentration across the portal-drained viscera together with the portal **blood flow** (this approach may underestimate absorption due to uptake of the nutrient by the tissue of the gut); (ii) isotopic techniques, for example **labelling**

the experimental animal with ^{15}N so as to distinguish (labelled) endogenous protein from (unlabelled) dietary protein (this gives a direct measure of the **real digestibility** of dietary protein, uninfluenced by endogenous protein loss, but there may be some recycling of (unlabelled) nutrient from the diet into endogenous secretions during the feeding period); and (iii) chemical modification of the dietary protein, for example treatment with *o*-methyl-isourea in order to guanidinate **lysine** to homoarginine and then to determine lysine digestibility (this method assumes that the chemical reaction is distributed equally between digestible and indigestible lysine, that the treatment does not influence the general digestibility of the protein, and that homoarginine is digested and absorbed to the same extent as lysine).

Other methods include predictions from: (i) *in situ* digestibility based on incubation in bags (***in sacco***) in the digestive tract, for example after incubation in the rumen or throughout the intestine (mobile nylon bag) with collection at the end of the ileum through a cannula, or in the faeces; (ii) *in vitro* digestibility based on incubation in the laboratory with enzymes similar to those occurring in the digestive tract; (iii) **gas production** where the volume and rate of gas production are related to the extent and rate of digestion in the rumen; (iv) **chemical composition**; and (v) physical methods based on **near-infrared** reflectance spectroscopy (NIRS), **nuclear magnetic resonance** or other methods, alone or in combination with chemical analyses.

In **fish**, digestibility is measured by several different methods for **faeces collection**, including dissection, stripping (i.e. pressing

digesta out of the rectum with the fingers) or anal suction of the individual fish, or, alternatively, immediate pipetting, continuous filtration, or decanting of tank water.

In poultry, the fraction of each nutrient ingested can be determined as the digestibility coefficient, obtained by measuring both the amount of nutrient present in the feed and the amount of nutrient present in the faeces (not the excreta), or more exactly in the ileum. The difference between the two, commonly expressed as a percentage or in relation to 1 (with 1 indicating complete digestion), is the proportion of the nutrient digested by the bird. The digestibility of an ingredient or a complete feed can also be measured. The measurement of digestibility in the bird is more complicated than in mammals, since faeces and urine are excreted together as 'droppings' through the **cloaca**. As a result, it is necessary to separate the faeces and urine, usually by performing a surgical operation on the bird that allows collection of faeces in a **colostomy** bag. Digestibility measured in this way is known as **apparent digestibility**, since the faeces and ileal digesta contain substances originating in the fluids and **mucin** secreted by the gut and associated organs, and also cellular material abraded from the gut wall as the digesta pass. Correction for these endogenous losses allows for the '**true digestibility**' to be measured. Generally, the digestibility values listed in feed tables refer to apparent digestibility unless stated otherwise.

Availability is often used as a synonym for digestibility but also has a different meaning. (SB; RB; GMcLD)
See also: Markers; Protein digestibility; Apparent digestibility

Further reading

D'Mello, J.P.F. (2000) *Farm Animal Metabolism and Nutrition*. CAB International, Wallingford, UK, 438 pp.

Dryden, G.McL. (2021) *Fundamentals of Applied Animal Nutrition*. CAB International, Wallingford, UK, pp. 40–41.

Digestible energy

That part of the **gross energy** of a food substance or complete ration which is not expelled as the gross energy of **faeces**. It is widely used to express both the **energy value** of a diet and the **energy requirement**s of animals. (JAMcL)

See also: Energy balance

Digestible organic matter:

see D value

Digestion

The process of breaking down dietary components to make them available for **absorption** from the gastrointestinal lumen by epithelial cells. Food particles are reduced in size by mechanical and chemical means. The mechanical breakdown is performed by **chewing** in the mouth and by contractions of the muscular walls of a bird's **gizzard**. Macromolecules such as **starch** and proteins need to be degraded to absorbable units, i.e. **monosaccharide**s and **amino acid**s. This is done by the digestive **enzymes** of the animal as well as those of **gastrointestinal microflora**. A large number of specific enzymes are involved in their breakdown. In **carnivore**s and omnivores, the animal's own enzymes predominate, whereas in non-ruminant **herbivore**s microbial

activity plays an important role. Microbial activity in the rumen and **large intestine** converts food nutrients into microbial matter and **volatile fatty acid**s, both of which are then utilized by the host animal.

Most digestive enzymes are found in all species. However, their activity varies with age and responds to variations in the diet. The digestion of the food may be initiated in the mouth, where it may be disintegrated by chewing. Although birds have no teeth, they may use their beaks to reduce the size of food components. During the process of **mastication**, **saliva** is added. In the saliva of many animals an α-**amylase** initiates the enzymatic degradation of starch. In very young pigs, salivary amylase is low; it increases slightly between 2 and 3 weeks of age and then falls to very low levels. In young (**suckling**) animals, a **lipase** initiates the degradation of milk **lipids**. The saliva provides a source of N (from **urea** and mucoproteins), P and K, which in ruminants are essential for the microorganisms in the rumen. Saliva also helps to **buffer** the rumen liquor and maintain an environment suitable for **rumen microorganism**s.

Some species have a forestomach: birds have a **crop** which serves as a storage organ in which microbial **fermentation** may occur together with a continued action of salivary amylase on starch degradation; in ruminants the rumen, together with the **reticulum** and **omasum**, are considered as forestomachs to the **abomasum**, which corresponds to the true (gastric) **stomach** of non-ruminants.

Protein digestion begins in the stomach, where pepsins cleave

some of the **peptide** linkages. Like many of the other enzymes involved in protein digestion, pepsins are secreted in the form of inactive precursors (proenzymes) and activated in the **gastrointestinal tract**. The **pepsin** precursors are called pepsinogens and are activated by gastric **hydrochloric acid**. Pepsins are most active at pH 1.5 to 3 and hydrolyse the bonds between aromatic amino acids, such as **phenylalanine** or **tyrosine**, and a second amino acid. A gelatinase that liquefies **gelatin** is also found in the stomach. **Rennin** (chymosin), a milk-clotting enzyme, is present at birth and disappears after **weaning**. Pepsin activity is very low (or absent) during the first 2 weeks after birth but then increases rapidly, together with HCl production.
In the **small intestine**, shortly after passing the pylorus, the **digesta** are mixed with an alkaline juice that neutralizes the acid digesta from the stomach and also contains a variety of digestive enzymes from the **pancreas**: proteases, amylase, lipases and nucleases for digesting proteins, starch, lipids and **nucleic acid**s. In some species the pancreatic duct is joined by the hepatic duct that transports **bile** from the **liver**. Bile salts are important for **lipid absorption**.

Polypeptides formed by digestion in the stomach are further degraded in the small intestine by the proteolytic enzymes of the pancreas and **intestinal mucosa**. The pH is about 6.5. **Trypsin**, the **chymotrypsin**s and **elastase** act at interior peptide bonds in the peptide molecules and are called **endopeptidase**s. The **carboxypeptidase**s of the pancreas and the **aminopeptidase**s of the **brush border** are **exopeptidase**s that hydrolyse the

amino acids at the carboxy- and amino- ends of the polypeptides. Some amino acids are liberated in the intestinal lumen, but others are liberated at the epithelial surface by the aminopeptidases and dipeptidases in the brush border of the mucosal cells. Some di- and tripeptides are actively transported into the intestinal cells and hydrolysed by intracellular peptidases, with the amino acids entering the bloodstream. Thus, the complete digestion of protein to amino acids occurs at three locations: the intestinal lumen; the brush border; and the cytoplasm of the mucosal cells.

Starch consists of **amylose** and **amylopectin**. Large quantities of pancreatic amylase are secreted from the pancreas into the **duodenum** in most non-ruminants, except the horse. In bovine species there is generally little pancreatic amylase. Thus, the pre-ruminant calf cannot utilize starch, and adult cattle fed diets rich in grain may develop digestive disturbances when large amounts of starch enter the small intestine. Carnivores have little or no amylase activity. α-Amylase does not hydrolyse the chain branches of amylopectin or the terminal bonds. Therefore, the products of amylase action in the intestinal lumen are disaccharides such as **maltose** and **isomaltose**, trisaccharides and limit dextrins with at least five and an average of eight **glucose** units. These products must be further hydrolysed to their monosaccharide constituents before they can be transported into the epithelial cells. The enzymes for performing these last hydrolyses are attached to the membranes of the microvilli of the brush border and include **maltase**, **isomaltase**, **glucoamylase** and limit dextrinase. Other saccharases are **lactase**, **sucrase** and **trehalase**. Lactase activity

is high in mammals at birth and remains high for the first 2–3 weeks of life, after which it declines rapidly. Birds do not have lactase activity and ruminants do not have sucrase activity. In pigs, sucrase and maltase activities are low at birth and then rise with age. Enzyme changes in early-weaned pigs occur more rapidly than in sow-reared pigs, but age has a greater effect than diet on the development of intestinal brush-border enzymes.

Lipids are hydrophobic and need to be emulsified (breakdown of **fat** globules into smaller globules) before they can be digested by the hydrolytic enzymes, lipase and **phospholipase**s. They are initially emulsified in the stomach as a result of stomach motility and are further emulsified in the small intestine by bile salts and **lecithin** secreted from the liver. The major component of lipids, triglycerides, are only partly digested before absorption. **Fatty acid**s in position 1 and 3 are hydrolysed and, after forming micelles (microemulsions), become available for absorption, together with the remaining 2-monoglyceride, **glycerol**, **cholesterol** and other lipids.

Nucleic acids, DNA and RNA, are digested by **deoxyribonuclease** and **ribonuclease** secreted from the pancreas and are further degraded to **pentoses** and **purine** and **pyrimidine** bases by nuclease and related enzymes attached to the brush border. Absorption of digested products is completed in the **ileum**.

In the large intestine, microbial enzymes contribute to the digestion in all animal species and are in many cases of significant importance. The major microbial end-products of fermentation are

short-chain fatty acids (SCFAs) and **ammonia**, which are absorbed. SCFAs are an important **energy source** for the epithelial tissue but may also contribute considerably to the general energy supply of herbivorous animals, for example up to 75% in the horse. In ruminants, microbial digestion plays a particular role because the major part of digestion takes place in the rumen. (SB; RB)

See also: Digestibility; Intestinal absorption

Digestive disorders

The function of the **digestive system** is to break down food particles, physically and chemically, into a form that is suitable for **absorption** into the blood system and subsequent utilization for metabolic processes. There are many digestive disorders in modern animal farming systems, principally because the nature of the food supply is different to that available to their ancestral progenitors. The digestive system of farm animals evolved to digest foods that were often very different to those that can be easily provided in modern farming systems. In addition, the genetic modification of farm animals to increase productivity requires that the nutrient density of the diet be increased above that which the wild ancestors of farm animals would have consumed. This is important for the energy and protein supply for ruminants, which evolved to utilize coarse grasses.

In the case of lactating cows, a diet of coarse grasses and browse material has been necessarily replaced by lush **grass**, with a high water-soluble **carbohydrate** content, and **cereal grain**s containing **starch** that is rapidly digested in the **rumen**. Excessive

processing of cereals exposes the starch to rapid **fermentation**. After a meal, the rapid production of **fatty acid**s as a result of bacterial growth on the readily available **substrate** can lead to a reduction in rumen pH below the normal 6–7 (clinical acidosis), which reduces the potential growth of cellulolytic bacteria in particular and is manifested as loss of **appetite** and production. Also in dairy cows, the inadequate supply of **acetate** and **butyrate**, which are the precursors of **milk** fat synthesized *de novo* in the **mammary gland**, leads to a low milk fat syndrome, which can be rectified by reducing the quantity of rapidly digestible substrate fed at any one time. The feeding must be changed either to fibre-based **energy source**s, such as **fodder beet**, or to a starch-based energy source in small quantities at regular intervals of the day. Some benefit can also be obtained by feeding the cereals in a mixture with forages.

The fermentation of food particles produces gases, principally **carbon dioxide** and **methane**, which are liberated via the mouth by eructation. The rapid digestion of starch can lead to the production of excessive gas which, with diminished contractions of the reticulorumen, result in the animal becoming bloated. This ruminal tympany can be observed on the left-hand side of the animal, when viewed from behind. Some **legumes**, such as **lucerne** or clovers, produce a stable foam in the rumen, through which the gases cannot be liberated. Others, such as bird's-foot trefoil, contain **tannins** that effectively bind the proteins to reduce the rate of digestion and make them 'bloat-safe'. The feeding of fibrous forages will be beneficial in cases of **bloat**, as it reduces the

rate of digestion. Ruminants will go to considerable lengths to consume adequate fibre to stimulate **rumination**. Ruminal atony predisposes ruminants to tympany, but the consumption of pseudofibrous material can cause digestive disorders, such as calves that lick each other's coats and develop hairballs, or chickens that get an impacted crop. Cattle also develop abscesses when they consume plants with awns that irritate the **gastrointestinal tract**.

Salivation is an essential process to add moisture to the food, which together with **mastication** prepares the food for passage into the gastrointestinal tract. It also adds digestive enzymes, principally **amylase**s and **buffer** salts. The salts are particularly important to increase rumen pH in cattle and sheep, which allows digestion of fibre to proceed. Excessively wet feeds, such as lush grass, which may have a **dry matter** concentration of only 10–12%, may promote acidotic conditions in the rumen. **Saliva** also contains mucins, which are believed to counteract ruminal tympany – a problem that is worst following consumption of herbage of low dry matter content.

Vomiting is a digestive disorder that functions to reduce the digestion of potentially harmful material. It can also be triggered by motion sickness in animals in lorries or suffering from intense fear or an infection. A stereotyped vomiting disorder can develop in primates in stressful conditions. **Diarrhoea**, too, functions to reduce the time for which potentially toxic elements are present in the gastrointestinal tract, but can also be triggered by gastrointestinal infection, typically by parasites or bacteria.

Parasites may damage the absorptive surface of the gastrointestine, especially the intestinal **villi**, thus reducing **mineral** uptake. Diarrhoea is commonly caused by an excessive intake of rapidly digestible nutrients. One of the most common instances occurs when ruminants graze lush pasture in spring. In this case the absorption of some critical minerals, such as **magnesium**, can be reduced by the short **turnover** of feed in the rumen.

Stress, which is common in many intensively managed farm animals, will exacerbate several digestive disorders, including diarrhoea and vomiting. The frequency of defecation, as well as the dry matter content of the **faeces**, will indicate stress. The extent to which dairy cows are stressed by contact with their herdsperson can be estimated by whether they defecate when they are milked by that person. **Gastric ulcers** develop in pigs in intensive housing, due to excessive acid production.

Low intakes of food can reduce **digestibility**, at least in the short term, due to insufficient nutrients to support an adequate concentration of **microorganism**s in the rumen. In the long term, digestibility usually increases, due to increased **chewing** of the food and reduced losses of **nitrogen** and other nutrients in faeces. Excessive intakes of food, apart from the problems of bloat referred to above, can cause difficulties if the food particles enter the wrong compartments. In milk-fed calves the **milk** normally bypasses the rumen to be digested in the **abomasum**; but if the reticular groove does not function adequately, such as is common in calves drinking large quantities of milk from buckets with the head facing downwards, rather than **suckling** with the head held horizontally,

milk may enter the rumen and cause diarrhoea, or 'calf scours'. Specific nutrients consumed in excessive quantities, such as **lipids**, can upset the bacterial digestion in the rumen. Similarly, the consumption of some minerals (e.g. **potassium**) in excess can reduce the absorption of others (e.g. magnesium) through competitive inhibition.

Digestive disorders are a serious problem in farm animals and can lead to low growth rates and low milk production. This is particularly the case in high-producing ruminants, where there is a significant difference in the diet fed from that available to their ancestral progenitors. Further research is required to devise feeding regimes for farm animals that cater for their level of productivity. (CJCP)

Digestive enzyme inhibitors

Substances that inhibit the activity of one or more digestive **enzymes**. Nutritionally, the most important of these are the **protease inhibitors**, which are widespread in the seeds of many plants, especially **legumes**. They are proteins that form stable inactive complexes with digestive **enzymes**, especially **trypsin** and **chymotrypsin**, and are called **trypsin inhibitors**. The activity of these inhibitors, in both their relative and their total amounts, varies greatly amongst species of legume, and between varieties of the same species. They are inactivated by appropriate **heat treatment** and such treatment often forms part of the processing of the seeds for inclusion in feeds, especially for non-ruminants. Diets containing large amounts of trypsin inhibitors cause hypersecretion and enlargement of the **pancreas**, reduce

the digestion of dietary proteins and increase the loss from the gut of endogenous **nitrogen**.

Amylase inhibitors also occur in certain legume seeds but do not appear to be of great nutritional importance.
The actions of digestive enzymes on plant proteins can also be impaired by the presence in the diet of other **antinutritional factors**, such as **non-starch polysaccharide**s and **phenolic compound**s, and by the physical barrier of indigestible plant cell walls which impede access of digestive enzymes to the **substrates** within the cells. (MFF)

Digestive system, introduction
The complex of organs that participate in the **digestion** of food. The system comprises the entire **gastrointestinal tract** and its accessory organs. These include the salivary glands, the **pancreas** and the **liver**, which secrete **enzymes**, **bile** acids and other substances into the gut lumen, and the portal circulation, which carries away the products of digestion to the rest of the body. (MFF)

Digestive system, poultry
Birds have a modified gut, in comparison with other non-ruminant species such as pigs. The digestive system is relatively simple, due probably to an evolutionary need for a light body weight related to the ability to fly. The mouth is modified into a narrow, pointed **beak** to facilitate eating of seeds and small insects, and does not allow for the presence of **teeth** to permit grinding of the feed into

smaller particles for swallowing. Instead, mechanical breakdown of feedstuffs is performed mainly by a grinding action in the **gizzard** (which is attached to the **proventriculus**) and contractions of the muscles of the gastrointestinal walls. The function of the proventriculus is analogous to that of the **stomach** in the pig. Chemical breakdown of the feed particles is achieved by **enzymes** secreted in digestive juices and by gut microflora. The digestive process reduces feed particles to a size and **solubility** that allows for absorption of digested nutrients through the gut wall into the portal blood system.



A chicken's beak is designed to eat seeds and small insects. Photo courtesy of Oleksandr Pidvalnyi. Licensed under CC0 1.0.

Digestion begins in the mouth, where fluid produced by the salivary glands moistens the dry feed so that it is easier to swallow. At this point the feed, if accepted, is swallowed whole. The feed then passes quickly to a pouch in the oesophagus, the crop, which is a storage organ from which feed can be filtered into the lower oesophagus for passage into the next section of the gut, the proventriculus. There is only minimal **amylase** activity in the **saliva** and crop, indicating little digestion of **carbohydrates** in

this organ, and no digestion of **protein**.

The softened feed passes down the oesophagus by a series of muscular contractions (**peristalsis**) to the next section, the proventriculus, which represents the glandular stomach. Secretion of digestive juices containing HCl and the enzyme precursor (**zymogen**) pepsinogen takes place here. Pepsinogen is converted to the active enzyme**, pepsin**, in the acidic (pH 2.5) conditions in this organ. This initiates **protein digestion**, which is continued in the attached gizzard. HCl also serves to dissolve **minerals** ingested with the feed, such as **calcium** salts, and it helps to inactivate pathogenic bacteria present in the feed. Mucus is released by the proventriculus to protect the inner wall from acid damage. A grinding action in the gizzard, which is facilitated by the ingestion of grit, continues the process of digestion further by exposing a greater surface area of the feed to chemical breakdown. Partially digested feed in a semi-fluid form known as **chyme** then moves from the gizzard into the next part of the gut, the **small intestine**.

The small intestine is a long tube-like structure connecting the gizzard to the **large intestine**. This is where digestion is completed and absorption of nutrients takes place. The first part of this section is the **duodenum**, in which glands produce an alkaline secretion that acts as a lubricant and also protects the duodenal wall against HCl from the gizzard. The **pancreas** (which is attached to the small intestine) secretes fluid containing **bicarbonate** and several enzymes (**amylase**, **trypsin**, **chymotrypsin** and **lipase**) that act on **carbohydrates**, proteins and **fats**. The duodenal wall also secretes enzymes, which continue

the breakdown process on **sugars**, protein fragments and fat particles. **Bile** synthesized by the **liver** passes into the duodenum via the bile duct. It contains bile salts, which provide an alkaline pH in the small intestine and fulfil an important function in digesting and absorbing fats. These processes comprise emulsification, action of pancreatic **lipase** and formation of mixed micelles which are required for absorption into the intestinal cells. As a result of these activities the ingested carbohydrates, protein and fats are broken down to small molecules suitable for absorption (**monosaccharide**s, **amino acid**s (AA) and monoglycerides, respectively).

In contrast to digestion in the pig, the **disaccharide**, **lactose** (milk sugar), is only partly utilized by chickens because they lack the enzyme (**lactase**) necessary for its breakdown. As a result, most milk products are not ideally suited for use in poultry diets.

Absorption also takes place in the second section of the small intestine, known as the **jejunum**, and in the third section, known as the **ileum**. Digestion and absorption are complete by the time the ingesta have reached the terminal end of the ileum. This area is therefore of interest to researchers studying nutrient bioavailability (relative absorption of a nutrient from the diet) since a comparison of dietary and ileal concentrations of a nutrient provides information on its removal from the gut during digestion and absorption.

Minerals released during digestion dissolve in the digestive fluids and are then absorbed either by specific absorption systems or by passive **diffusion**.

The processes for the digestion and absorption of fat- and **water-soluble vitamins** are different, due to their **solubility** properties. **Fat-soluble vitamins** and their precursors (A, β-carotene, D, E and K) are digested and absorbed by processes similar to those for dietary fats, mainly in the small intestine. Most water-soluble vitamins require specific enzymes for their conversion from natural forms in feedstuffs into the forms that are ultimately absorbed. Unlike fat-soluble vitamins that are absorbed mostly by passive diffusion, absorption of water-soluble vitamins involves active carrier systems to allow absorption into the portal blood.

The ingesta, consisting of undigested feed components, intestinal fluids and cellular material from the abraded wall of the intestine, then pass to the next section of the intestine, the large intestine, which consists of a short **colon**, and a pair of blind caeca attached at the junction with the small intestine. The colon is attached to the **cloaca** (vent), the common opening for the release of faeces, **urine** and eggs. Poultry, like other birds, do not excrete liquid urine. Instead they excrete urine as uric acid, which is excreted as a white paste or a dry, white powder. Very little water is required for this process in birds, compared with the excretion of urine in cattle or pigs, which is related to their ancestry from reptiles. The process also explains the absence of a bladder in poultry. The contents of the large intestine move slowly and no enzymes are added. Some microbial breakdown of fibre and undigested material occurs in the caeca, but is limited. The extent of breakdown may increase with age of the bird and with

habituation to the presence of fibre in the diet. Thus, fibrous feeds, like **lucerne**, have a relatively low feed value, except in **ratites** such as the **ostrich**, which are well adapted for the utilization of high-fibre diets. Remaining nutrients, dissolved in water, are absorbed in the colon.

The large intestine absorbs much of the water from the intestinal contents into the body, leaving undigested material which is formed into faeces, then mixed with urine and later expelled through the cloaca. Caecal waste is also deposited on the excreta (droppings), appearing as a light-brown froth, which should not be confused with **diarrhoea**.

The entire process of digestion takes about 2.5–25 h in most species of poultry, depending on whether the digestive tract is full, partially full or empty when feed is ingested. Because of fowls' high **metabolic rate**, a more or less continuous supply of feed is required. This is provided for by the crop, which acts as a reservoir for the storage of feed prior to its digestion. Poultry tend to eat meals at about 15 min intervals through the daylight hours. Larger portions are eaten at first light and in the late evening. A meal of normal feed takes about 4 h to pass through the gut in the case of young stock, 8 h in the case of **laying hen**s and 12 h for broody hens. Intact, hard grains take longer to digest than cracked **grain**. (RB; CJCP; MFF)

Dihomo-γ-linolenic acid

All-*cis*-8,11,14-eicosatrienoic acid, molecular structure $CH_3{\cdot}(CH_2)_4{\cdot}(CH{=}CHCH_2)_3{\cdot}(CH_2)_5{\cdot}COOH$, molecular weight 306.5, shorthand designation 20:3 n-6. A **fatty acid** of the n-6

family synthesized from **linoleic acid** by successive Δ6 desaturation and chain elongation; it is also called homo-γ-**linolenic acid**. (DLP)

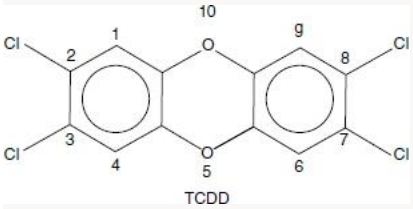
Dihydrofolate
$C_{19}H_{23}N_7O_6$, the first intermediate in the conversion of folic acid (a B vitamin) to its **tetrahydrofolate** form by the enzyme, **folate** reductase. After modification by addition of γ-glutamyl residues, tetrahydrofolate is the **coenzyme** form of the vitamin. Tetrahydrofolate and the folate system are critical to the synthesis of the **purines** used in DNA synthesis. (NJB)

Dilution rate
The rate at which fluid or solids in the freely mixing, constant-volume content of a compartment of the gut (e.g. reticulorumen) is replaced. Units are % h^{-1}, fraction h^{-1}, etc. (RNBK)

Dimethylsulphoxide (DMSO)
$(CH_3)_2{\cdot}SO$, a hygroscopic liquid that is miscible with water. It readily penetrates tissues and is used as a solvent for delivery of drugs to the bloodstream by topical application. (NJB)

Dioxin
A family of more than 70 chemical compounds, known as polychlorinated dibenzo-*para*-dioxins, that have an identical carbon–**oxygen** 'skeleton' and contain one to eight chlorine atoms. The most widely studied is 2,3,7,8-tetrachlorodibenzo-*p*-dioxin (TCDD), a known **carcinogen**, teratogen and mutagen. There is a

range of similar compounds broadly classified as polychlorinated dibenzo-*p*-dioxins (PCDDs, including TCDD), polychlorinated dibenzofurans (PCDFs), and **polychlorinated biphenyl**s (PCBs). Dioxins were found as contaminants in the herbicide trichlorophenoxyacetic acid (2,4,5-T) and also as a component of the defoliant 'Agent Orange' and in wood preservatives (pentachlorophenol). They are deposited on agricultural land from **pesticide**s and herbicides and enter the human **food chain** via animals that consume contaminated feed. Open incineration of rubbish also releases dioxins, because it is formed by combustion at low temperature in the presence of carbon and chlorine. They persist in the environment and accumulate in the fatty tissue of living organisms and some organs, such as the **liver**. Nearly all human contamination comes from food. In humans, dioxins are potentially carcinogenic, and they also disrupt reproductive, immune and endocrine systems. (JEM; CJCP)



TCDD

Dipeptidase

A **peptidase** that specifically hydrolyses dipeptides. Dipeptidases are located together with **tripeptidase**s and **aminopeptidase**s in the **brush border** of the epithelial cells of the **small intestine**, mainly the **jejunum**. (SB)

See also: Digestion

Dipeptide

R·C=O·NH·C·R, a molecule formed of two **amino acid**s linked by a **peptide** bond. In the **digestion** of **protein**, some dipeptides are formed and absorbed into the **enterocyte** prior to being hydrolysed to single amino acids. In special cases dipeptides are formed from cellular amino acids. These include **carnosine** (β-alanylhistidine), anserine (β-alanyl-1-methylhistidine) and **balenine** (β-alanyl-3-methylhistidine). (NJB)

Direct calorimetry

Direct calorimeters not only measure the total heat given off by animals, but also partition it into its two components, evaporative and non-evaporative. Non-evaporative or sensible heat is heat given off from an animal by radiation to surrounding surfaces, by convection to the surrounding air and by conduction to any objects with which the animal is in contact. **Evaporative heat loss** occurs because the conversion of liquid water into vapour requires heat energy. The latent heat of vaporization is the heat required to vaporize unit mass of water; it varies from 2490 to 2390 J g^{-1} (595–572 cal g^{-1}) within the temperature range 0–40°C. When water is vaporized in the respiratory passages during normal respiration and panting, or at the skin surface during perspiration, the latent heat of vaporization is given up by the animal. This heat loss by the animal is transferred to the air in the form of increased humidity; the enthalpy of the air (which is a measure of its energy content and depends on temperature, humidity and pressure) is increased.

Direct calorimeters are classified into four types (isothermal,

heat-sink, convection and differential) according to how sensible heat is measured. In isothermal calorimeters the sensible heat is measured as it passes through the walls, floor and ceiling of the animal chamber; these surfaces have heat-sensitive linings that generate voltages proportional to the heat passing through. In heat-sink calorimeters the chamber surfaces are thermally insulated and the sensible heat from the animal is taken up by a heat exchanger; the heat is measured as the product of the temperature rise of the coolant and its rate of flow. Convection calorimeters also have insulated surfaces and ideally all sensible heat from the animal is taken up by the ventilating air, whose temperature increase multiplied by flow rate provides the measure of the heat. This method tends to be slow in response, because after a change in the level of heat output there is a delay while the chamber itself, especially its insulated walls, adjusts to the new level. To overcome the delay, differential calorimeters employ two similar chambers, one containing the animal and the other an electrical heat source; the power provided to the heater is controlled to produce the same increase in air temperature as that in the animal chamber and it thus represents the sensible heat output of the animal. In heat-sink, convection and differential calorimeters, evaporative heat is measured as the increase in humidity of the ventilating air, usually sensed by dewpoint hygrometers or wet-and-dry-bulb thermometers.

The earliest calorimeters for farm animals were of the heat-sink type and much pioneering work was done in them 100 years ago. None of today's sophisticated electronic control systems were

available and most calorimeters required a team of three or four scientists for their operation. The precision was truly remarkable and demonstrated (over periods of days) agreement between direct and **indirect calorimetry** to within 1%. At the time this was hailed as proof that the first law of thermodynamics applied to living systems as well as to mechanical ones. Nowadays that would be accepted as axiomatic and the agreement between direct and indirect calorimetry would be regarded as proof of the accuracy of the measuring systems.

In recent years the technique of heat-sink calorimetry has been revived and refined but mainly applied to studies on humans. For animals, recent use of heat-sink, convection and differential calorimeters has been confined to studies on **laboratory animal**s and poultry. The most favoured method for farm animals has become the isothermal one, the modern form of which is the gradient-layer calorimeter.

In the gradient-layer calorimeter the sensible heat from the animal generates a small temperature gradient across a thin uniform layer, usually of plastic material, as it passes into a water-cooled jacket surrounding the chamber. The mean temperature gradient (i.e. temperature difference) across the layer is measured by multiple and/or widespread sensors on either side (thermocouples, thermistors or resistance thermometers) and generates a voltage output that is proportional to the integrated heat flow through all surfaces, i.e. the sensible heat output from the animal. Evaporated water is reconverted into liquid by passing exhaust air between cooled plates that return its humidity to the

original level it had before entering the chamber; the heat of re-condensing it, which is equal to the evaporative heat loss of the animal, is again measured by gradient layers covering the plate surfaces. Because the gradient layers are thin and the temperature differential across them no more than a fraction of a degree, the time response to changes in heat output is only a few minutes. The principal limitation to the speed of response of a gradient-layer calorimeter is not the calorimeter itself, but the relatively slow response to heat changes of any cage or bars fixed inside it to restrain the animal.

Ventilation of a direct calorimeter has to be sufficient to ensure control of air temperature inside the chamber and to avoid condensation of evaporated water inside it. Pre-conditioning all the ventilating air and then exhausting it to the environment would be wasteful of power and so most of the air is usually recirculated round a closed circuit, with only a small proportion being voided to the atmosphere and replaced with fresh air. The **oxygen** and **carbon dioxide** concentration differences between fresh and exhaust air can be made of the order of 1%, and conveniently measurable so that indirect and direct calorimetry may be performed at the same time. (JAMcL)

See also: Heat balance

Further reading

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Disaccharidases
Enzymes that hydrolyse molecules made up of two **sugars**. In animals they are found in the **brush border** of the **enterocyte**s of the **small intestine**. The enzyme that hydrolyses the two-sugar unit **maltose** from **starch** digestion is **maltase**; that hydrolysing **lactose** is **lactase**; and that hydrolysing **sucrose** is **sucrase**. (NJB)

Disaccharides
Sugars made up of two **monosaccharide** molecules. They can be **reducing sugars**, which have a potential carbonyl carbon, or non-reducing sugars, which do not. Disaccharides important in animal nutrition include the reducing sugars **maltose** (made up of two **glucose** units) and **lactose** (made up of glucose and **galactose**) and the non-reducing sugar **sucrose** (made up of glucose and **fructose**). Another non-reducing disaccharide of note is **trehalose**; other reducing disaccharides include cellobiose, gentiobiose, **melibiose** and turanose. (NJB)

Disorders, nutritional:
see Nutritional disorder

Dispensable amino acids:
see Non-essential amino acids

Dispersion strategy

Animals often have to leave their site of origin and settle in a new area to avoid competition with conspecifics for food. Such animals are known as dispersers. Exposure to particular cues can lead to habitat imprinting that helps to guide territorial dispersers to suitable new territory. Understanding dispersal tendencies can be helpful to successfully relocate groups of animals. Microorganisms and weeds are facilitated in moving the necessary distances for successful dispersion by animal carriers. In many cases, passage through the animals' **gastrointestinal tract** increases the survival of weed seeds. This has major implications for pasture quality in stock routes, for example those in Australia down which stock have travelled to markets for a hundred years or more. (CJCP)



Cattle disperse on rangeland to find new feed sources. Photo courtesy of USDA government. Licensed under Public Domain Mark 1.0.

Displaced abomasum

In cattle, the **abomasum** or true **stomach** normally lies at the

base of the abdomen, but it may fill with gas and become displaced, rising to the top of the abdomen. This leads to entrapment between the **rumen** and abdominal wall, usually on the left side, and ileus and abomasal ischaemia may ensue. The normal passage of feed is rendered impossible. If it twists on itself (abomasal volvulus), the blood supply may be cut off, in a particularly serious condition. This usually occurs in the first three months of **lactation**. Factors predisposing to displaced abomasum include feeding a separate concentrate rather than mixed into a **total mixed ration**, a concomitant episode of **ketosis**, **hypocalcaemia**, hypokalaemia and high milk productivity. (CJCP)

Distillers' residues

Materials that arise from (or remain after) the distilling process. Distilling, which is basically the conversion of cereal **starch** into ethyl alcohol, takes two forms. Malt distilling uses only malted **barley** as a **substrate** and **grain** distilling traditionally used **maize** and malt but recently, in Scotland at least, increasing proportions of **wheat** have been used. Residues suitable for use as animal feeding stuffs arise at all stages of the distilling process, from the initial screening of malt or cereal grains to the liquids remaining after the alcohol has been distilled off.

As in brewing, ground malt, other cereals or both are mixed with hot water to form a '**mash**' in which the enzymatic conversion of starch to **disaccharide** sugar takes place or is completed. The liquid phase (wort) containing the soluble components, primarily **sugars** and some **protein**, may be separated prior to **fermentation** (usual in malt distilleries) or **yeast** may be added

to the whole mash. When fermentation is complete the alcohol is distilled off. The mix of liquid and solids remaining after fermentation of and distillation from the whole mash is known as thin stillage. Solids and liquid are separated when distillation is complete.

The solid residues, which are primarily the fibrous portion of the cereal grain, wh**e**ther extracted before or after fermentation and distillation, are known in Scotland as draff whilst the liquids are known as 'pot ale' (malt distilling) and 'spent wash' (grain distilling). These liquids contain disrupted **yeast** cells as well as residues of substances solubilized from malt and cereal grains and are usually concentrated by evaporation to produce pot ale and spent wash syrups. Traditionally much of the syrup was dried to produce a fine, mildly hygroscopic meal known as dried distillers' solubles. More usually now, the syrups are mixed back with the solid residues. This mix may be made available at 'super draff' or dried and pelleted to produce distillers' dark grains (distillers' grains with solubles). Occasionally, though rarely now, the solid residues may be dried without the addition of a syrup, when they are referred to as distillers' light grains. Syrups may also be used directly or blended with other materials such as **molasses** to produce liquid feeding stuffs.

Composition of distillers' residues.

	Dry matter (g kg^{-1})	**Crude protein** (g kg^{-1} DM)	**Ether extract** (g kg^{-1} DM)	**Crude fibre** (g kg^{-1} DM)	**Ash** (g kg^{-1} DM)	**MER** (MJ kg^{-1} DM)
Pot ale syrup	450	360	30	< 5	100	14.5
Spent wash syrup – maize	360	300	70	< 10	80	16.0
Spent wash syrup – wheat	300	350	20	25	60	15.0
Malt distillers' dark grains	890	260	60	140	55	12.0

	Dry matter (g kg^{-1})	**Crude protein** (g kg^{-1} DM)	**Ether extract** (g kg^{-1} DM)	**Crude fibre** (g kg^{-1} DM)	**Ash** (g kg^{-1} DM)	**MER** (MJ kg^{-1} DM)
Maize distillers' dark grains	890	300	100	90	50	14.0
Wheat distillers' dark grains	890	300	60	75	50	12.5

DM, dry matter; MER, metabolizable energy for ruminants.

When referring to distillers' residues it should always be made clear from which cereal they were derived, e.g. malt screenings, maize distillers' light grains, pot ale syrup or wheat distillers' dark grains.

Distillers' residues are used in the diets of pigs, poultry and ruminants but their fibrousness and the nature of the protein make them most suited to feeding ruminants. Typical crude analyses of three syrups and three types of dark grains are as shown in the table.

Other distillers' products used in animal feeding are dunder

(also called **vinasse** or **molasses** distillers' solubles) and maize (corn) distillers' dried grain and solubles. Dunder is a **yeast**-rich end-product of molasses distillation for rum production. It has about 63% **crude protein**, but it is not rich in essential **amino acid**s – the main amino acid is **glutamate** (29% of the total protein). Dunder has a ruminant metabolizable energy content of 11 MJ kg^{-1} DM and it contains about 10% total mineral, of which much is **calcium sulphate**. It is best used as a **protein source** for ruminants, although it can be used in pig and poultry feeds in small amounts.

Maize distillers' dried grains with solubles (DDGS) is a product from **ethanol** production. DDGS has 31% protein, 10% fat and 1.5% starch (Caldas *et al*., 2020) and 13.3 MJ ME kg^{-1} DM (ruminants) and 10.3 MJ AMEn kg^{-1} DM (poultry). It is widely used in poultry, pig and ruminant feeds. (CRL; GMcLD)

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Diurnal rhythm
A term applied to numerous **circadian rhythm**s and used to describe predictable daily variation in the intensity of a physiological function. This variation is thought to occur in all living organisms. The 24-hour light/dark cycle is involved in setting the daily rhythms of neural activity, body temperature cycle, sleep, feeding and fasting, physical activity cycle, blood concentrations of hormones and metabolites, etc. (NJB)

Docosaenoic acids **Unsaturated fatty acid**s with 22 carbons. In the n-3 (or ω3) family the first double bond occurs on carbon 19 (i.e. 22–3) whereas in the n-6 (ω6) family the first double bond is on carbon 16. (NJB)

Docosahexaenoic acid (DHA)
An unsaturated 22-carbon **fatty acid** with six double bonds (22:6, $\Delta^{4,7,10,13,16,19}$), a member of the n-3 family. In **metabolism** it can be synthesized from α-**linolenic acid** by sequential desaturation and two-carbon elongation reactions. DHA can be obtained directly from **fish oils** and is in high concentrations in the brain, retina and testis. In the retina it is a component of the membrane **phospholipid** fraction and is thought to lead to the enhanced fluidity needed for the visual process. It is particularly concentrated in the *sn*-2 position (i.e. 2-carbon of **glycerol**) of **phosphatidylethanolamine**. (NJB)

Docosapentaenoic acid

A 22-carbon **unsaturated fatty acid** with five double bonds (22:5, $\Delta^{7,10,13,16,19}$), a member of the n-3 family. (NJB)

Dog nutrition

Dietary requirements for companion dogs include those common to all species: **calorie**s, water, and nutrients of **protein** (**amino acid**s and **nitrogen**), **lipids** (**fatty acid**s), **vitamins** and **minerals**. While not considered essential, both digestible **carbohydrate** (mainly **starch**) and fibre provide valuable health benefits, and fibre in particular is important for normal gastrointestinal function. The dog requires ten indispensable amino acids (**arginine**, **histidine**, **isoleucine**, **leucine**, **lysine**, **methionine**, **phenylalanine**, threonine, **tryptophan** and **valine**) in a bioavailable form; that is, they must be readily absorbed and utilized in metabolic processes. In addition to bioavailability, the quantity of indispensable amino acids provided must be sufficient to meet the body's need for those particular amino acids as well as provide precursors to synthesize the dispensable amino acids. Amino acids can be provided by a range of dietary **protein source**s, which can vary with regard to quality. If amounts or bioavailability of the amino acids in the diet are insufficient, this can result in cardiac and retinal abnormalities, reduced growth rate, muscle atrophy, aberrant behaviour and impaired healing. Dietary lipids improve **palatability** of the diet and provide both energy and the omega-6 **essential fatty acid**, **linoleic acid**, critical for cellular function, which impacts many aspects of health, including skin and coat quality. Linoleic acid also serves as a precursor for other important fatty acids, such as

arachidonic acid, that are incorporated into cell membranes, play a role in cellular signalling and contribute to **hormone** synthesis. Certain omega-3 fatty acids are also essential during growth and development, and some regulatory authorities have established minimum dietary concentrations of these nutrients in commercial diets used for canine growth and reproduction.

Essential vitamins are necessary in trace amounts in the diet; these nutrients contain carbon molecules and are therefore considered **organic compound**s. Vitamins are integral to physiological metabolic reactions ranging from DNA synthesis to energy synthesis, cellular growth, neurological signalling, blood coagulation and protection from oxidative damage. Dogs require the **fat-soluble vitamins** (A, D, E, and K), the B vitamins (**cobalamin** (B_{12}), folic acid (B_9), **niacin** (B_3), **pantothenic acid** (B_5), **pyridoxine** (B_6), **riboflavin** (B_2), **thiamine** (B_1)) and **choline**. Fat-soluble vitamins can be stored in the body's **adipose tissue**, whereas **water-soluble vitamins**, when in excess, are excreted in **urine**. The storage of some vitamins in the body is important for continued availability, although these can accumulate and become toxic with excessive intake. With the varied role of the many vitamins in the body, deficiency symptoms reflect each vitamin's function in the physiological processes. As two examples, **vitamin K** is crucial for normal clotting function, and deficiency can result in bleeding disorders; while niacin is essential in the **metabolism** of other nutrients such as **glucose**, fatty acids and amino acids, and deficiency results in a whole host of symptoms ultimately leading to death.

Minerals, which in their natural form are inorganic compounds because they do not contain carbon molecules, are important in catalysing metabolic reactions as well as providing structural support. These nutrients are often categorized as macrominerals, which are required in substantial quantities (typically grams per day), and trace minerals, required in only small amounts (mg or µg per day). Required macrominerals include **calcium**, **chloride**, **phosphorus**, **potassium**, **magnesium** and **sodium**, while trace minerals include **copper**, **iodine**, **iron**, **manganese**, **selenium** and **zinc**. As well as absolute requirements, the ratio of elements is important. For example, the ratio of dietary calcium to phosphorus should be between 1:1 and 2:1 to maintain proper calcium abundance for cell signalling, muscular contraction and bone integrity. Like vitamins, minerals have a diversity of roles within the body, with deficiencies of a specific mineral reflecting its role in physiology and metabolism. For example, iron is critical for red blood cell production, and a deficiency can result in **anaemia**, whereas calcium deficiency can result in poor **bone density** and even fractures, which reflect its role in skeletal structure. Since most minerals play more than one role in the body, deficiencies tend to impact more than one system and the degree of the impact depends on the severity of the deficiency as well as the status of other nutrients, the dog's life stage and health status and many other factors.

Carbohydrates in the form of fibre and starch maintain normal gastrointestinal tract **motility** and ideal stool quality and provide energy. Most carbohydrate sources provide a range of essential

nutrients as well, including essential fatty acids and amino acids along with vitamins and minerals. Digestible carbohydrate (**sugar** and starch, although the former is not typically fed to dogs) is digested to **glucose**, which is necessary for body functions, including normal brain function.

Most pets are fed commercial diets bought at stores for the majority of their intake. However, there is no product that is the ideal for every animal – the most appropriate diet will depend on the individual dog's **body condition**, life stage, activity level, dog and owner preference, availability, cost and any diseases present. Importantly, the selected **diet** should be formulated for the life stage of the pet (puppy, maintenance, reproducing female). Diets made by large, experienced manufacturers are backed by extensive research, comprehensive quality control programmes and rely on the knowledge and expertise of a team of scientists. As such, they are safe, convenient and effective for satisfying the nutritional needs of dogs. Treats or foods used as meal toppers are appropriate if limited to less than 10% of the daily calories, in order to avoid unbalancing the diet by nutrient dilution (treats will add calories but not the equivalent essential nutrients).



Wild dogs feed infrequently on animal carcasses, every two or three days or even less often, in contrast to domestic dogs, which are usually fed once or twice a day. Photo courtesy of Tambako the Jaguar. Licensed under CC BY-ND 2.0.

Homemade pet foods have both advantages and disadvantages, and adherence to a balanced and appropriate diet is crucial. Although there are many recipes on the internet and in books, most are unbalanced and not recommended. Some recipes are vague in instruction, contain errors or omissions in formulation, incorporate potentially toxic or otherwise problematic ingredients, or feature outdated strategies for managing diseases. Consultation with a board-certified veterinary nutritionist to develop a customized homemade diet is a wise investment, due to the complexity of diet formulation.

Regardless of whether the diet is homemade or commercial, the feeding of raw animal products is not recommended, due to the significant risk of **contamination** with bacteria that are pathogenic, zoonotic and resistant to antibiotics.

Many US states have adopted as law the guidelines for pet foods that are established by the Association of American Feed Control Officials (AAFCO). As such, commercial pet foods sold in these states must have a nutritional adequacy statement on the label. This provides the following information: (i) whether the diet carries a complete and balanced claim; (ii) if it does, how the claim was substantiated (formulation method or feeding trials); and (iii) species and life stage for which the diet is intended. Similarly, pet foods sold in the European Union must also carry label claims that

specify if the product is complete and the species and life stage for which it is intended. In other regions, such as Canada, labelling and compliance with specific guidelines is voluntary.

Puppies and reproducing females are in the most demanding life stages in terms of both energy and nutrients and they should be fed diets appropriate for those needs. According to current AAFCO guidelines, diets formulated for growth or for all life stages must state, as part of the nutritional adequacy statement, whether or not they are adequate for puppies expected to be 32 kg or larger at adult size. This distinction is based on a maximum calcium concentration of 4.5 g per 1000 kcal for large-breed puppies; diets that exceed this value are only recommended for growth in smaller breeds. While energy density of the diet must be adequate to allow for meeting calorie requirements, **obesity** should be avoided during growth and before and during pregnancy, due to the negative impacts on skeletal development and normal parturition, respectively.

An adult dog should be fed the amount necessary to meet its energy needs and maintain ideal body condition. Within this amount of food, all essential nutrients must also be provided in adequate concentrations. For complete and balanced diets in the USA, this is verified by pet food manufacturers either by feeding trials or by meeting the AAFCO Dog Food Nutrient Profiles. Commercial diets intended for adult dogs may contain more moderate concentrations of many essential nutrients compared with those for more nutritionally demanding life stages. However, not all essential nutrients have higher minimum values for growth

and reproduction. Furthermore, individual products, while meeting the minimum required for a given life stage, are highly variable in nutrient content, making generalizations across products difficult. The quantity of diet to be fed for maintenance will vary by the specific caloric content, as well as by the needs of the individual dog. According to AAFCO guidelines, the pet food label must provide feeding directions that include the daily amounts based on the weight of the dog. Given the wide variation in individual energy needs, which depends on breed, activity level, age and other factors, the label's feeding directions should be considered only as a general starting point. The amount fed should be adjusted for individual dogs as needed to maintain ideal body condition.

Senior dogs may experience important physiological effects of ageing, but most studies have not shown significant differences in nutrient absorption. Dietary energy density should be considered on an individual basis, since some senior dogs tend to become overweight while others need more calories to maintain ideal body condition. Of course, any disease that develops with age should be considered when choosing a diet. There is some evidence that nutritional interventions can help manage cognitive dysfunction, such as **supplementation** with medium-chain triglycerides. There are no regulatory guidelines for senior diets, so products marketed for senior dogs are highly variable in their nutrient profiles. In addition, since every dog is an individual with specific needs, any diet changes to address age-related concerns should be carefully considered.

Obesity in dogs may contribute to **insulin** resistance, cardiovascular and pulmonary disease, exercise or heat intolerance, as well as increasing surgical and anaesthetic risk and the risk of developing orthopaedic disease (or it can cause progression of pre-existing orthopaedic disease). Most importantly, being overweight reduces health and shortens a dog's lifespan. Reversal of obesity is challenging for a variety of reasons, and weight regain is common even after successful weight loss plans, thus prevention is critically important. Prevention of obesity starts during puppyhood, with neutering in particular being a risk factor for unwanted weight gain. Monitoring of body condition throughout the growth period and beyond is necessary to quickly and effectively address inappropriate gain.



Obesity in dogs. Photo joegoauk73 and is licensed under CC BY-SA 2.0.

Many dogs require significant energy restriction at the end of growth and when they transition to senior years, even if neutering is not performed. Regardless, the diet fed should still be appropriate for the life stage, and a change to an adult diet should

not be implemented until adult size is achieved. Diets with a lower caloric density, yet still formulated for growth, can be used if diet volume is an issue, to avoid excessive **hunger** and begging or scavenging behaviour. (JAL; AMO)

Further reading

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Domestic fowl

A bird of the order Galliformes that is kept as a source of eggs, meat or feathers/down. These birds include **laying hens** and **broiler chickens** (*Gallus gallus domesticus* derived from the wild red junglefowl of Southeast Asia); **turkeys** (*Meleagris gallopavo* developed from wild species native to North America); **ducks** (mainly *Anas platyrhnchos domesticus*); geese (*Anser anser domesticus* and *Anser cygnoides domesticus*); and several species of quail, mainly *Coturnix* spp. (e.g. Japanese quail) and *Colinus* spp. (e.g. bobwhite quail). (RB)

Domestic junglefowl

The genus *Gallus*, belonging to the order Galliformes, suborder Phasiani, family Phasianidae, subfamily Phasianinae. Progenitors of modern poultry. The four species in the genus, which have the common name junglefowl, have their origin in South-east Asia: the red junglefowl, *Gallus gallus*; the grey junglefowl, *Gallus sonneratii*; the Ceylon junglefowl, *Gallus lafayetii*; and the green junglefowl, *Gallus varius*.



Red junglefowl in Hawaii, descended from birds that were brought by the first Polynesian settlers. Photo courtesy of Richard Morgan. Licensed under CC BY-ND 2.0.

The most widespread is the red junglefowl, within which there are five subspecies: *G. g. murghi, G. g. spadiceus, G. g. jabouillei, G. g. gallus* and *G. g. bankiva*. As a species the red junglefowl is not threatened. It is most numerous in Thailand, where *G. g. spadicus* and *G. g. gallus* have part of their habitat range. Recent DNA analyses of these subspecies have indicated that *G. gallus* was the originating species of the **domestic fowl**. Domestication, from

about 6000 BC, exploited the bird for sport and food. Breed development across Asia and Europe was limited until the 19th century, when the larger Chinese breeds arrived in Europe and the USA. The majority of breeds are for show purposes. Those developed for commercial purposes have a mature body size ranging from 1.5 to 6.5 kg. Breeds at the lower end of the range are used for **egg production** and those at the upper end are used for **meat**.

Both **laying hen**s and meat chickens are derived from the same species. The modern hybrid layer can be divided into two main groups: the light breeds and the heavy breeds. The former are mainly derived from White Leghorns, laying white eggs, while the heavy, less feed-efficient brown layers come mainly from Rhode Island Red stock. Worldwide there are currently some ten major breeds, with most breed companies offering a choice of at least three strains: brown and white egg layers and a more traditional strain for extensive/alternative systems.

Modern breeds are capable of producing 20 kg of egg mass output to 76 weeks, with a **feed conversion ratio** (FCR) of 2–2.2:1. This is typically obtained by producing 320+ eggs, average weight 63 g, on a daily consumption of around 112 g of feed. Breeds may differ in average egg weight and have different shell quality characteristics. Some are more feed efficient than others but no one strain is perfect, since different markets require different products. Alternative systems require greater egg size; shell egg markets emphasize shell quality; while for the liquid-egg market, feed efficiency is most important.

The world market for meat birds, be it **chicken** or **turkey**, is now dominated by five major companies, along with some smaller organizations producing speciality products. Several companies offer a choice of products, depending on market requirements, while others have only a simple compromise bird. Heavy meat breeds now dominate the world stage. Historically there were light breeds where the breeder bird produced large numbers of chicks, which grew less efficiently, with lower **meat yield**s. With the huge worldwide demand for **poultry meat** and the move away from whole carcasses to portions or stripped meat, the high-yielding feed-efficient breeds have succeeded.

A modern **broiler breeder** produces 140 chicks to 65 weeks of age with a **feed intake** per chick of about 350 g. The broilers can be slaughtered over a wide weight range, typically from 32 days to 50 days of age. This is to provide everything from whole small chicken carcasses to heavy males for meat stripping. Males and females are normally grown separately to allow maximum efficiency of production. The breeds differ in their growth pattern and yield characteristics but are very similar in weight for age, FCR and mortality.

Birds are normally kept in controlled environment sheds on the floor with *ad libitum* access to feed and water. Broiler performance is continuously improving, due to genetic selection, with birds typically reaching target weight 1 day earlier each year. This gives a corresponding improvement in feed efficiency of several points per annum.

Metabolism does not differ greatly between breeds, although the

pattern of early growth is breed specific. The **nutrient requirement**s are set out in manuals provided by the breed companies. In practice, integrated companies with more than one breed tend to produce only one set of diets. (WKS; KF)

Donkey meat:
see Horse and donkey meat, effects of nutrition

Donkey milk, effect of nutrition
Equine **milk** is known for its potential health-promoting properties and these are strictly related to equine (donkey and horse) metabolic utilization of the diet. Equines are **monogastric** species and, for these reasons, are reported to be good utilizers of **metabolizable energy** of the diet (Miraglia *et al.*, 2020). Being monogastric, there is a more direct influence of the diet on milk composition compared with ruminants. Management, farming system, pasture and **forage** utilization are all crucial for their potential effect on milk production and quality. The composition of the diet does directly affect donkey milk composition, particularly the **fatty acid** profile, considering the negligible biohydrogenation before **absorption**. Hence C18:3 n-3 is increased in donkey milk when donkeys are pasture fed, compared with **hay**.

Related to this, **supplementation** with **eicosapentaenoic acid** (EPA) and docosahexaenoic acid (DHA) does not affect the linoleic and linolenic content in milk, but increases the **arachidonic acid**, EPA and DHA concentrations in milk. Aromatic odours and related compounds have been identified in donkey milk when the animals were fed fresh forage (Miraglia *et*

al., 2020). (PDP)

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Dopamine

Dopamine (3-hydroxytyramine or 3,4 dihydroxyphenethylamine) is one of the **catecholamines** and is a **neurotransmitter**. It is produced by hydroxylation and **decarboxylation** of the aromatic **amino acid** L-**tyrosine** in the substantia nigra in the brain. In Parkinson's disease, production of dopamine is insufficient to maintain dopaminergic neuron function. (NJB)

Double isotope techniques

Also called double **labelling**, used to trace the fate of nutrients or **metabolite**s in the body. For example, an **amino acid** labelled with both ^{15}N and ^{13}C can provide information on the metabolic fate of both the **nitrogen** and the carbon in the amino acid molecule. **Doubly labelled water** is used to estimate CO_2 production. (MFF)

Doubly labelled water
Water containing isotopes of both **hydrogen** and **oxygen**, usually **deuterium** (^{2}H) and ^{18}O. Its usual use is for the estimation of **carbon dioxide** production. The principle of this method is that when doubly labelled water ($^{2}H^{18}O_2$) is introduced into the body, both elements are lost as water but oxygen is lost additionally as CO_2. By measuring the rate of decline in the concentrations of both isotopes in the **body water** pool, this additional loss of oxygen can be estimated and, from it, the rate of CO_2 production. The method can integrate CO_2 production over a period of days or weeks and is thus particularly suitable for measurements in free-living animals. (MFF)

Draught animals:
see Working animals

Dressing percentage
This is determined as **carcass** weight as a proportion of the **liveweight** at slaughter. Carcass weight may include the head, feet, tail, etc., but sometimes does not. (MFF)

Dried grass
The procedure for drying grass differs from **hay** and barn-dried haymaking because it involves the rapid evaporation of plant juices by hot air with minimum losses of nutrients. Although this process is the most effective in retaining the nutritional value of the fresh grass, it is also extremely costly. Both capital outlay and running costs are high. The nutritive quality of dried grass is high and the

process is commanding greater attention due to the need to rely less on imported concentrates. Dried grass is normally marketed with **protein** contents of between 14% to 20% **dry matter** (DM), **metabolizable energy** > 10.8 MJ kg^{-1} DM, and a DM content > 90%. The final dried grass material may be sold finely chopped or in the form of pellets. Dried grass is a very palatable feed and the **forage** substitution rate (kg reduction in forage DM intake per kg DM of **supplement** fed) is similar to that of average grazed grass and better than good-quality **silage** of **maize** or grass. (RJ)

Dried lucerne

Lucerne (alfalfa, *Medicago sativa*) is usually chopped and then dried at a very high temperature (800°C) before further processing by pressing or **pelleting**. The high-temperature drying process removes the water content of the plant and at the same time reduces the degradability of the proteins, protecting approximately 50% of the protein from degradation in the **rumen**, making it available for **digestion** in the **small intestine**. Dried lucerne contains only 10% of **crude protein** as **non-protein nitrogen** (NPN), against 55% of crude protein as NPN for lucerne when it is ensiled. (RJ)

Typical analysis of dried lucerne.

Dry matter (DM)	88%
Protein	18–20% of DM
Metabolizable energy	10.0 MJ kg^{-1} DM
Neutral detergent fibre	42–45% of DM

Acid detergent fibre	32–35% of DM
Oil	3% of DM
Ash	11% of DM
β-Carotene	80 mg kg^{-1}
Vitamin E	120 mg kg^{-1}
Calcium	3% of DM
Phosphorus	0.3% of DM

See also: Lucerne

Dried milk
Milk (whole or skimmed) dried to a powder by spray drying or roller drying. (PCG)

Dried skimmed milk
Skimmed milk dried to a powder, usually by spray drying. (PCG)

Dried whey
Pasteurized fresh liquid **whey** dried to a powder by spray drying. It contains all constituents, except moisture, in the same relative proportions as in the whey. Before being dried, the whey concentrate is usually treated to form small **lactose** crystals, resulting in the creation of a non-hygroscopic product, preventing lump formation when it absorbs moisture. Dried whey is a quality **protein source** used as an ingredient in many food applications. (PCG; DB)

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Drinker

A device for providing fresh drinking water to domestic livestock. This can range in size from a bath tub or trough with a ballcock mechanism for flow control, as used for cattle or sheep out at grass, to a tiny nipple, as used by caged laying hens. A drinker can be as simple as a manually filled basin for extensive ducks, or as complex as a time-regulated bell drinker that allows broiler breeders to consume only a set volume of water each day. Sheep and cattle drinkers tend to be large vessels with simple ballcock mechanisms to stop wastage. Some are shallow and allow rapid refilling, to prevent solids build-up; others are deep and must be cleaned out regularly. In **rangeland**s, the holding tank may be connected to an internet signalling device to alert the farm manager to dangerously low water reserves, which may stem from a leak in the system.



Cattle drinkers often allow storage of large volumes of water, with a ballcock mechanism to control the refilling. Regular cleaning out is required to ensure that solids do not accumulate in the bottom of the trough. Photo courtesy of Michael Dibb. Licensed under CC BY SA 2.0.

For pigs and small numbers of cattle, drinkers often incorporate a pressure switch activated by the nose or snout to control the flow of water. For intensive poultry also it is important to avoid wastage. Spillage from nipple drinker systems is often reduced by the use of a cup hung underneath. Access to automatic water supplies may be cut off for poultry that become unable to walk, which occurs in a small proportion of birds in intensive housing systems. In most production systems smaller and more refined drinkers are used with infant livestock, such as mini jars for poultry, small nipples for pigs and plastic teats for calves and lambs. (KF; CJCP)

Drinking behaviour

There are several methods of drinking used by domesticated animals. While cattle, horses and sheep form their lips into a tube and suck, pigs gulp water and poultry depend on gravity for transferring water to the alimentary tract.



A cow drinks water by partially immersing her muzzle into the water and sucking during an inspiratory breath. Photo courtesy of Erik Cleves Kristensen. Licensed under CC BY 2.0.

When drinking from bell or cup drinkers (usually situated below head height), domestic fowl make a series of angled dips of the open **beak** into the water and raise the head between each dip to let the water pass from the mouth into the oesophagus. When drinking from nipple drinkers (usually above head height), they extract water with varying efficiency and let it trickle down while keeping the head raised. Typically, fowl spend more time drinking from nipples (about 6% of time) than from bell or cup drinkers (about 3%), because water flow rate is limited with nipple drinkers.

The main determinant of water requirement is **feed intake**, when ambient temperature is within the thermoneutral zone. Most drinking occurs in close association with spontaneous meals. Typically, animals consume about 1.6–2.2 times as much water as food per day, by weight. However, some drink more than would be expected from their daily food intake, possibly as a consequence of

environmental stress, and such excessive drinking (polydipsia) can be very marked in animals subjected to chronic food restriction. When ambient temperature is above the thermoneutral zone, animals need to drink more water to replace evaporative water loss due to sweating and panting. Physiological control of water intake is based mainly on changes in cellular hydration, through osmoreceptors, but also on changes in plasma volume, through the **rennin**–angiotensin system. Water consumption and the ratio of water to food intake are increased by high dietary mineral and protein concentrations. (JSav; JMF)

Drinking water:
see Water

DroughtExtended dry period in the natural **climate** cycle where an area or region experiences below-normal precipitation. Drought occurs anywhere in the world where the supply of water, either rain or snow, falls below the critical demand in an area over a prolonged period. The demand is usually a function of human activities and droughts can therefore be considered at least partly due to humans. In contrast, an area with low rainfall is described as arid, but the ecology of the flora and fauna are adapted to the periodic absence of water.



Drought leaves cattle dead and dying in Kenya. Photo courtesy of Oxfam International. Licensed under CC BY-NC-ND 2.0.

Droughts lead to feed shortages and loss of production, principally in grazing stock, and usually have their origin in the rainfall and plant production of the preceding season. It can cause reduced soil moisture or groundwater, diminished stream flow, crop damage, and a general water shortage. Drought impacts feed and **fodder** availability, animal productivity and **welfare**, farm economics and farmer well-being. The declaration of drought should be made after a short dry period in the case of high-output stock, such as dairy cows, whereas as little as one month without rain may substantially reduce production, and after a long period in the case of stock of low productivity, such as Merino sheep, for whom a drought may extend for several years before a serious loss of productivity is experienced. Thus intensification of pasture and animal production will increase the risk of drought and increase the variation in profitability of the enterprise. Drought will also

influence the diseases affecting grazing stock, with plant **poisoning** being common as animals search for fodder, as well as osteomalacia and **botulism**. The congregation of livestock around small waterholes can facilitate the spread of infectious diseases such as tuberculosis and brucellosis.

The impact of droughts can be buffered by feeding **supplement**s to livestock, by sale of stock or their agistment or, in highly intensive systems, by the use of artificial irrigation for livestock crops. Usually grain or hay is used as a supplement. It is important that a drought management strategy is prepared in years between droughts. The strategy should include estimates of drought frequency, the cost of supplementation, the financial gain from maintaining livestock growth and the impact on stock welfare. Drought frequency can now be estimated in many regions, since rainfall records have been kept for at least 100 years. For example, in Australia, the second driest continent in the world with annual rainfall of less than 600 mm for more than 80% of the country, it can be determined that a major drought will occur in central east Australia every 7 years, whereas in the south-east of that country it will only occur once every 11 years. Often the Australian droughts last for a period of 2–3 years. Droughts are expected to become more prevalent in the future as pressure to increase food and feed production increases and global climate change reduces the productivity of **rangeland**s. (CJCP; DB)

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Dry matter

One of the terms used to describe the proximate composition of feedstuffs. Most feedstuffs have water as part of their weight. In most cases dry matter is determined by the weight loss of samples dried in an oven at temperatures above 100°C for 12–24 h. Weight loss is equated to water and dry matter is calculated accordingly. (NJB)

Dry season

A time when no rain is expected. In the tropics either one or two dry seasons are normal. The long dry season is usually relatively cool and can last many months. Plant growth ceases; termite

damage and senescence reduce standing biomass. Livestock depend on crop residues. In extreme years, stock losses are common. (TS)
See also: Wet season

Drying feed crops
The purpose of drying crops for animal feed is to allow safe storage with minimal losses and **contamination**.
Grain
Some advantages of drying grain are that it: (i) increases quality of harvested grain by reducing crop exposure to weather; (ii) reduces **harvesting** losses, including head shattering and cracked kernels; (iii) reduces dependency on weather conditions for harvest; (iv) allows use of straight combining for small grains; (v) reduces size and/or number of combines and other harvest-related equipment and labour required due to extending harvest time; and (vi) allows more time for post-harvest field work. Some disadvantages are: (i) the original investment for drying equipment and annual cost of ownership; (ii) the operating costs for fuel, electricity and labour; and (iii) possible need for further investment in equipment for the extra **grain** handling that is required.

The length of time for which grain can be stored without significant deterioration is determined by the temperature and the moisture content at which it is stored. Table 1 shows the maximum recommended moisture contents for storage with duration for some typical feed grains. Short-term storage generally refers to storage under winter conditions, while long-term storage includes the effect of summer conditions.

Table 1. Recommended moisture contents (%) of selected grains for storage

	Short term (less than 6 months)	Long term (more than 6 months)
Barley	14	12
Maize	15.5	13
Oats	14	12
Rye	13	12
Wheat	14	13

Grain can be stored at a higher moisture content without significant **fungus** development when stored at colder temperatures. Table 2 shows the relationship between moisture and temperature and its effect on allowable storage time for cereal grains.

Table 2. Guidance on storage time (days) for cereal grains

	Temperature (°C)					
Moisture content (%)	−1	4	10	16	21	27
14	*	*	*	*	200	140
18	*	200	90	50	30	15
22	190	60	30	15	8	3

	Temperature (°C)					
Moisture content (%)	−1	4	10	16	21	27
26	90	35	12	8	5	2
30	60	25	5	5	3	1

* Storage time may exceed 300 days.

Airflow rate, air temperature and atmospheric relative humidity will influence drying speed. In general, higher airflow rates, higher air temperatures and lower relative humidities increase drying speed. Raising the temperature of the drying air increases the moisture-carrying capacity of the air and decreases the relative humidity. As a general rule of thumb, increasing the air temperature by 7°C doubles the moisture-holding capacity of air and cuts the relative humidity in half.

The drying rate depends on the difference in moisture content between the drying air and the grain kernel. The rate of moisture movement from high-moisture grain to air with low relative humidity is rapid, but the moisture movement from wet grain to moist air may be very small. At high relative humidities, dry grain may pick up moisture from the air.

There are a number of different grain driers available commercially, including natural air, low temperature and high temperature, or batch and continuous flow. Driers can also be classified according to the direction of airflow through the grain:

cross-flow, counter-flow and concurrent-flow. These driers are normally operated by specialist contractors or installed on large arable farms.

Forage

Some drying is essential for the preservation of **forage crops** such as grasses, **legumes** or whole-crop cereal silage for livestock winter feed. As forage crops mature and the succulent leafy material is replaced by stem and seed heads, the moisture content will decline naturally. With grass and legume crops, a further field curing or **wilting** of mown crops will be required in order to reduce the moisture content and reduce the potential effluent loss during storage as baled **silage** or bunker silage. High moisture (> 80%) of forage crops may lead to an undesirable clostridial **fermentation**, which may increase losses and reduce the feed nutritional value and **palatability**. Reducing the moisture content of forage crops to < 70% will ease the method of transportation of harvested crop from field to storage, with higher levels of **dry matter** being transported per trailer load. In the UK the main method of reducing forage crop moisture content is field wilting.



Turning hay with a tedding machine in the UK to aerate it and accelerate drying. Photo courtesy of pszz. Licensed under CC BY-NC-SA 2.0.

Field wilting

Field **wilting** of forage crops is the most common method of reducing moisture content of crops using natural resources of wind and solar energy. Wilting of crops for **silage** or haymaking requires herbage to be cut with a mower and left in the field for varying periods of time prior to baling or ensiling. In poor weather conditions, dry matter content of crops will increase only slightly; and in extended wilting periods soluble **sugars** and **protein** content will be reduced because of continued plant cell respiration. In contrast, during good weather conditions, wilting will be rapid, with minimum losses in soluble sugars and protein content. Under these conditions the dry matter content of the crop may exceed 350 g kg^{-1}.

Natural dry matter losses in wilted crops are normally small,

provided that the wilting period is up to 2 days. If the pre-wilting period is extended and accompanied by poor weather, then losses of DM up to 10% of the total crop have been reported.

Mechanical treatment of field-mown crops using turning and tedding the swath can substantially increase the drying rate. Spreading of mown grass within 1 h can increase the rate of water evaporation by up to five times, mainly as a result of water evaporation through open stomatal guard cells. Following this time period, the stomata will close and plant water loss will need to pass through the thick cell walls.

Barn-drying

Barn-drying was popular in the UK during the 1960s, both in methods of ventilation and in a shift from batch drying to storage drying. However, even at its peak barn-drying accounted for no more than a small proportion of the total hay crop made in the UK and, as field haymaking declined from 1970 onwards, it was replaced by ensilage. Thus few large-scale units were installed and most of the limited number of barn-drying installations still operating are likely to be storage driers, holding between 50 and 100 t of hay.

High-temperature drying

High-temperature drying is undoubtedly the most efficient method of conserving a green forage crop. Total loss of dry matter, from standing crop to dried product, can be as low as 3%; furthermore, because the crop can be cut for drying at a much more immature growth stage than is practicable for either **hay** or silage, the **nutritive value** of the dried product can be much higher. High-

temperature drying is also largely independent of weather conditions. Because of this potential, a considerable programme of research on high-temperature drying was conducted during the 1960s. Largely as a result of this research, production of **dried grass** in the UK rose from 65,000 t in 1965 to over 200,000 t in 1972, and further major expansion was predicted. However, grass-drying is based on the burning of fossil fuel, generally oil, to evaporate the water in the fresh crop, with up to 300 l of oil being needed to produce 1 t of dried grass from a crop cut at 80% moisture content. Sharp increases in the price of oil during the 1970s made grass-drying much more expensive and greatly reduced the economic benefits of dried grass as a livestock feed. As a result, there was a steady fall in the amount of dried grass produced in the UK, down to the present annual level of about 70,000 t. Most of this is from drying specialized crops such as **lucerne**, with an annual output of more than 5000 t, and the operators who have continued in production have remained competitive by wilting the cut crops in the field before bringing them to the drying plant, thus greatly reducing fuel consumption and increasing drier output. The situation in the UK contrasts sharply with that in a number of other EU countries, and since 1980 total EU production has more than doubled, to 4.5 million tonnes of dried green crop a year, mainly as a consequence of EU support for dried green crops. (RJ)

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Ducks

Ducks have been domesticated for over 2000 years and kept for meat, table eggs, feathers and down and the production of fatty liver. There are many local breeds of ducks kept around the world but the predominant breeds commercially used today are highly selected genetic lines derived from the white Pekin breed. Other commercial breeds include Muscovy or Barbary, Tsaiya (Taiwan), and Mule or Mullard (infertile cross of Muscovy and Pekin or Tsaiya) reared predominantly for fatty liver production.

Ducks, unlike most other avian species, do not have a distinct crop. Instead, there is a widening of the oesophagus where food remains temporarily. They feed briefly, then drink copious amounts, resulting in watery excreta (which can lead to wet litter problems).

Ducks are hardier than chickens; they are less prone to avian diseases, have a high reproductive rate, run in flocks and are easier to manage. Common viral diseases are hepatitis, enteritis (duck plague), avian influenza and fowl cholera, a bacterial infection.

Over the past 30 years duck production around the world has seen significant changes and investment in production systems, which have seen duck production numbers approximating 5 billion annually. Most of this production is in China. These changes have been driven by financial investment in Asian countries, particularly China, Thailand and Vietnam, predominantly in response to local demand for **protein** and in responses to disease outbreaks (such

as highly pathogenic avian influenza). These changes have resulted in a shift away from the traditional breeds and farming systems integrating duck production with **rice** and **fish** farming, to modern environmentally controlled poultry production systems very similar to modern facilities used for **broiler chicken**s.

The main difference between duck and broiler housing is the management of water, particularly waste water. Ducks consume and use significantly more water than other commercial poultry species and the management of their wetter droppings is often the limiting factor for stocking densities and it is very uncommon to exceed 25 kg m^{-2}, unless the ducks are on 100% slatted floors and have access to nipple-type drinkers. Cherry and Morris (2008) described the many different productions systems used around the world.



Intensive duck farming in Kerala, India. Photo courtesy of Shankar S. Licensed under CC BY 2.0.

Broiler ducks

The continued selection and education by the primary breeding companies has seen significant improvements in terms of **liveweight** at a given age, **feed conversion ratio** (FCR) and **carcass** conformation in terms of breast meat and **fat** content in meat-type ducks, as shown in Table 1.

Table 1. Improvements in growth and meat composition of ducks 2000–2015 (Cherry Valley Farms, 2020)

Year	Liveweight (g) at 42 days	(FCR, empty)	Breast meat (% of carcass)
2000	3200	2.08	13.7
2007	3335	1.96	15.6
2015	3550	1.88	17.2

Nutrition

Like any other commercial poultry species, if the genetic potential of the modern selected duck breeds is to be met, they need to be fed a high-quality diet, balanced for all key nutrients at the different stages of production. Tables 2 and 3 summarize the latest published scientific recommendations and the author's established nutrient profiles developed and applied over the past 25 years for commercial broiler ducks and **broiler breeder** ducks.

Table 2. Recommended specifications for broiler duck diets

	Starter	**Grower**	**Finisher**

	Starter		Grower		Finisher	
Age fed (days)	0–14	15–28	29–Slaughter			
Amounts per kg						
ME kcal	2900	2950	3000			
ME MJ	12.13	12.34	12.55			
	Total	**Digestible**	**Total**	**Digestible**	**Total**	**Digestible**
Crude protein (g)	220.0	189.0	185.0	159.0	170.0	146.2
Amino acids (g)						
Lysine	12.5	11.3	10.0	9.0	8.5	7.7
Methionine + Cystine	9.4	8.9	8.0	7.2	7.5	6.8
Methionine	5.5	5.0	4.5	4.3	4.0	3.8

	Starter		Grower		Finisher	
Threonine	8.8	7.3	6.7	4.9	5.3	4.9
Valine	9.8		8.1		6.4	
Arginine	12.4		10.5		8.3	
Tryptophan	2.5		2.0		1.7	
Minerals (g)						
Calcium	10.0		8.0		8.0	
Available phosphorus	5.0		4.0		4.0	
Sodium	2.0		1.8		1.8	
Chloride	2.0		1.7		1.6	
Potassium	6.0		6.0		6.0	

	Starter	Grower	Finisher
Trace minerals (mg)			
Copper	10	10	10
Iodine	0.2	0.2	0.2
Iron	60	60	60
Manganese	100	80	80
Selenium	0.40	0.40	0.40
Zinc	80–120	80–120	80–120
Added vitamins			
Vitamin A (IU)	8000–11000	8000–11000	7000–9000
Vitamin D_3 (IU)	2500–3500	2000–3000	2000–3000

	Starter	Grower	Finisher
Vitamin E (IU)	50–100	50–100	50–100
Vitamin K (mg)	2	2	2
Thiamin (mg)	2	2	2
Riboflavin (mg)	5–10	4–8	4–8
Nicotinic acid (mg)	50	50	50
Pantothenic acid (mg)	20	20	10
Pyridoxine (mg)	2–4	2–4	2–4
Biotin (mg)	0.25	0.21	0.21

	Starter	Grower	Finisher
Folic acid (mg)	1.0	1.0	1.0
Vitamin B_{12} (mg)	0.02	0.02	0.02
Minimum specifications			
Choline (mg)	750–1500	750–1500	750–1500
Linoleic acid (g)	10.0	7.5	7.5

Table 3. Recommended specifications for broiler breeder duck diets

	Starter		Grower		Breeder 1	Breeder 2
Age fed	0–6 w	7–20 w	21–40 w	41 w–end of lay		

	Starter		Grower		Breeder 1		Breeder 2	
Amounts per kg								
ME kcal	2900	2850	2700	2650				
ME MJ	12.13	11.92	11.30	11.09				
Crude protein g	22.0	19.05	16.50	14.27	18.50	16.00	17.50	15.05
Amino acids g	**Total**	**Digestible**	**Total**	**Digestible**	**Total**	**Digestible**	**Total**	**Digestible**
Lysine	12.5	11,3	8.5	7.7	12.0	10.8	11.4	10.3
Methionine + Cystine	9.4	8.9	6.0	5.4	9.0	8.1	8.6	7.7

	Starter		Grower		Breeder 1		Breeder 2	
Methionine	5.7	5.1	3.5	3.3	5.5	5.2	5.2	5.0
Threonine	8.8	7.3	5.5	4.0	7.5	6.2	7.1	5.9
Minerals g								
Calcium	10.0		9.0		37.5		42.5	
Available phosphorus	5.0		4.0		4.0		4.0	
Sodium	1.8		1.8		1.8		1.8	
Chloride	0.18		0.14		0.18		0.18	
Potassium	6.0		5.0		6.0		6.0	

	Starter	Grower	Breeder 1	Breeder 2
Trace minerals mg				
Copper	10	10	10	10
Iodine	0.2	0.2	0.5	0.5
Iron	60	60	50	50
Manganese	100	100	100	100
Selenium	0.40	0.40	0.40	0.40
Zinc	80–120	80–120	100	100

	Starter	Grower	Breeder 1	Breeder 2
Added vitamins mg unless stated				
Vitamin A IU	8000–11000	8000–11000	10000–12500	10000–12500
Vitamin D3 IU	2500–3500	2000–3000	2500–4000	2500–4000
Vitamin E IU	50–100	50–100	50–100	50–100
Vitamin K mg	2	2	10	10

	Starter	Grower	Breeder 1	Breeder 2
Thiamin	2	2	5	5
Riboflavin	5–10	5–10	16	16
Nicotinic acid	50	50	75	75
Pantothenic acid	20	20	20	20
Pyridoxine	2–4	2–4	4	4
Biotin	0.25	0.25	0.25	0.25
Folic acid	1.0	1.0	2.5	2.5
Vitamin B_{12}	0.02	0.02	0.020	0.020

	Starter	Grower	Breeder 1	Breeder 2
Minimum specifications				
Choline	750–1500	750–1500	750–1500	750–1500
Linoleic acid	10.0	10.0	15.0	15.0

Subject to final processing age, it is common practice to feed up to three feed stages during the production cycle. Commercial duck diets routinely contain feed **enzymes**, particularly a **xylanase** and a **phytase**.

Ingredients used to make duck diets are similar to those used in **chicken** diets, except that **groundnut** meal should be avoided because it is often contaminated with **aflatoxin** (a **mycotoxin**). Ducks are highly sensitive to aflatoxin (more so than broilers or turkeys), particularly when diets are low in protein. Great care should be taken with selection of feed ingredients and feed storage, particularly in hot and humid environments. For breeding ducks, a chicken layer–breeder diet with increased **vitamin** fortification can be used successfully.

Ducks are filter eaters. They naturally shovel, sieve and then swallow. Feed form is therefore very important for ducks to achieve a good FCR. To achieve efficient production and minimize feed wastage, ducks should be fed a good-quality **pelleted feed**. Physical durability should be maximized and ideally exceed 94% if liveweight gain and FCR are to be optimized.

For starter feeds the pellet diameter should be between 3 and 3.5 mm and the length less than 10 mm. A crumb feed can be fed for the first 7 days, but feed wastage will be increased if continued beyond 7 days. For grower and finisher feeds, pellet diameter can be increased to 4 mm and length 10–15 mm.

Laying ducks

Common egg-laying breeds in North America and Europe include the Khaki Campbell and Indian Runner. The Tsaiya and Lonhyan breeds are used in Asia. Some flocks produce over 300 eggs per duck per year.

Duck eggs are not popular in most western countries, because they have a stronger flavour. They contain 30% more fat than chicken eggs, are normally larger (about 60–80 g), and vary in colour from white to brown to blue-green. Although they have a higher fat and **cholesterol** content than chicken eggs, they have a higher omega-3 **fatty acid** content and stay fresher longer. In Asia, they are eaten in many forms. In the Philippines, the 'balut', an embryonated egg, incubated to day 19, is a delicacy. Salted eggs and century eggs are traditional methods of preserving duck eggs, giving them a characteristic taste. In Taiwan, 95% of duck eggs are processed in these ways but in Indonesia most are eaten fresh.

Nutrition

The ingredients used in diets for layer ducks are similar to those used in diets for meat-type ducks and chickens. Pelleted diets are also recommended, with a supply of drinking water provided close to the feeders. The NRC (1994) publication did not include tables of **nutrient requirement**s of egg-layer ducks. In their absence various industry groups have developed suggested nutrient specifications (as shown in Table 4). (BPK)

Table 4. Recommended nutrient specifications for layer duck diets

Amounts per kg	0–3 w	4–6 w	Laying/Breeding[a]
ME kcal	2900	3000	2500–2900
Crude protein g	200	180	175
Amino acids g			
Arginine	11.0	10.0	ND
Isoleucine	6.3	4.6	3.8
Leucine	12.6	9.1	7.6
Lysine	11.0	10.0	8.5
Methionine	5.0	5.0	4.0
Methionine + cystine	7.6	7.5	8.0
Threonine	7.5	7.5	6.0
Tryptophan	2.3	2.1	2.1

Amounts per kg	0–3 w	4–6 w	Laying/Breeding[a]
Valine	7.8	5.6	4.7
Minerals g			
Calcium	10	9.0	30
Phosphorus (non-phytate)	4.0	3.5	4.0
Chloride	1.2	1.2	1.2
Magnesium	0.5	0.5	0.5
Sodium	1.5	1.5	1.5
Trace minerals mg			
Copper	10	10	10
Iodine	2.0	2.0	5.0
Iron	60	60	50
Manganese	50	60	60
Selenium	0.3	0.3	0.4
Zinc	60	60	90
Vitamins, IU	60	60	50
Vitamin A	10,000	8,000	12,000
Vitamin D_3	3,000	3,000	4,000
Vitamin E	20.0	20.0	35.0
Vitamins, mg			

Amounts per kg	0–3 w	4–6 w	Laying/Breeding[a]
Biotin	0.2	0.2	0.15
Folic acid	1.0	1.0	1.0
Niacin	55	55	55
Pantothenic acid	20.0	10.0	30.0
Pyridoxine	4.0	4.0	6.0
Riboflavin	10.0	8.0	10.0
Vitamin B_{12}	0.02	0.02	0.03
Vitamin K	2.0	2.0	1.0
Linoleic acid	10	10	15

[a] The vitamin levels shown are for layer diets. Breeder diets contain increased levels. ND = not determined.

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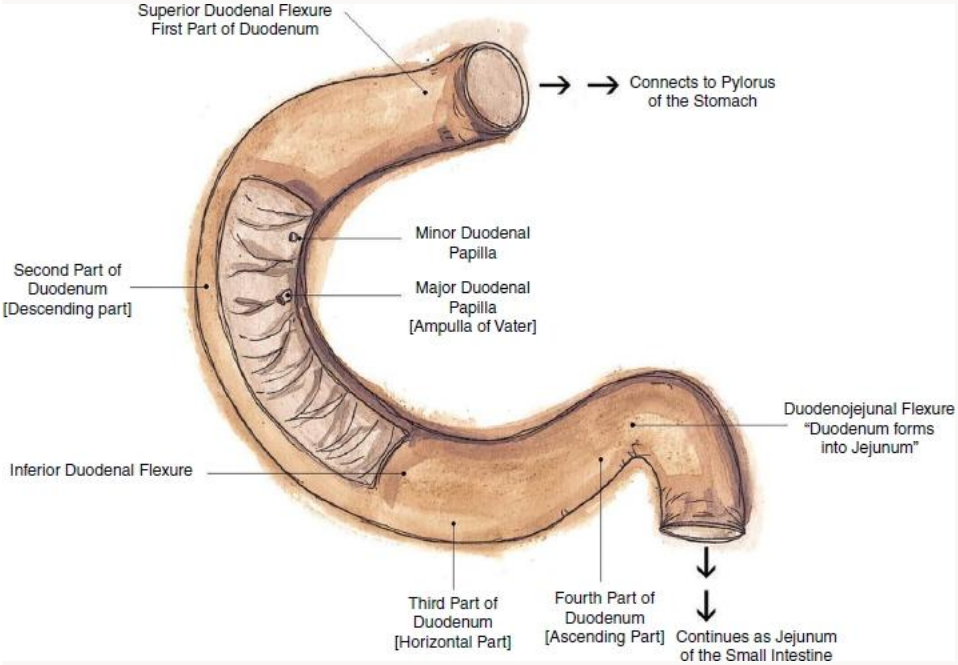
Dumas method

A method for measuring the amount of **nitrogen** in **organic compound**s. A weighed amount of **sample** is mixed with **copper**(II) oxide and heated in a tube. All **nitrogenous compound**s present in the sample are converted into nitrogen gas, which is separated from other gases and collected. The volume of nitrogen gas is measured and from this the total mass of nitrogen in the sample is calculated. For nutritional studies it is an alternative to the **Kjeldahl** method. (SPL)

Duodenum

The proximal section of the **small intestine**, between the pylorus and the **jejunum**, where **digesta** leaving the **stomach** are mixed

with secretions from the pancreatic and **bile** ducts. (SB)



The stages of the duodenum in humans. Photo courtesy of Luke Guthmann. Licensed under CC BY-SA 3.0.

Dyschondroplasia

Dyschondroplasia (chondrodystrophy, osteochondrosis) occurs as a congenital lesion in **manganese** deficiency in calves, associated with impaired synthesis of chondroitin **sulphate**, and seen as enlarged joints and deformed limbs. **Copper** deficiency with molybdenosis causes overgrowth of epiphyseal **cartilage**, associated with impaired activity of lysyl oxidase, and seen as **lameness** with obvious swellings, in calves, foals and deer. (WRW)

See also: Leg weakness

E

Early weaning

Removal of young mammals from their mother at a time before that which is normal under natural conditions. If left undisturbed, piglets will not wean themselves until 12–16 weeks of age. In farm practice, the **age at weaning** can vary widely and the term 'early weaning' has different meaning in different countries. Within the European Community, animal welfare legislation specifies that weaning may not take place at less than 3 weeks of age. Commercial weaning ages typically vary between 3 and 5 weeks. However, weaning at much younger ages is possible and is practised in some countries as a means of improving both sow output and herd health management. The practice of segregated early weaning involves weaning piglets at 10–18 days of age, whilst still protected by maternally derived **antibodies**, and removing them to a clean site, away from infectious challenges of the breeding herd. The nutritional requirements of the piglets depend heavily on the age at weaning. Younger pigs have little experience of eating solid food and have an immature digestive **enzyme** system. They are very susceptible to enteric disorders and therefore require highly digestible diets containing **milk** products and cooked **cereal**s. (SAE)

See also: Piglets

Eating disorders
Mental health conditions in which food is used to control feelings and other situations. Symptoms include worrying about body weight and shape, avoiding eating socially, overexercising, mood changes. (CJCP)
See also: Belly nosing; Bulimia nervosa; Coat licking; Comfort eating; Crib biting; Cross-sucking; Feather pecking; Inappetence; Obesity; Tongue rolling; Sucking

Echinacea (*Echinacea purpurea*)
A herbaceous and perennial flowering plant with cone-shaped purple flowers, belonging to the Asteraceae family.



Echinacea 'PowWow Wild Berry. Photo courtesy of Swallowtail Garden Seeds. Licensed under CC BY 2.0.

The origin of this plant is in North America but nowadays it is spread and cultivated all over the world (Burlou-Nagy *et al.*, 2022). It has a wide range of bioactive compounds, including alkylamid, **polysaccharide**s, glycoproteins, flavonoids and **phenolic compound**s (such as caffeic acid, chicoric acid, caftaric acid,

chlorogenic acid and echinacoside). Due to the diverse and wide range of bioactive compounds, this plant is claimed to have natural antioxidant, immune-system-modulating, anti-inflammatory, antibacterial, antiviral and anti-osteoporosis properties (Burlou-Nagy *et al*., 2022). As such it is also claimed to remove toxic substances from the blood (Zargari, 1997). In poultry, it is believed to have **immunity**-stimulating properties and, as a result, to be a potentially valuable phytobiotic and alternative to antibiotics (Nosrati *et al*., 2017; Saeed *et al*., 2018). (AS; BH-G; CJCP)

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Ectoparasites

Parasites, such as flies, ticks, lice and mites, that live on the external surfaces of an animal are called ectoparasites and they have many influences on its nutrition. In particular, the ectoparasites may disrupt **feeding behaviour**, they have their own **nutrient requirement**s and they transmit diseases that affect the animal's nutrition. They increase stress levels in cattle, in particular, and reduce **nitrogen retention**. Cattle engage in tail swishing and regular, sudden movements of their ears, heads and limbs in response to flies landing. Flies congregate in greatest numbers when cattle are kept at high stocking density in **feedlot**s. Baits, sprays and traps are used in an attempt to control the flies, and prompt removal of manure and cleaning of pens, particularly under the fence lines, will also assist in controlling fly breeding. Treating livestock with insecticides is of some benefit in grazing animals, but resistance has been detected and will in the long run render the insecticides of little value. (CJCP)

Eel

Some species of the freshwater eel family (Anguillidae) are of importance to **aquaculture**, with the Japanese eel (*Anguilla japonica*) and the European eel (*A. anguilla*) being the principal cultured species. The family has a worldwide distribution, with the greatest number of species in South-east Asia and the south-western Pacific. All species are catadromous, living in **fresh water** but returning to sea to spawn. The larvae have not been reared successfully and so all culture relies on the availability of wild juveniles (elvers) returning from the sea.



Eels can be successfully cultured and are particularly popular for human consumption in Japan and the Republic of Korea. Photo courtesy of Cheetah100. Licensed under CC BY 2.0.

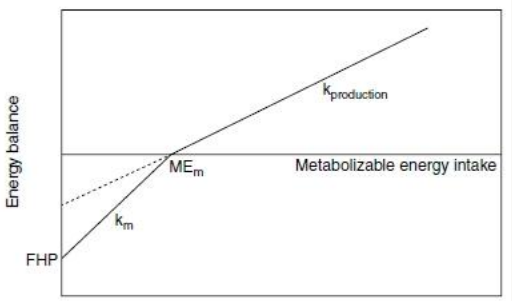
Since the optimum temperature for eel growth is 24–30°C, their culture in temperate climates requires the use of recirculation systems for most efficient use of heated water. Pond culture is practised in China and South-east Asia. Eel larvae supply, **cannibalism** and variable growth are problems in eel culture. About 250,000–300,000 t of cultured eels are marketed annually, with over two-thirds being consumed in Japan and the Republic of Korea. China and Myanmar are the world's major producers of eels. At present the major problem for eel aquaculture is seedling supply, since artificial reproduction has not succeeded and it is usually forbidden to harvest natural eel seedlings from rivers such as the Yangzi and Qiantang Rivers. From 2021 this has been forbidden in China. (RHP; QS)

Efficiency of energy utilization

Energy efficiency is eliminating energy waste by using less energy to perform the same task or function. Energetic efficiency is

defined as the ratio between energy output (in useful end-products) and the corresponding energy input. It can be obtained from the relationship between **energy balance** and **metabolizable energy** (ME) intake (see figure). The slope of this line is interpreted as the efficiency of **energy utilization** (k). Historically, the relationship has been represented as having two linear segments. Below **maintenance**, the slope of the line between fasting **heat production** (FHP) and the metabolizable energy intake for maintenance (MEm) indicates the efficiency with which dietary nutrients are used for maintenance purposes, relative to mobilizing body reserves for that purpose. This relative efficiency has been called the efficiency for maintenance (k_m) and depends on both the diet and the body reserves used when the animal is actually fed below maintenance. The slope of the line above maintenance is the energetic efficiency for production (e.g. growth, lactation).

With increasing ME intake, growing animals deposit an increasing fraction of energy as **lipid** (relative to protein). As the energetic efficiencies of protein and lipid deposition differ, the linear relation is therefore overly simple.



Relation between the energy balance and metabolizable energy intake.

Because k_m is a relative efficiency, its value typically exceeds that of the efficiency of production and may even exceed unity. The maintenance **energy requirement** is essentially a requirement for **adenosine triphosphate** (ATP). It is difficult to express the efficiency of ATP synthesis as a fraction of energy input 'retained' as ATP; nevertheless, the (relative) efficiency with which nutrients can be used for ATP synthesis can be compared (see table). It appears that **glucose** and lipids can be used relatively efficiently for ATP synthesis, whereas **volatile fatty acid**s are used 10–18% less efficiently. The efficiency of using **amino acid**s for ATP synthesis is considerably lower. Part of this inefficiency is due to the incomplete **oxidation** of amino acids. The **nitrogen** of amino acids is excreted as **urea**, which involves a physical loss of energy (as urea) as well as the **energy expenditure** to synthesize it (2 ATP/N).

Protein and energy output per hectare (data from Spedding and Hoxey, 1975)

	Protein (kg ha^{-1} per year)	Energy (MJ ha^{-1} per year)
Plant products		
Dry grass	1100	180,000
Cabbage	1100	33,500
Corn	430	83,700
Wheat	350	58,600
Rice	320	87,900

	Protein (kg ha^{-1} per year)	Energy (MJ ha^{-1} per year)
Potatoes	420	100,460
Animal products		
Rabbits	180	7400
Chickens	92	4600
Lamb	43	4800
Beef	42	7900
Milk	115	10,460

The theoretical efficiency of **protein synthesis** is approximately 85% (*see* Energy costs) but the actual efficiency is often lower, due to **protein turnover**. The efficiency of depositing protein in animal tissue appears to be considerably lower (approximately 60%) than that of depositing protein in animal products such as milk or eggs (75%). Part of this difference may be due to difference in protein turnover between these types of production. In the 20th century, considerable research was carried out on the energetic efficiency of **fat** deposition. In ruminants, a major part of the energy supply is derived from the end-products of **fermentation**. For instance, cows rely on **rumen** microbes to convert feed components into useable source of energy and protein such as fermenting **carbohydrates** into **volatile fatty acid**s and gases. The metabolic utilization of these end-products (and the associated cost of fermentation) is less efficient than that observed in non-ruminant animals. As with the efficiency

for ATP synthesis, the efficiency for fat deposition in non-ruminants increases in the order protein, carbohydrate, lipid.

Efficiency of energy utilization can also be measured from the land area required to achieve a given quantity of output. By this means different farmed products can be compared. Because of their inherent inefficiency, beef and lamb production have low output of protein and energy per hectare (Spedding and Hoxey, 1975). However, the highest-output farming system, of **dried grass**, requires considerable processing energy inputs. Some livestock production systems utilize land that cannot be easily used for plant products but many do not, particularly if they rely on large inputs of **cereal**s. Some animals have a low output of **meat** from the entire animal, typically 50% for terrestrial animals, but for **fish** it can be as high as 86%, increasing the efficiency of energy utilization for an edible product. In addition, unlike terrestrial farm animals, fish are mostly poikilothermic and therefore do not need large amounts of energy to maintain a body temperature above the ambient temperature.

Meat for human consumption also utilizes large amounts of energy because it is often frozen to preserve it, whereas more plant products are sold fresh or in the dried form. **Freezing** requires the temperature to be decreased initially to –29°C (commercial) and then –18°C (household). With careful freezing of post-rigor mortis meat, preservation for 1–2 years is achieved, but with some loss of **taste** characteristics. Traditional (more energy-efficient) meat preservation methods of curing, salting, drying, smoking and canning are increasingly less common. Method of cooking also has

major implications for protein and energy efficiency. For example, frying of meat induces loss of energy in the form of fat, and toasting of bread also incurs a significant energy input. (JvanM, CJCP)

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Efficiency of feed conversion (FCE)

The efficiency of conversion of feed into productive output (e.g. meat or eggs) is directly related to the major cost in most animal enterprises (i.e. feed) and so it is often used to indicate the efficiency of the system. A major source of variation in FCE is **feed digestibility**. Ruminants rely on a complex community of microbes in their rumen to assist in the conversion of host-indigestible feed into nutrients, following their digestion in the **small intestine**. Considerable loss of energy occurs through **methane** output, depending on the concentration of methanogens in the rumen. Efficiency is commonly expressed as the weight of productive output divided by the weight of feed eaten (the term gain:feed is also used in growing animals). Differences in feed conversion efficiency therefore indicate differences in the availability and utilization of the feed supplied, the proportion of

the available nutrients that are required for body maintenance and the nutrient composition of the productive output (the ratios of protein:**lipid**:**ash**). **Feed conversion ratio** (FCR) (feed:gain) is inversely related to FCE (gain:feed) and is also used to describe the efficiency of feed utilization. (SPR; DB)

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Egg

As a source of nutrients the egg presents the consumer with a number of benefits over many other foods. Eggs are rich in balanced proteins (with a **biological value** of 93.7%) and are a good source of **unsaturated fatty acid**s, **vitamins** A, B, D, E and

K, **iron**, **phosphorus** and trace **minerals**. Concerns about the effect on blood **cholesterol** of eating eggs are now considered to have been overemphasized: dietary cholesterol intake has little effect on plasma cholesterol levels in healthy individuals.

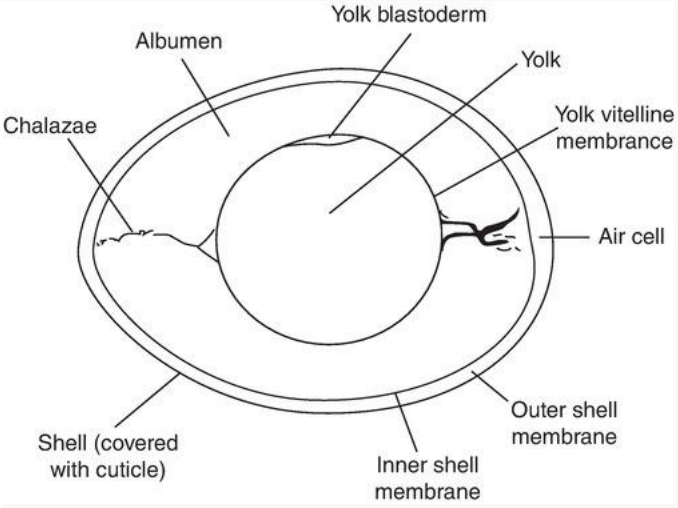
Cooking may destroy some nutrients or can enhance nutrient availability. Thus, **riboflavin** levels have been shown to be reduced by up to 20% by some forms of cooking. While unlikely to have a significant impact in healthy adults eating a balanced diet, the egg proteins ovomucoid and ovoinhibitor have been shown to have anti-tryptic activity. Similarly, the protein **avidin** binds to **biotin**, making in unavailable. **Heat treatment** can destroy these antinutritive factors and thus release vitamins, improving their availability.

Eggs are used in foods not only for their **nutritive value** but also for their functional properties. The albumen proteins allow eggs to be used as coagulators (e.g. in custards, scrambled egg) and foaming agents (e.g. in cakes, meringues) while the yolk is used extensively as an emulsifying agent in, say, batter, mayonnaise and salad dressings. The yolks may also be used as colorants; for example, the xanthophylls provide the pale golden colour associated with cakes and pasta. (NS)

Egg composition

An egg consists of three main parts: the shell, the egg white and the egg yolk. The structure of a hen's egg is shown in the figure below. This structure allows the developing embryo (in a fertilized egg) to be protected from drying out and to survive without external access to nutrients and water. The yolk and the albumen provide a source

of water and nutrients. Wastes are released to the allantois, which is an extension of the embryonic gut. **Oxygen** diffuses though the outer shell of the egg, regulated by the chorion which forms the outer layer surrounding the yolk. It functions to protect the embryo by providing it with a stable fluid environment. The allantois also assists in gas **diffusion**. Food for the developing embryo comes from the **yolk sac**, which reduces in size as the embryo matures. Surrounding all the other membranes is the chorion, providing an overall enclosure for the developing **chick** and protecting it from bacterial invasion. The air cell (at the blunt end) usually rests between the outer and inner membranes and grows larger as the egg ages.



The domestic hen's egg has a yolk with a solids content of approximately 50%, of which **lipid** accounts for 31–36%, **protein** 15–17%, **carbohydrate** 0.2–1.0% and **ash** 1.1%. The composition of the yolk lipid is approximately 66% triglyceride, 29% **phospholipid** and 5% **cholesterol**. The **energy** content of the hen's egg is approximately 623 kJ 100 g^{-1} compared with, for example, 776 kJ 100 g^{-1} for the duck's egg. While the duck's egg

contains more total lipid than the hen's egg (13.8 g 100 g^{-1} cf. 10.0 g 100 g^{-1}, respectively), the amounts of total **saturated fatty acid**s differ only slightly. The amounts of total monosaturated **fatty acid**s are significantly greater in duck's eggs (6.5 g 100 g^{-1} cf. 3.8 g 100 g^{-1}), with **cholesterol** levels in the duck's egg being more than double those in the hen's egg (884 mg 100 g^{-1} cf. 425 mg 100 g^{-1}). In a hen's egg the yolk contains most of the vitamins and minerals. These include **iron**, **vitamin A**, **vitamin D**, **phosphorus**, **calcium**, **thiamine** and **riboflavin**. Yolk colour can range from pale yellow to deep orange, depending on the type of feed and the breed of the hen.

The albumen in the hen's egg consists primarily of water (on average 88%), the remainder being protein (approximately 10%); lipid, carbohydrate and ash each account for less than 1%.

The fibrous shell membranes are proteinaceous and are characterized by high contents of **histidine**, **cystine** and **proline** while being relatively low in **glycine**. The shell may be white or coloured, depending on breed. Nearly all the shell (approximately 98%) is inorganic in nature, being predominantly calcium carbonate in the form of calcite. The organic matrix accounts for the remainder of the shell. The matrix permeates the shell and is linked to the shell membranes via the organic cores that are embedded in the cone layer. The shell may be capped by either an organic (e.g. chicken, grouse) or inorganic (e.g. gannet, shag) layer. The glycoprotein cover on the shell of the hen's egg is constructed from spheres (< 1 μm) forming an uneven layer up to 13 μm thick. The spheres are mainly protein (90%), the **amino acid**s having a

high glycine content.

Eggs in some countries are unwashed so that the outer cover is retained as a protective layer. In this case it is necessary for the hens to be provided with clean laying facilities. Other countries require that eggs be washed before marketing to the public, which has the advantage that the possible presence of pathogens on the egg surface is reduced. Unfertilized eggs are generally used for human food use, although fertilized eggs are used as a delicacy in some countries.

There is an extensive literature on eggs, one of the most famous and comprehensive being a 918-page book *The Avian Egg* by Alexis L. Romanoff (a descendant of the former ruling Russian family) and his wife Anastasia J. Romanoff of Cornell University, first published by John Wiley & Sons Inc., New York, in 1949. (RB)

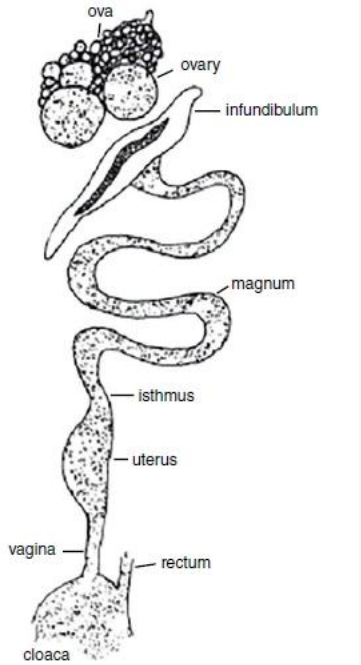
See also: Egg formation

Egg formation

Egg formation is a natural process in sexually mature hens and does not require the presence of males. The hen, unlike most animals, has only one functional ovary – the left one – located in the body cavity near the backbone. At the time of hatching, the ovary of the female **chick** has more than 12,000 tiny ova but only a small proportion (*c.* 500) of these acquire **lipids** and later develop into mature ovulatory sacs (follicles). The follicles, attached to the ovary by a narrow avascular strip called stigma, are thin-walled, and richly supplied by blood. With the onset of sexual maturity, follicles of different sizes develop, resulting in a hierarchy that

ensures the release of only one follicle per day. The number of ova recruited into the ovarian hierarchy at any one time is fewer than ten. When ova are in hierarchy, massive accumulation of yolky material (2 g per day), produced by the liver under the influence of **oestrogen**, occurs over a period of 4–6 days. This accretion process is completed 24 h prior to ovulation. During the final day of follicular development, plasma **progesterone** in the follicular blood supply rises, inducing the release gonadotropin-releasing hormone (**GnRH**), which, in turn, stimulates the release of **luteinizing hormone** (LH) by the anterior pituitary, triggering ovulation. At ovulation, the follicle splits along the stigma to release the **ovum**. The empty follicle starts to degenerate within a day of ovulation and produce **oxytocin**, a hormone that plays the primary role in the expulsion of the fully formed egg from the vagina.

Once released from the ovary, the mature yolk is engulfed by the funnel-shaped proximal end of the oviduct called the infundibulum. If live sperm is present, fertilization occurs in the infundibulum. If no males are present, as in commercial production of table eggs, no fertilization takes place and the ovum travels down the oviduct and proceeds with the formation of an egg. The oviduct is divided into five distinct segments (see figure), each with a specific role in the formation of egg components (see table).



Different segments of the oviduct

Functions of the five segments of the oviduct

Segment	Time spent	Function
Infundibulum	15 min	Capture of the ovum
Magnum	3 h	Formation of layers of albumen (egg white) around the yolk
Isthmus	1 h	Formation of inner and outer shell membranes

Segment	Time spent	Function
Shell gland (uterus)	21 h	Initially the accumulation of electrolytes and water. Calcification of shell (98% calcium carbonate). Addition of pigments in brown-shelled eggs.
Vagina/cloaca	< 1 min	Addition of bloom

Laying hens have a unique mechanism of **eggshell** calcification. **Calcium** ions for shell formation may be supplied from the diet, via the upper small intestinal blood system or, from a labile form of **calcium phosphate** in medullary bone stores in the long bones. About 20–40% of calcium required for calcification is estimated to be mobilized from the bone, and the depleted calcium is replenished when the shell gland is empty. The calcium absorbed from the intestine is fully available during this period for the rejuvenation of bone matrix. In brown-shelled eggs, the pigment porphyrin is secreted and added to the shell during the final 6–10 h of egg formation. The final step prior to oviposition is the deposition of a shiny, waxy material called the bloom (or cuticula) on the surface of eggshell during passage through the vagina. The purpose of bloom is to prevent the penetration of microbes into the

egg and to limit the loss of water after oviposition. Time taken for the formation of egg from ovulation is generally about 24–25 h. Within 60 min of oviposition, the next hierarchical follicle is released, and the ovulation cycle is repeated. This physiological mechanism ensures that a hen lays only one egg a day. (VR)

Further reading

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Egg production

The egg production industry is an important component of the supply of food worldwide. According to the International Egg Commission the total recorded output grew from 61.7 million tonnes in 2008 to 76.7 million tonnes in 2018, from over 6.0 billion **laying hens** (in rearing and production). China continues to be an industry leader, producing 466 billion eggs in 2018, which represents 34% of the global market. Other important producing countries and regions are the EU, USA and India. Consumption of eggs varies from country to country, being around 76 per person per year in India to over 250 in China. Although domestic hen eggs dominate the world table-egg market, other types of poultry are also kept for their eggs. Some **duck** breeds, such as the Indian Runner, are used for egg production, particularly in Asia.

The choice of breed of hen for commercial egg production

should be made on the basis of the market being served and the type of housing and management system to be used. Typically the breeds of chickens that produce white-shelled eggs are smaller and eat less but are more flighty and aggressive than the breeds that lay brown-shelled eggs.

There are two main stages in the laying hen production cycle: the pullet rearing period following hatching of fertile eggs; and the laying period. In commercial production the **chicks** are hatched at hatcheries, the males and females are sexed and separated, and the female chicks are vaccinated against diseases. It is usual also for **beak** trimming to be done at this time, to minimize later injuries from **pecking** and **cannibalism**, during the laying period. (The male chicks of egg-laying breeds are of little economic value and are usually killed and disposed of after hatching, commonly as **hatchery waste**.) The female chicks are then transported directly to the farm or to a pullet grower, who rears the chickens until they reach approximately 18 weeks of age. During this time a series of crumbled/pelleted diets is fed according to the recommendations of the breeder supply company: commonly a starter ration to 4 weeks; grower ration 4–10 weeks; pullet developer ration 10–16 weeks; pre-lay ration 16 weeks until 2% of the birds are laying.

On average, hens will begin egg-laying between 18 and 20 weeks of age. Therefore, it is recommended that the pullets are housed in the laying accommodation at about 16 weeks of age, before egg production starts. This allows for recovery from the stress of handling and possible change of housing, and it avoids depression of ovarian development that occurs during the late pre-

lay stage. Control of lighting is important at this time, an increasing **photoperiod** stimulating the flock to come into lay. A common schedule is to increase the period of lighting gradually to 14–16 h per day. An important change to the diet during the late pre-lay stage is to raise the level of **calcium** from around the previous 1% to 2–2.5%. This allows for medullary bone development and calcium storage, providing a labile source of calcium for **eggshell** formation when the intake of this mineral is inadequate. A laying hen needs to ingest sufficient calcium to provide about 2 g for eggshell formation, and an inadequate supply of this mineral from the diet or from bodily storage will result in a deficiency. Typical signs of deficiency include a reduction or cessation of egg-laying, shell-less eggs, and, if prolonged, skeletal problems such as cage layer fatigue and osteoporosis. **Energy intake** is usually the limiting factor for egg production and completion of growth during the early laying period, therefore it is usual to provide a diet with about 2750–2850 kcal ME kg^{-1} at this time until the birds have reached about 35 weeks of age. The **protein** requirements of the laying hen vary according to the number and size of eggs being laid, being increased to around 19% at peak production and reduced gradually to about 15–16% as the birds age. Factors such as **environmental temperature** can affect **feed intake**, resulting in the need to adjust energy and protein levels in the diet to maintain a correct intake of nutrients. In addition, the **amino acid**s need to be maintained in ideal balance during the laying period. Layers allowed to range outdoors can adjust their appropriate intakes of energy and protein by the provision of

choice feeding.

By about 35 weeks of age the birds will have achieved and passed peak production (at 28–30 weeks) and have attained sexual maturity. During the post-peak phase, egg production begins to decline slowly, and the feeding programme should be designed to maintain the birds at a high rate of egg production, while supporting an increase in egg size and maintaining satisfactory eggshell quality. During this stage until depletion of the flock, energy concentration of the diet is decreased to maintain an appropriate body weight and improve feathering and liveability. The ability to absorb calcium is reduced as the hen ages, therefore shell quality needs to be monitored to ensure that high-producing birds continue to receive an adequate calcium intake. The form in which the calcium is present in the diet is important. Shell formation takes about 18 h and tends to take place during the hours of darkness, with the egg being laid soon after the lights are switched on. Calcium should be provided, therefore, in a form that can be resorbed by the bird during the hours of darkness, when the bird is unlikely to be eating. If calcium is provided as a finely ground powder, it is likely to pass rapidly through the **gizzard** and be unavailable to the bird at the time when it needs it most. For this reason, the majority of the calcium should be provided as coarsely ground **limestone** or **oyster shell**. Yolk colour should be monitored throughout the laying period to ensure it meets the requirements of the market being served. The colour can be intensified by an appropriate change in feed ingredients or by **supplementation** of the feed with approved pigmenting agents.

In late lay, care must be taken to guard against excessive feed intake and egg size, which can result in an increased number of downgrades (cracked shells). Protein and **amino acid** levels generally have to be adjusted in this phase to help control egg size. After being in lay for almost one year and the birds having produced about 320 eggs, production and shell quality decline and the flock is considered 'spent'. The entire flock is then removed, the housing disinfected and left vacant for a downtime of at least 7 days before a new flock of chicks or pullets is introduced. Alternatively, the flock may be moulted and retained for a second production cycle.

The housing and management of commercial layer flocks has undergone significant changes in the period following the end of World War II. Until that time it was traditional for many farms and smallholdings to have backyard chickens and produce their own eggs. As the population grew and became more urbanized, commercial layer farms developed in the 1960s. Larger flock sizes forced producers to find new ways to house and manage bird numbers, while dealing with losses from predators and diseases. This was achieved by housing hens indoors on raised wire floors that separated them from their manure and reduced disease transmission. Keeping the birds in smaller social groups reduced injuries from aggression. The application of an increasing amount of research findings on nutrition and related sciences, as well as on breeding and disease control, allowed for the introduction of intensive units that permitted efficient year-round egg production to supply an increasing consumer demand. It mainly involved the

birds being housed permanently indoors in automated caged systems rather than in the traditional systems of **free range** or deep-**litter** systems, which were more difficult to intensify and which led to increased problems of predator losses and disease control. Initially the battery cage (aviary) system that allowed for groups of layers to be housed per cage seemed to be the ideal system, in that it was labour-saving and allowed for **automatic feeding**, drinking, egg collection and manure removal. The hens laid more eggs and the wire flooring enabled separation of the hens from their droppings, which resulted in cleaner eggs (an important issue especially in countries that do not require eggs to be washed before marketing); it allowed easy inspection of the birds; mortality rates dropped from a common 20% to less than 6%; and caged housing broke the cycle of infection and reduced the incidence of disease. Consequently, it became the main housing system used in commercial egg production worldwide.

However, it was not too long before ethologists pointed out that battery cages interfered with some of the natural behaviour activities of the birds and there was a growing public sentiment that the system amounted to animal cruelty. These sentiments were expressed most powerfully in the book *Animal Machines*, published by Ruth Harrison in 1964. This book was very critical of intensive farming in general, and of battery cages in particular because the cages restricted the hens' ability to express natural behaviour. The result was increased research activity on the broader **welfare** implications of battery cages and it intensified public opinion about the practice. This led to legislation being

introduced in several countries to require improved systems that provided more space per hen than conventional battery cages and enabled the birds to perform natural behaviours such as nesting and perching, or to ban the use of cages altogether.



Intensive egg production in battery cages, where birds are fed, excreta is removed and eggs are collected automatically. Photo courtesy of Secretaria de Agricultura e Abastecimento do Estado de São Paulo Agriculturasp. Licensed under CC BY 2.0.

An alternative to the caged system is the free-run system in which the birds are housed entirely indoors on a barn floor, commonly on deep-litter and providing nesting boxes, perches and feeding and watering systems. Free-run housing that provides deep-bedding is often referred to as a deep-litter system. Some of these systems allow the birds to range outdoors during the day. Well-managed free-run facilities with appropriate stocking densities allow the hens to roam freely in the barn and explore their surroundings. If these systems provide nest boxes, perches

and dust bathing areas in sufficient quantity, the hens in the flock are able to fulfil their complete range of natural behaviours. Provision of perches is important, since it results in improved bone structure and foot condition. It is recommended that feed in this type of free-run system be provided in **mash** form rather than in pelleted form, in order to encourage food-directed **pecking** behaviour, which decreases the likelihood of feather-**pecking**.

In a free-range system the birds are allowed to roam freely and to range outdoors, preferably on good pasture. However, it requires more land and birds to produce similar egg numbers as in caged systems and mortality is generally higher. This type of system allows the birds to express their natural behaviours fully. Adequate feeders and drinkers need to be provided and checked regularly. It is recommended that feed be provided in pelleted form to reduce feed spillage from outside feeders, or that **choice feeding** be used. As the birds in a flock establish their hierarchy, aggressive behaviour by more dominant birds may cause fearfulness in birds lower in the **pecking** order, which can be mitigated by the provision of 'escape' areas. Flocks with access to outdoors must also be protected from external threats such as predators. As with free-run and deep-litter systems, it is necessary to prevent the increased transmission of diseases such as avian TB and salmonella, and parasites such as coccidia and parasitic worms. Range access can be linked to health benefits such as improved plumage condition and reduced incidence of footpad dermatitis, but there are also health risks associated with free-range systems, such as greater susceptibility to disease (e.g. spotty **liver disease**), **heat stress**,

predation and potentially parasites in comparison with free-run or cage housing systems. This type of system is more labour-intensive and although the eggs are more expensive to produce, they generally have a greater consumer appeal. A beneficial feature of the free-run system is that it can be adapted readily to organic production. (RB)

See also: Egg composition; Egg formation; Moulting; Yolk pigments.

Further reading

Campbell, D.L.M, Bari, M.S. and Rault, J.-L. (2020) Free-range egg production: its implications for hen welfare. *Animal Production Science* 61(10), 848–855. doi: 10.1071/AN19576

Eggshells

Eggshells consist primarily of **calcium** carbonate in the form of calcite. Shell mineralization commences in the isthmus region of the oviduct, immediately prior to the **egg** entering the uterus or shell-gland where the bulk of mineralization takes place over about 18 h. During this period the opportunity exists for shell formation to be disrupted by a number of events or conditions.

Disease (e.g. infectious bronchitis) or nutritional factors (e.g. high levels of lathyrogens) can cause wrinkled shells. The wrinkled shell results from either the failure of the shell membranes, which form the foundation for the shell, to tension correctly during plumping (e.g. as caused by infectious bronchitis) or the structure of the membranes being perturbed (e.g. as caused by lathyrogens). The normally smooth texture of the shell results from the distinct outer layer of the shell (surface crystal layer) being overlaid by an

organic layer – the so-called cuticle.

If the bird is stressed it is possible that the egg can be expelled from the oviduct before the mineralization process has been completed. The resultant partially formed shell will, depending on its thickness, feel rough when compared with normal shells, mineralization having proceeded as far as the formation of the cone or palisade layers. Also, where mineralization has not proceeded beyond the fusion of the cone tips, the shell will be flexible: the form and strength are provided by the shell membranes and influenced by the underlying albumen.

The presence of two eggs in the oviduct at the same time can also cause thin-shelled eggs. If both eggs arrive at the same time in the oviduct they will have equally thin shells, but if one arrives much earlier than the other it will have all, or almost all, of its full complement of calcium carbonate while the other egg will have little or no shell. In the former circumstance the eggs will have a 'slab-sided' appearance caused by the two eggs pressing against each other in the shell gland.

So-called equatorial or shoulder bulges (where the shell has a thickened appearance around the equator) are the result of the shell being broken around the equator during the early stages of mineralization. Typically this is caused by the bird being stressed; the consequent constriction of the oviduct results in the shell being broken. The crystalline calcium carbonate shell is formed by a process known as epitaxis. Thus the existing crystal face dictates the crystal form. If the mineralizing face is disrupted, as occurs when the shell is broken, subsequent mineralization will take place

on an uneven surface, both physically and in terms of activation energy, causing the uncontrolled and irregular deposition of calcite.

Mineralization in the shell gland is terminated in part by a rise in the concentration of phosphate; however, if stressed, the bird may secrete excess phosphate into the shell-gland, causing **calcium phosphate** to be deposited as a 'white dusting' or 'splashing' over the surface of the shell. (NS)

Eicosanoids

A group of physiological substances derived from 20-carbon **unsaturated fatty acid**s. The source of the fatty acids for the biosynthesis of these compounds is from the two position of membrane **phosphatidylcholine**. Eicosanoids are classified as **prostaglandins**, **thromboxanes**, **leukotrienes** and **lipoxins**. They are local **hormone**s and act through cell membrane receptors and signal transduction to elicit cellular change. Two pathways are involved in their synthesis: the cyclo-oxygenase pathway results in the production of prostaglandins and thromboxanes; and the lipoxygenase pathway produces leukotrienes and lipoxins. **Dihomo-γ-linolenic acid** (eicosatrienoic acid, $\Delta^{8,11,14}$) gives rise to a series of prostaglandins, thromboxanes and leukotrienes. **Arachidonic acid** (eicosatetraenoic acid, $\Delta^{5,8,11,14}$) gives rise to a separate series of prostaglandins, thromboxanes and leukotrienes and lipoxins. Finally, α-**linolenic acid**, after being converted to a 20-carbon unsaturated fatty acid (eicosapentaenoic $\Delta^{5,8,11,14,17}$), gives rise to a

separate series of prostaglandins, thromboxanes and leukotrienes. These compounds are potent and can have physiological effects at concentrations as low as 1 ng ml^{-1}. (NJB)

Eicosapentaenoic acid
A 20-carbon **fatty acid** with five double bonds (C20:5 $\Delta^{5,8,11,14,17}$), a member of the n-3 family. It can be formed from α-**linolenic acid** (C18:3 $\Delta^{9,12,15}$) by 2-carbon elongation and desaturation and is involved in production of prostanoids via the cyclo-oxygenase pathway and **leukotriene**s by the lipoxygenase pathway. It is an **essential fatty acid** for most marine aquatic animals. (NJB; QS)
See also: Eicosanoids

Elaidic acid
An 18-carbon **unsaturated fatty acid**, $CH_3{\cdot}(CH_2)_7{\cdot}CH{=}CH{\cdot}(CH_2)_7{\cdot}COOH$, the *trans* form of **oleic acid**, the form encountered in nature. (NJB)

Elastase
An **endopeptidase** (pancreatopeptidase E; EC 3.4.21.36) that hydrolyses those **peptide** bonds that involve neutral **amino acid**s: it is particularly active on elastin. It is secreted from the **pancreas** as the precursor proelastase, which is activated in the **duodenum** by **trypsin**. (SB)

Electrolytes
Soluble ions in **body fluid**s. Electrolytes participate in maintaining electrochemical gradients and osmotic pressure. **Sodium**,

potassium, **magnesium** and **calcium** are the major cations and **chloride**, phosphate, **bicarbonate**, **organic acid**s and **protein** are the major anions. Sodium is the major extracellular cation; potassium and magnesium are the major intracellular cations. Phosphate, proteins and bicarbonate make up the majority of the intracellular anions. It is the unequal distribution of ions across cellular membranes that generates electrochemical potentials and the osmotic pressure required for cells to function. (NJB)

Elimination behaviour
Undigested or surplus nutrients need to be voided on a regular basis and this is done primarily by two processes: **defecation** and urination. Some minerals are voided in the sweating process. The regularity of location for eliminatory activity varies between species, with some routinely using the same locations, which if concentrated into a single location is called a latrine. This helps to concentrate parasites into a single ungrazed location. **Herbivore**s, including both terrestrial and aquatic animals, typically defecate in similar locations. Some migratory animals defecate at random locations. Repeated elimination in the same area results in transfer of soil fertility to these areas. As mammals age, the frequency of urination increases and that of defecation decreases. (CJCP)

Embden–Meyerhof pathway:
see Glycolysis

Embryonic development:
see Fetal growth

Emergency feeding

Livestock are kept in large numbers on modern farms and a big quantity of feed is required on a regular basis to sustain the animals, particularly if it is of low **dry matter** concentration. Feed availability may be disrupted on a large scale by many factors: war, landmines (even though illegal under the Ottawa treaty), failure of access roads, fire, disease outbreaks, political issues, extreme weather events (including hurricanes and floods) and many other emergencies. On a smaller scale, individual animals, or small groups of animals, may be without feed for numerous reasons, such as when the owners are away, necessitating some emergency measures to provide feed, often by an inspectorate who become aware of the situation.



Delivering hay to stranded livestock during floods in the USA. Photo courtesy of Oklahoma National Guard. Licensed under Public Domain Mark 1.0.

The stages in getting feed to livestock for a large-scale

emergency can be drawn out and require experienced personnel. There should be an initial assessment, usually based on field observations, then the creation of a proposal for field operators to address the problem, obtaining approval, finding funding sources and potential partner agreements, intervention and the monitoring of progress and, finally, evaluation post-emergency. If large numbers of livestock have been killed, disposal of bodies is required and ultimately farmers need replacement stock. Aid agencies may assist in the latter. Local governments may help or hinder, and there may be other political, religious or societal hurdles to overcome. Veterinary services are often limited or non-existent locally and facilities for providing **fodder** are scarce. Transport vehicles are usually in short supply in such circumstances, and adequate maps and relief staff may not even be available. Furthermore, it may not only be feed that is restricted in availability; water too may be scarce and intake needs are often more pressing. Four days is the most we can expect cattle to survive without water, depending on ambient temperatures.

Livestock Emergency Guidelines and Standards (LEGS, 2009) have been developed to assist in managing large-scale emergencies. Governments may assist in providing funds for livestock feed, for example in drought-declared lands in Australia. However, most livestock are kept in developing regions of the world where government assistance is not available. It may be necessary to involve large international organizations, such as the United Nations (UN). In emergencies, human survival is understandably the first priority. However, as humans depend on their livestock, a

partnership between humanitarian aid providers and animal-focused charities should address the needs of both together. The World Society for Animal Protection often spearheads the provision of support for livestock and is experienced in dealing with other NGOs, often those locally prominent, in a collaborative effort. In all emergencies, the UN appoints a coordinator, who may involve the Food and Agriculture Organization (FAO) to coordinate livestock response teams. Animals other than livestock may be involved. Zoos do not usually function during emergency situations, yet the animals require a continuous source of feed. Evacuation plans for farmers may be needed in extreme circumstances, such as the shelling of a region and the impact on remaining animals must be considered. Some may be injured by flying shrapnel and the long-term provision of feed supplies is likely to be disrupted. Many will show signs of stress. In the event of war, fields growing livestock feed are unable to be managed and harvests are impossible. Armed non-state operators, otherwise known as bandits or freedom fighters, may hinder rescue missions. Controlled slaughter of livestock may be necessary if evacuation proves impossible. This may even be beneficial for humans caught in a siege, providing a source of food. Direct targeting of property, including animals, is illegal under the UN charter, unless that property is being used to perpetrate war, such as a horse carrying weapons. It is also illegal to use food as a weapon of war against humans, but sieges have remained a prominent part of modern warfare. Similarly, the destruction of livelihoods is illegal and compensation for lost livestock has been part of negotiations post-

war on previous occasions. (CJCP)

Key references

LEGS (Livestock Emergency Guidelines and Standards) (2009) *Project Report*. Practical Action Publishing, Bourton on Dunsmore, UK

Roeder, L.W. (2016) Providing feed to livestock during emergencies. In: Phillips, C.J.C. (ed.) *Nutrition and the Welfare of Animals*. Springer International Publishing, Cham, Switzerland, pp. 199–217.

Emulsifier

A substance used to stabilize an emulsion, in animal feeding most commonly to make a liquid mixture of fat and water. The table gives emulsifiers that are listed in the Feedingstuffs (UK) Regulations 2000. (MG)

Emulsifiers listed in Feedingstuffs (UK) Regulations 2000

Emulsifier	E number
Lecithins	E322
Propylene glycol alginate	E405
D-Glucitol	E420
Mannitol	E421
Glycerol	E422
Sodium, potassium and calcium salts of edible fatty acids	E470
Monoacyl and diacylglycerols	E471
Esterified monoacyl and diacylglycerols	E472

Emulsifier	E number
Sucrose esters of fatty acids	E473
Mixture of sucrose esters and monoacyl and diacylglyerols	E474
Polyglycerol esters of non-polymerized edible fats	E475
Propylene glycol esters of fatty acids	E477
Stearoyl-2-lactylic acid	E480
Sodium stearoyl-2-lactylic acid	E481
Calcium stearoyl-2-lactylic acid	E482
Stearyl tartrateq	E483
Glycerol poly(ethylene glycol)ricinoleate	E484
Dextrans	E486
Sorbitan monostearate	E491
Sorbitan tristearate	E492
Sorbitan monolaurate	E493
Sorbitan mono-oleate	E494
Sorbitan monopalmitate	E495

Endocrine glands

Ductless glands that secrete **hormone**s into the bloodstream. Unique hormones are released by each of the endocrine glands. The pineal gland is in the brain near the third ventricle, and the

pituitary is in the brain near the base of the skull. The thymus is at the base of the neck near the heart and the thyroid lies on each side of the trachea. There are two **parathyroid**s, on the left and right sides of the trachea, next to the thyroid. The two **adrenal** glands are located above the kidneys and the **pancreas** is located near the **liver**. The two ovaries are located in the lower abdomen, while the two testes are normally outside the body in the scrotum. (NJB)

Endogenous protein in faeces

Endogenous protein comprises all non-dietary **nitrogen** (N) compounds entering the lumen of the digestive tract. These N compounds include enzymes, the glycoproteins of **saliva**, gastric juice, **bile** and pancreatic secretions and mucus (mucopolysaccharides) secreted from the mucus cells throughout the intestinal tract. The largest component is contributed by desquamated intestinal cells, which can amount to 30–60% of the total protein that enters the intestinal lumen. **Trypsin** is the most abundant of the pancreatic enzymes, and proteases the most abundant class of enzymes. **Urea** is an important non-protein component of endogenous nitrogen.

Most endogenous proteins are digested by pancreatic proteases and are processed identically to dietary proteins. A few proteins (such as intrinsic factor that is necessary for absorption of B_{12} in the **ileum**) largely escape luminal **digestion**.

Generally, most of the endogenous protein from the **stomach** and **small intestine** is reabsorbed (at least 0.65–0.75) in the **ileum**. Most un-reabsorbed endogenous protein is converted to

microbial protein, some in the ileum but more in the **large intestine**. N from fermented endogenous protein utilized for energy by the bacteria is either incorporated into microbial protein or absorbed as **ammonia** in the hindgut, increasing apparent overall N **digestibility**.

Endogenous protein loss changes with **feed intake** and, in **feed evaluation**, it is practical to express endogenous protein loss in relation to the dietary intake, i.e. in g kg^{-1} dry matter (DM) intake. The amount and **amino acid** composition of endogenous protein are influenced by a number of dietary factors, in particular fibre and **antinutritional factors** (ANFs). In the pig, endogenous protein losses from the ileum vary from less than 10 to more than 30 g kg^{-1} DM intake. Endogenous losses in the faeces are smaller and less variable. In ruminants, metabolic faecal N (MFN) is the amount of endogenous N excreted in faeces. The MFN loss is 15.2 g kg^{-1} DM intake.

Endogenous protein in faeces can be considered to be composed of two fractions: a minimal (basal) loss and a feed-specific (extra) loss, mainly resulting from the effects of dietary protein, fibre and ANFs. The total loss (ileal or faecal) can be measured after a preliminary **labelling** of the experimental animals with ^{15}N and measuring the dilution of dietary ^{14}N in the **digesta** or faeces by comparing the ^{15}N:^{14}N ratio in the digesta or faeces with that of the blood. The basal loss can be measured by feeding N-free diets (or diets with 100% digestible protein at ileal level) that do not contain fibre or ANFs. In situations where feeding an N-free diet is impracticable, the alternative is to feed diets with

varying levels of N and to find the minimum faecal loss of endogenous N by regression of faecal N excretion on dietary N intake.

Endogenous protein loss has a significant influence on experimentally determined values for the digestibility of protein and amino acids. Their digestibility is now commonly measured at the terminal ileum, because amino acids are practically not absorbed in the large intestine but are metabolized by the microflora which change the amount and composition of the resulting protein that appears in faeces. In pig nutrition, correction for the basal endogenous losses of amino acids is now commonly used for the calculation of true or standardized ileal digestibility of amino acids. Endogenous protein in the ileal digesta of growing pigs has a characteristic amino acid composition, with a relatively low contribution of most essential amino acids (except threonine, **cystine** and **tryptophan**) compared with **ideal protein**. (SB; GMcLD)

See also: Protein digestibility; Protein digestion

Further reading

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Endopeptidase

A proteolytic enzyme that has the capacity to hydrolyse internal **peptide** bonds in a protein, in contrast to an **exopeptidase**, which hydrolyses terminal peptide bonds. Important endopeptidases in the digestive tract include **pepsin** and **rennin**

in gastric secretions, **enterokinase** from duodenal epithelial cells and **trypsin**, **chymotrypsin** and **elastase** from the **pancreas**. (SB)

Endorphins
Peptides produced by the brain and having a morphine-like effect. They are part of the pro-opiomelanocortin **peptide** family and are derived from the 31-amino-acid carboxyl terminal of the 91-amino-acid β-lipotropin. β-Endorphin contains the full 31-amino-acid sequence; α- and γ-endorphins have 15 and 14 **amino acid**s, respectively. Endorphins bind to the same receptors as do opiates and play a role in pain perception. (NJB)

Endosperm
In angiosperm seeds, the tissue that surrounds the embryo. The endosperm and embryo together comprise the inside of cereal grains, with the endosperm forming the major component. **Starch** and **protein** stored within the endosperm support the initial growth of the germinating embryo. The endosperm accounts for the nutritional and economic importance of cereal grains and **oilseed**s. (ED)
See also: Cereals; Grain

Endotoxaemia
The presence of **endotoxin**s in the blood. This generally occurs with the proliferation of Gram-negative bacteria, such as that seen with ***Escherichia coli*** mastitis. Endotoxins are highly inflammatory and pyrogenic and result in massive increases in

vascular permeability. A common result of endotoxaemia is loss of circulating blood volume and loss of cardiovascular function (shock). (BLS)

Endotoxins

Heat-stable bacterial toxins produced primarily by Gram-negative bacteria. They are included in the bacterial **lipopolysaccharide** cell wall. Endotoxins are highly pyrogenic and cause extensive increases in vascular permeability. They are similar regardless of the species of bacteria and have similar activity and pathogenicity. (BLS)

Energy

The capacity to do work. Energy exists in many forms, including chemical energy, mechanical energy and heat. On earth, the primary source of energy is the sun. Solar radiation warms up the atmosphere and surface of the planet and some of it is absorbed by **chlorophyll** in growing plants to synthesize organic material from **carbon dioxide** and water. This process, photosynthesis, stores energy in chemical form as plant tissue. The chemical energy of plants may in turn be used in the short term as fuel for fires or as food for humans and animals, or it may be stored over millennia, building up reserves of fossil fuel. **Metabolism** of food makes energy available for the **maintenance** of essential body functions, such as respiration and circulation of the blood, and for **growth**. Metabolism is an oxidative process in which carbon from the food is combined with atmospheric **oxygen**, with the release of energy as heat, but the total amount of heat or energy produced from the

oxidation of any food material is very nearly the same whether it is burned quickly or digested in the body. It may not be identical, because the final state (temperature and pressure) of the products of the reaction may differ between the two processes.

In the body, some of the energy of food is converted into other forms of chemical energy (body growth, milk, eggs, etc.) and by draught animals into mechanical energy, but a high proportion of the total **energy intake** is returned to the environment as heat or as the residual chemical energy of excreta. Even mechanical energy is rarely retained in a useful retrievable form, but lost as heat in overcoming, say, the friction of a plough or cartwheels; an exception is when animal power is used to raise loads, such as water out of a well.

Because of its many diverse forms, energy may be measured in a variety of units. Mechanical energy is defined in terms of the energy expended when a mass of material is moved a given distance against a specified force; electrical energy is that expended when a given level of power is consumed for a specified time; thermal definitions of energy relate to the heat required to increase the temperature of a mass of water by one degree. All energy units are precisely related to one another and some useful conversion factors include the following.

1 joule (J) = 1 watt-second (W s) = 0.239 calories (cal)

1 kilojoule (kJ) = 0.278 watt-hours (W h) = 0.239 kilocalories (kcal)

1 megajoule (MJ) = 0.278 kilowatt-hours (kW h)

1 calorie = 4.184 joules (J)

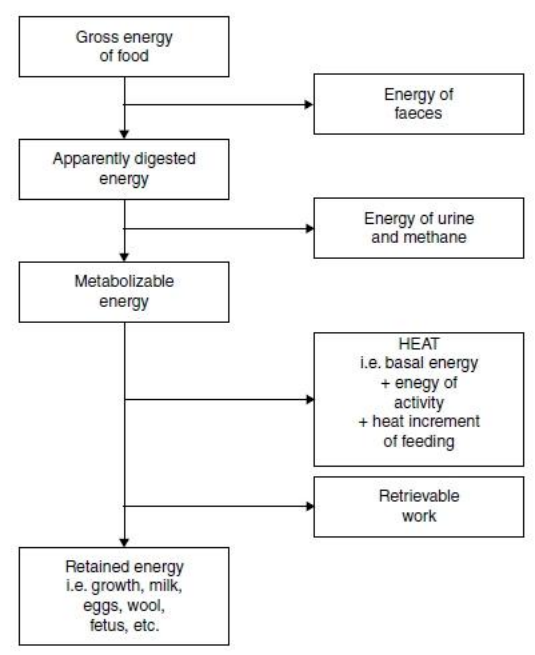
1 kilocalorie (kcal) = 4.184 kilojoules (kJ) = 1.162 watt-hours (W h)(JAMcL)

See also: Energy balance; Energy costs; Energy metabolism; Energy units; Energy utilization; International units

Energy balance

The principle of conservation of energy necessitates that food **energy intake** is balanced by energy retained or lost. The partition of the gross (chemical) energy of food into its major subdivisions is illustrated in the figure. Some food is undigested, resulting in loss of energy as **faeces**. The difference between the energy content of the food and the energy content of the faeces is termed the apparently digested energy; the adjective 'apparently' being included because some faecal material is not of immediate dietary origin but consists of cells or secretions of the alimentary tract. **Cellulose** and other complex food constituents that are not susceptible to **digestion** by the animal's own digestive enzymes are converted into digestible end-products by bacterial **fermentation**, especially in the **rumen** but also in the gut of all species. This results in the production and expulsion of combustible gases **methane** and, to a lesser extent, **hydrogen**. The **digestible energy** consists of nutrients that are absorbed from the gut. Waste products from their further **metabolism** are lost as energy excreted in **urine**; the remaining energy is the **metabolizable energy** of the food. It has to provide for the **energy requirement**s of the body. Firstly, there is the basal energy requirement for maintenance of respiration, blood circulation and other vital functions. The minimal rate of **energy**

utilization by a resting animal in a comfortable environment is known as the basal **metabolic rate**; to this must be added the extra **energy cost** that occurs after taking a meal (the **heat increment of feeding**) and any additional energy required for activity, **thermoregulation** or other muscular work. Any metabolizable energy left over from meeting these demands may be retained in the body as new tissue growth or used for the production of milk, wool or eggs.



Partition of the gross energy of food into its major subdivisions

If the metabolizable energy of the food is insufficient to meet the demand, energy retention can be negative and the body consumes its own energy reserves. Normally the level of food intake is regulated to meet the demands of maintenance plus growth in the young, or production in the pregnant or feeding mother; otherwise excess food intake leads to the deposition of **body fat**. Conversely, a deficiency leads eventually to emaciation.

The **gross energy** of food, the energy retained in the body and

the energy of faeces, urine and combustible gases are all forms of chemical energy. The energy concerned with body function and activity is non-chemical and is generally converted into heat. In most forms of exercise, mechanical work (like the work involved in vital body functions) is transformed into heat in the course of its execution. The rate at which metabolic heat is produced in the body is known as the metabolic rate or as the rate of **heat production**.

In accordance with the principle of conservation of energy, the **heat balance** equation may be written as follows:

Gross energy of food=energy of faeces+ energy of urine+ energy + retained energy+ retrievable mechanical work+ heat production.

It is possible, with varying degrees of difficulty, to measure all of these energy components in a living animal. Food, faeces and urine may be collected and sampled; their energy contents can then be measured using a **bomb calorimeter**. Heat production can be measured by one of the techniques of **calorimetry**. Using **indirect calorimetry** by enclosing the animal in a **respiration chamber** or by employing a mask technique, heat production is calculated very accurately from the rates of **oxygen consumption** and **carbon dioxide** production. The energy loss as combustible gases can also be measured in a respiration chamber. **Energy retention** can be measured using the **carbon and nitrogen balance** method, or by the difference between metabolizable energy and heat production.

In addition to the overall energy balance, there must also be a balance between the rates of heat production and heat loss,

otherwise body **temperature** alters. Healthy warm-blooded animals usually have an efficient thermoregulatory system for maintaining deep body temperature within close limits but alterations in the temperature of regions close to the skin surface and in the limbs can be considerable, resulting in some storage of heat. The rate of heat loss by an animal can be measured in a **direct calorimeter**. When a direct animal calorimeter also has a facility for indirect measurements, it is possible to measure the differences between rates of heat production and loss and to relate these to changes in body temperatures. (JAMcL)

References and further reading

Nigussie, T. (2018) A review on the role of energy balance on reproduction of dairy cows. *Journal of Dairy Research & Technology* 1, 003. doi:10.24966/DRT-9315/100003

Westerterp, K.R. (2013) Introduction. Energy balance in animals. In: Westerterp, K.R. (ed.) *Energy Balance in Motion*. Springer Briefs in Physiology. Springer, Berlin, Heidelberg. doi: 10.1007/978-3-642-34627-9_1

Energy content:
see **Energy value**

Energy costs

It is difficult to give a precise estimate for the energy cost of **maintenance** functions. According to Baldwin (1995), nervous tissues contribute 15–20% to the maintenance **energy requirement** and **protein turnover** contributes 10–15%; Na^+ **resorption** by the kidneys, heart function and respiration

contribute 6–11% each. Part of the energy cost is due to the utilization of **adenosine triphosphate (ATP)** for physiological functions; another part is related to an inevitable loss of energy (as heat) in the biochemical transformation of dietary nutrients to ATP and animal products. For example, when **glucose** is used, 81% of the energy input can be conserved as **lipid**. However, as ATP is formed during this synthesis, the overall efficiency is slightly higher (84%). Theoretically, the efficiency of using dietary lipid for lipid deposition exceeds 97%. The only cost involved is the ATP utilized for the resynthesis of triacylglycerides from **fatty acid**s and **glycerol**.

The efficiencies mentioned above are based on the minimal costs of converting one nutrient to another. Other costs (i.e. related to **digestion**, **absorption** and transport) are not specifically accounted for but are included in experimental values of efficiency. For example, after a meal, part of the digested energy is stored (temporarily) as **glycogen** in the **muscle** or **liver**. Depending on how the energy of glycogen is recovered, this temporary storage of glucose is associated with an additional energy cost of 3–5%. Likewise, animals may store energy as body lipid, which may be used later for ATP synthesis. Baldwin (1995) calculated that storing glucose temporarily as fat is associated with an additional energy cost of 23%. Apparently, this is the price paid for storing energy in a very compact form.

Protein turnover (i.e. the repeated synthesis and **hydrolysis** of **peptide** bonds) also represents a considerable energy cost. If it is assumed that 100 g of protein is the equivalent of 1 mol of **amino**

acids and that five ATP (from glucose) are required for **protein synthesis**, the maximum efficiency is 2380/(2380 + 5 × 74) = 87%. Using sources other than glucose for ATP further reduces the efficiency of protein deposition. One additional cycle of degradation and synthesis requires (at least) another five ATP, thereby reducing the efficiency to 76%. The value of k_p derived from experiments (approximately 60% for protein deposition in growth) suggests that considerably more ATP is required. The extent of protein turnover is affected by several factors. Visceral organs (especially the **gastrointestinal tract**, liver and kidneys) contribute to protein turnover and to the overall **energy expenditure**. There are also indications that dietary protein increases protein turnover. (JvanM)

See also: Basal metabolism; Efficiency of energy utilization; Energy balance

Key reference

Baldwin, R.L. (1995) *Modelling Ruminant Digestion and Metabolism.* Chapman & Hall, London, 578 pp.

Energy deprivation:

see Starvation; Undernutrition

Energy expenditure

Synonymous with **heat production**. That part of the metabolized energy which is not productively retained as growth, milk, eggs, etc., but is lost as heat. (JAMcL)

Energy intake

Energy intake is a function of species, breed, body mass, age, physiological state, the form and composition of the diet and environmental factors. Energy intake can be expressed in terms of gross, digestible, metabolizable or **net energy**. Because of the relatively wide differences in **digestibility** coefficients of feeds, particularly for ruminants, it is generally preferable to express energy intakes as **digestible energy** (DE) or **metabolizable energy** (ME) intake, both of which are reasonably easy to measure.

One way of describing energy intake is in terms of multiples of the **energy requirement** for **maintenance**, i.e. the amount of energy needed to maintain zero **energy balance**. Growing pigs and high-producing lactating cows and sows can consume up to about 3 times maintenance (3 M), whereas egg-laying breeds of domestic poultry voluntarily consume about 1.5 M and mature non-lactating animals tend to consume between 1 and 1.5 M. Whilst energy intake increases as body weight increases, the response is not linear. With pigs, for example, a study on individually fed growing boars from 20 to 300 kg showed that DE intake (MJ per day) was 4.0 $W^{0.5}$ but some studies have erroneously concluded that intakes peak around 100 kg liveweight and subsequently decline. Similar results to those for the boars have been reported for sheep fed very highly digestible diets. Animals tend to eat to a predetermined energy 'ceiling' unless there is a physical limitation to intake, such as low digestibility of the feed. Such a situation is more likely with ruminants on high-forage diets. With non-ruminants, increasing the energy content of the feed tends to

reduce dry matter intake but energy intake tends to increase. For example, a 10% increase in energy content of a broiler diet gives approximately a 5% increase in energy intake.

Energy intake is also affected by the physical form of the feed; for example, chop length of forage affects the voluntary intake of ruminants. Poultry, particularly broilers, consume up to 10% more energy as **pelleted feed** compared with **mash**. Energy intake is also affected by **environmental temperature**: at low temperatures (outside the thermoneutral zone) energy intake tends to increase to cover the additional heat loss incurred. The opposite effect occurs at high temperatures, as the animal has difficulty in disposing of the heat increment arising from **metabolism** of feed. Domestic fowl have a poorly defined thermoneutral zone and energy intake tends to increase linearly with falling temperature below 30°C. Within the range 15–30°C, the reduction in intake per °C increase in temperature averages approximately 1.6%.

Other environmental factors that affect energy intake include feed accessibility, trough design and group size. Pigs in groups tend to consume 10–15% less energy than those housed singly and large group size and limited trough space further reduce energy intake. Large differences in intake between individual animals under uniform conditions have been reported in several studies. For example, the average DE intake of pigs over the liveweight range 35–90 kg was 28 MJ per day but individual intakes varied from 20 to 38 MJ per day.

Under normal production conditions cattle are usually encouraged to maximize energy intake and this applies, in most

cases, to pig and poultry **meat production**. However, sows are normally restricted during gestation to about 26 MJ DE per day to avoid excessive weight gain and maintain fecundity. After peak **egg production** it is usually desirable to restrict **laying hen**s to approximately 1.2 MJ ME per day to maximize feed efficiency. **Broiler breeder**s have to be restricted during growth and the laying cycle to prevent leg and **fertility** problems. (KJMcC)

See also: Environment–nutrition interactions; Voluntary food intake

Key references

Barzegar, S., Wu, S.-B., Choct, M. and Swick, R.A. (2020) Factors affecting energy metabolism and evaluating net energy of poultry feed. *Poultry Science* 99, 487–498.

National Research Council (NRC) (2012) *Nutrient Requirements of Swine*. National Academies Press, Washington, DC.

Energy metabolism

All the energy exchanges that occur in a living animal or cell. They originate from the chemical energy of food, which is the prime source of energy for all body processes and activities, including **growth**.

Only part of the chemical energy of food can be utilized in the body; some food constituents can be assimilated immediately through the intestinal walls into the bloodstream; some have first to undergo chemical transformation in the **gastrointestinal tract** into a more digestible form; some are totally indigestible. Indigestible and waste **by-product**s are voided as **faeces** and **urine**. In all species, but especially in herbivorous animals, which

pre-digest food by **fermentation** in the **rumen**, a further waste product is **methane**. The remaining energy is **metabolizable energy**, which is involved in many chemical transformations in the organs of the body. This part of the process is termed intermediate **metabolism**. It includes some reactions that build up energy-rich compounds (anabolism) and others that break down energy-rich compounds to release energy (**catabolism**). Anabolic and catabolic processes are continuous and simultaneous, with an equilibrium between them. A prime example is the energy-rich compound **adenosine triphosphate** (ATP), which can release energy on being reduced to adenosine diphosphate (ADP). Such compounds may be used to provide energy quickly at high rates for, say, muscular movement, the energy store being replenished later by reconversion of ADP to ATP, this being coupled to the **oxidation** of food-derived nutrients that provide the energy required. This is an example of short-term energy storage; such temporary storage is quantitatively small in comparison with the overall level of energy metabolism. In a wider sense, growth is an anabolic process and consumption of **body fat** during undernourishment is a catabolic one; these are long-term and quantitatively large methods of energy storage and de-storage.

The metabolizable energy is available to promote synthesis of body tissue (meat or fetus), milk, wool or eggs; it can also be used by draught animals to do mechanical work. A large proportion is transformed into heat that is lost to the environment. The level at which metabolism proceeds is determined by both **energy requirement** and the availability of food. A minimal energy level

(**basal metabolism**) is needed to maintain essential body functions such as respiration and **blood** circulation. Eating itself involves further **energy expenditure** in finding, **chewing** and absorbing the food (known as the **heat increment of feeding**). Additional energy is required for activity and mechanical work. Only after these requirements have been met is excess metabolized energy available for retention in the body as growth or production (milk, eggs, wool or fetus). Production rates are generally increased up to a certain limit by additional food intake. Production and skeletal growth in the young, however, do not cease if food intake is insufficient, but proceed by catabolism of body reserves, mainly fat.

All metabolized energy not retained for production, growth or retrievable work is converted into heat. In warm environments, most of the heat produced is wasted and animals have to find means to get rid of the excess heat to the environment. Conversely, in a **cold environment**, heat is useful to the animal; indeed in very cold environments animals may be forced to metabolize additional food energy simply in order to keep warm. (JAMcL)

Energy requirements

In a thermoneutral environment, the energy requirement of an animal is the sum of the energy retained in animal products and the associated **adenosine triphosphate (ATP)** costs (i.e. the cost of ingestion, **digestion** and **metabolism**). The energy content of secreted animal products (e.g. milk or eggs) can be determined relatively easily in a **bomb calorimeter**, whereas the energy retained by the animal (e.g. growth or gestation) requires a **comparative slaughte**r technique or **indirect calorimetry**. It

is virtually impossible to determine directly the ATP required for physiological processes. The main problem is that energy is released as heat during the transformation of nutrients to ATP as well as during the actual ATP utilization. Consequently, energy requirements are expressed in terms of energy, such as **metabolizable energy** (ME) or **net energy**.

Maintenance

The **maintenance** energy requirement is defined as the energy requirement of a non-producing animal (i.e. no production of milk, eggs or wool, no fetal growth and no net deposition of body protein or lipid). In addition, it is assumed that the animal is healthy and is kept in a thermoneutral and stress-free environment. Physiological components of maintenance include blood circulation, nutrient transport and **absorption**, respiration, excretion and tissue **turnover** that is unrelated to production. Although there is general agreement on the conceptual and qualitative description of maintenance, it is more difficult to quantify maintenance unambiguously in farm animals. During fasting, animals catabolize body reserves in order to supply ATP for essential body functions and so fasting **heat production** is often used as an **indicator** of the maintenance requirement; however, it is an indirect measurement, because the efficiency with which body reserves are used for ATP synthesis is not considered. Maintenance energy requirements are often expressed as a metabolizable energy (ME) equivalent, which has the drawback that the value is not independent of the diet. A zero **energy balance** (i.e. either induced experimentally or by statistical extrapolation) ensures that

all metabolizable energy is used for maintenance functions. The maintenance energy requirement represents an important fraction of the **energy intake**, ranging from 25–30% of ME intake for very productive animals (such as high-producing dairy cows or rapidly growing pigs and poultry) to 100% of ME intake in mature non-producing animals. For mature species, maintenance requirements are typically expressed per kilogram of metabolic body weight (kg $BW^{0.75}$) and range from 290–330 for cattle to 400–440 kJ ME kg^{-1} $BW^{0.75}$ per day for sows. Normal physical activity is also considered part of the maintenance energy requirement and may represent an important fraction of it. In a comparison between species, the cost of activity (kJ kg^{-1} $BW^{0.75}$) has been found to range from 2.4 (rats) to 30 (pigs) per 100 min of standing. The heat generated in metabolic processes is usually sufficient to maintain a constant body **temperature** but animals in a **cold environment** may need to divert energy from productive processes to **thermogenesis** in order to maintain a constant body temperature. In that case, the energy requirement of the animal includes all the heat that is produced (i.e. the ME intake).

Weight gain (protein and fat deposition)

Most of the energy gain in farm animals is retained as protein and lipid. Although **glycogen** is important for the short-term storage of energy, it plays a minor role in the long-term energetics of gain. The energy requirement for body weight gain depends on the protein and lipid composition of the gain. The **gross energy** values of body protein and lipid are approximately 23.7 and 39.8 kJ g^{-1}, respectively. Although these values can be used to calculate the

energy content of body weight gain, they do not reflect the **energy cost** of gain. The latter also includes the cost of **nutrient absorption**, transport and **metabolism**. The cost of protein (PD) and lipid deposition (LD) has been estimated experimentally by a factorial approach:

$$ME=MEm+1/kpPD+1/kfLD$$

where ME_m is the maintenance energy requirement, k_p is the marginal efficiency of protein deposition and k_f the marginal efficiency of lipid deposition. Although it is acknowledged that there is considerable variation in reported values for marginal efficiencies, k_p is typically much lower than k_f (60% and 80%, respectively, in growing pigs). Consequently, more energy is required to deposit 1 kJ of energy as protein than as lipid. The greater energy requirement for protein deposition is due to the ATP needed for **peptide** bond formation (augmented by **protein turnover**). It is important to realize that k_p and k_f reflect the conversion of metabolizable energy to retained energy and are therefore diet dependent.

Gestation and egg production

From an energetic point of view, gestation in farm animals is a complex process. Apart from the development of the fetuses, maternal tissues such as the uterus, placenta and udder grow and become metabolically more active during gestation. Moreover, the female may not have reached maturity or may be in the process of restoring body reserves following a previous **lactation** and so fetal growth may be accompanied by growth of maternal tissues. The energy retention by the fetuses is typically assumed to be

proportional to the **birth weight** and number of young born. Fetal growth (mainly protein) and growth of the placenta and maternal tissues are relatively minor during the initial phase of gestation and are often described by exponential functions. During gestation, a considerable fraction of the **energy expenditure** is due to oxidative metabolism (i.e. ATP synthesis and utilization) by the uterus and placenta and this expenditure may even exceed that of the fetus(es). The complexity of gestation and methodological differences result in widely different estimates of energy requirements of gestation between species. It is less difficult to determine the energy requirement of **reproduction** in poultry. Based on the **energy value** of egg constituents, at least 7 kJ g^{-1} egg mass is needed. The metabolizable energy requirement for **egg production** is typically assumed as being 8.7 kJ g^{-1}. This requirement covers the synthesis of egg energy as well as the energy required for synthesis (e.g. formation of the **eggshell**).

Lactation

The energy retained in **milk** is a function of the protein, fat and **lactose** contents of the milk. The heat of combustion of these products is approximately 38.9, 23.9 and 16.5 kJ g^{-1}, respectively. In ruminants, lactose can be synthesized from gluconeogenic precursors such as **propionate**, whereas non-ruminants may use dietary **glucose**. The actual energy requirement for milk synthesis appears to be considerably greater than that calculated theoretically from transforming nutrients to milk components, especially in ruminants. The experimental efficiency of using dietary energy for milk production is 60–65% in ruminants and

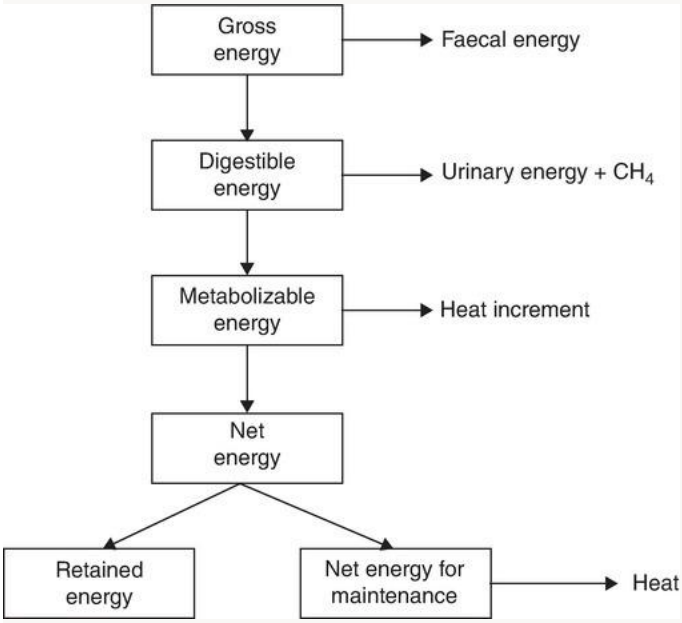
70% in sows. This difference is partly due to differences in the nutrients used for milk fat synthesis (for example, **volatile fatty acid**s obtained from **fermentation** vs. **carbohydrates**). In early lactation, the energy requirement for milk production (and maintenance) may exceed the intake capacity of the animal, resulting in mobilization of body reserves. The efficiency with which this occurs is relatively high (80–90%). (JvanM)
See also: Energy systems

Energy retention:
see Energy balance

Energy source
A **feed** included in diets primarily for the energy it supplies (in contrast to **protein source**s). The major sources of energy in animal feeds are **carbohydrates** (such as **starch** in cereal **grain**s and **cellulose** in **forages**) and **lipids** (such as the **oils** in **oilseed**s). (JMW)

Energy systems
Energy systems have been developed as a means of relating the supply of dietary energy to the animal's requirement (see figure). The objective of an energy system is to attribute a value to a feed that can be compared with a requirement expressed using the same units. Most current energy systems are based on (or variants of) **digestible energy** (DE), **metabolizable energy** (ME) or **net energy** (NE). It is important to realize that, in refining energy systems, **energy value**s become not so much a property of the

feed alone but more a function of both the diet and the animal's productive processes.



Relation between energy systems.

Digestible energy (DE)

The DE content of a diet corresponds to the **gross energy** (GE) content minus the energy lost in the faeces. The faecal energy corresponds to the energy of undigested dietary nutrients as well as a (small) endogenous fraction. DE values cannot easily be determined in poultry, because the urine is excreted with the faeces. DE values may be extremely variable and may range from 0 to 100% of the gross energy value. The (apparent) DE value may often be calculated from digestible nutrients. For example, the DE value of feeds (for growing pigs) has been determined by regression as:

$$DE=0.0229\times DCP+0.0389\times DEE+0.0115\times DCF+0.0175\times ST+0.01$$

where DCP is the digestible **crude protein** content, DEE the digestible **ether extract**, DCF the digestible **crude fibre** content,

ST the **starch** content, sugars the **sugar** content and DRes the digestible residue content (i.e. **organic matter** minus the other digestible nutrients), all expressed in g kg^{-1} dry matter (DM). It should be noted that the coefficients correspond to the (approximate) GE values for each nutrient. Several equations of this type have been proposed and are all built on the premise that digestible energy is supplied by the components of organic matter. It must be ensured that DE values are representative of the situation to which they are applied, as the **digestibility** of a nutrient may be affected by feeding level or physiological stage of the animal. Although DE values of feedstuffs can be easily determined, the biological basis for establishing DE requirements is rather weak.

Metabolizable energy (ME)

The ME value of a feed corresponds to the DE value minus the energy lost in the urine and as gas. All ME is retained in animal products or lost as heat. The energy losses in the urine, mainly as **urea** in mammals or as uric acid in birds, are principally due to the incomplete **oxidation** of **amino acid**s. Urinary energy represents 2–5% of GE for non-ruminant animals and 4–6% for ruminants. Urea has an **energy value** of 22.6 kJ g^{-1} N (34.4 kJ g^{-1} N for uric acid). Thus, each additional gram of protein that is not deposited as protein will theoretically result in an additional urinary energy loss of $0.16 \times 22.6 = 3.6$ kJ g^{-1} protein. Thus, the ME value of dietary proteins that are deposited as protein will equal the DE value (23.8 kJ g^{-1}), whereas that of oxidized amino acids will be $23.8 - 3.6 = 20.2$ kJ g^{-1}. Consequently, the ME value of protein is not a property

of the protein content per se, but depends on the utilization of the protein. This has led to the suggestion that ME should be corrected to zero balance or constant N retention. As with DE, ME also contains an endogenous component that is not (directly) of dietary origin. Also the gaseous energy (**methane** and **hydrogen** originating from microbial **fermentation**) cannot be used by the animal. Although this is a minor fraction for non-ruminants (0–2% of GE), it may represent 6–10% of the GE in ruminants. The measurement of methane and hydrogen production requires specialized equipment. Consequently, ME values are often calculated as a function of DE, digestible nutrients and/or **organic matter** digestibility.

Net energy (NE)

Net energy can be defined as the 'useful' energy for the animal and is equivalent to the ME value minus the **heat increment of feeding**. The latter is the heat loss associated with ingestion, **digestion** and metabolism of nutrients and can be obtained by regression of the **energy balance** (or **heat production**) on the ME intake. The slope of this line is the efficiency of production ($k_g = \Delta EB/\Delta ME$) and the NE value can then be calculated as $k_g \times ME$ (the heat increment is $(1 - k_g) \times ME$). The relation between the energy balance and ME intake is not necessarily linear and NE values are therefore not constant. The NE value of a diet can also be seen as the sum of the NE values for maintenance and production. The NE for production corresponds to the energy that is stored in animal products (e.g. growth, milk, eggs) whereas the fasting heat production is typically taken as an estimate for the NE

for maintenance. Although the energy retained in milk and eggs can easily be measured, measurement of the energy balance requires the **comparative slaughter** technique or **calorimetry**. Both techniques are costly and time consuming, which limits extensive measurement on feeds. For most species, NE values have been measured experimentally and this information has been exploited to predict the NE value from the **chemical composition** or ME value of the feed. These (statistical) relations explain a large fraction of the biochemical efficiency of nutrient transformation. In growing pigs, the NE/ME ratios (for maintenance and growth) for protein, **ether extract**, **starch** and **dietary fibre** correspond to approximately 0.58, 0.90, 0.82 and 0.58, respectively. The value for starch is similar, whereas that for **lipid** is slightly lower than the theoretical efficiency for lipid deposition. The value for protein is considerably lower than the theoretical value, suggesting that other processes (e.g. **protein turnover**) contribute to the efficiency. The observation that the efficiency of using protein for protein deposition is very similar (0.60, which is essentially an ATP cost) supports this idea. The result is that, relative to an ME classification, feedstuffs rich in protein and fibre have a low NE value (in pigs), whereas those rich in fat have a higher value. The advantage of using an NE system (relative to ME or DE) is that it corresponds more closely to the actual **energy utilization** by the animal. On the other hand, it results in different NE values for each type of production and therefore becomes less of a diet characteristic per se. (JvanM; JAMcL)

See also: Calorific factors; Energy; Energy units; International units

Energy units

The Standard International (SI) unit of energy is the **joule** (J), which is the work done when a force of 1 newton acts over a distance of 1 m. The **calorie**, another unit of energy, is the heat required to raise the temperature of 1 g of water through 1°C. The relationship 4.184 J cal^{-1} is known as the mechanical equivalent of heat.

Use of SI units is recommended whenever possible but calories (cal), **kilocalorie**s (kcal) and pounds (lb) are widely used in agriculture. The SI unit of time is the second (s) and the SI unit of power is the watt (1 W = 1 J s^{-1}). In agricultural practice, one is dealing with rates of heat output and food **energy intake** in the range 1 W to 10 kW, but food intake and requirements are usually reckoned per 24 h. This inevitably leads to the use of hybrid units such as **kilojoules** per hour, **megajoule**s per day, kilowatt-hours, kilojoules per pound, etc., as well as joules and calories. Some useful conversion factors are as follows. (JvanM; JAMcL)

Units of energy, including work and heat (mass × $distance^2$ × $time^{-2}$):

1 joule (J) = 1 watt second (W s) = 0.239 calories (cal)

1 kilojoule (kJ) = 0.278 watt hours (W h) = 0.239 kilocalories (kcal)

1 megajoule (MJ) = 0.278 kilowatt hours (kW h)

1 calorie = 4.184 joules (J)

1 kilocalorie (kcal) = 4.184 kilojoules (kJ) = 1.162 watt hours (W

h)

Units of power or work-rate (mass × distance^2 × time^{-3}):

1 watt (W) = 1 joule/second (J s^{-1}) = 3.6 kJ per hour (kJ h^{-1}) = 86.4 kJ per day = 0.239 cal s^{-1}

1 kilowatt (kW) = 1 kJ s^{-1} = 3.6 MJ h^{-1} = 86.4 MJ per day = 0.239 kcal s^{-1}

1 joule per second (J s^{-1}) = 1 W = 0.239 cal s^{-1}

1 kilojoule per hour (kJ h^{-1}) = 0.278 W

1 megajoule per day (MJ day^{-1}) = 11.6 W

1 calorie per second (cal s^{-1}) = 4.184 J s^{-1}

1 kilocalorie per hour (kcal h^{-1}) = 1.162 W

Units of energy/mass (distance^2 × time^{-2}, used for **energy value** of foods, heats of combustion, energy expended in doing mechanical work):

1 joule per gram (J g^{-1}) = 0.239 cal g^{-1}

1 kilojoule per kilogram (kJ kg^{-1}) = 0.239 kcal kg^{-1} = 0.454 kJ lb^{-1} = 0.1084 kcal lb^{-1}

1 megajoule per kilogram (MJ kg^{-1}) = 108.4 kcal lb^{-1}

1 kilojoule per pound (kJ lb^{-1}) = 0.239 kcal lb^{-1} = 2.205 kJ kg^{-1} = 0.527 kcal kg^{-1}

1 calorie per gram (cal g^{-1}) = 4.184 J g^{-1}

1 kilocalorie per kilogram (kcal kg^{-1}) = 4.184 kJ kg^{-1} = 0.454 kg lb^{-1} = 1.90 kJ lb^{-1}

1 kilocalorie per pound (kcal lb^{-1}) = 4.184 kJ lb^{-1} = 2.205 kcal kg^{-1} = 9.224 kJ kg^{-1}

Energy utilization

The **metabolizable energy** (ME) cost of forming an animal product (e.g. milk, eggs, body tissue) is the extra ME intake required for the formation of the product over and above the ME required for the animal's **maintenance** (ME_m). The **gross energy** of the product is its heat of combustion. For cows' milk this is approximately 3 kJ g^{-1}, for sows' and ewes' milk 5 kJ g^{-1} and for hens' eggs 6 kJ g^{-1}. For **growth** in most species the gross energy of weight gains is of the order of 6–10 kJ g^{-1} after birth when the gain is mainly protein, rising to 25–30 kJ g^{-1} at maturity when the gain is mostly fat.

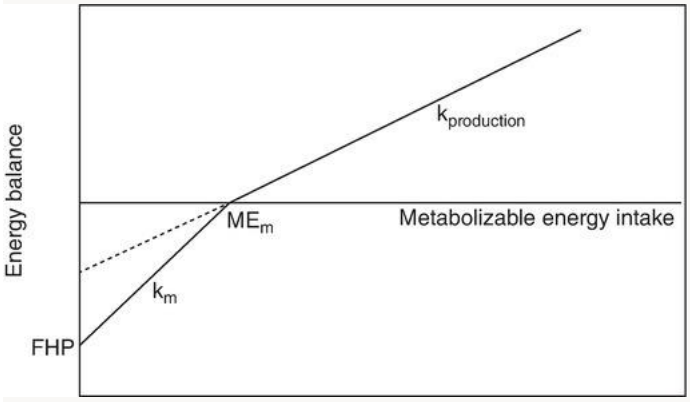
The **efficiency of energy utilization** is the ratio between energy output (in product) and the corresponding energy input. It can be obtained from the relationship between **energy balance** and metabolizable **energy intake** (see figure). The slope of this line is interpreted as the efficiency of energy utilization (k). The relationship is usually represented as having two linear segments and can be expressed by the equation:

ME requirement = (GE of the total product produced/$k_{production}$) + (fasting heat production/k_m)

where GE is the gross energy content of the product.

At ME intakes above maintenance, $k_{production}$ is the efficiency of utilization of ME for formation of product (k_L for **lactation**, k_F for **fattening**, etc.). Below maintenance, the slope of the line between fasting heat production (FHP) (a measure of the animal's **basal metabolic rate**) and the metabolizable energy intake for

maintenance (ME_m) indicates the efficiency with which dietary nutrients are used for mainten ance, relative to mobilizing body reserves for that purpose. This efficiency for maintenance (k_m) depends on both the diet and the body reserves used when the animal is actually fed below maintenance. With increasing ME intake above maintenance, growing animals deposit an increasing fraction of energy as **lipid** (relative to protein). As the energetic efficiencies of protein and lipid deposition differ, the linear relation is therefore overly simplified.



Relation between the energy balance and metabolizable energy intake.

The efficiency of utilization of ME is generally higher for higher-quality (i.e. higher **metabolizability**) foods. For maintenance, k_m is usually of the order of 0.65–0.85, for **lactation** k_L = 0.55–0.65, for growth k_G = 0.35–0.55 and for milk-fed growing animals up to 0.7. For **egg production**, k_E = 0.7. The ME cost of an entire pregnancy is approximately 7.5 J per J **gross energy** of a newborn calf, i.e. an efficiency of 0.13. If food intake is insufficient for essential needs such as fetal or skeletal growth or milk production, these functions still proceed, albeit at reduced rates, obtaining their energy from **catabolism** of body reserves

(mainly fat). The (relative) efficiency for this is usually of the order of 0.9.

Because k_m is a relative efficiency, its value typically exceeds that of the efficiency of production and even may exceed unity. The maintenance **energy requirement** is essentially a requirement for **adenosine triphosphate (ATP)**. It is difficult to express the efficiency of ATP synthesis as a fraction of energy input 'retained' as ATP. Nevertheless, the (relative) efficiency with which nutrients can be used for ATP synthesis can be compared (see table). It appears that **glucose** and **lipids** can be used relatively efficiently for ATP synthesis, whereas **volatile fatty acid**s are used 10–18% less efficiently. The efficiency of using **amino acid**s for ATP synthesis is considerably lower. Part of this inefficiency is due to the incomplete **oxidation** of amino acids. In mammals, the **nitrogen** of amino acids is excreted as **urea**, which involves both a physical loss of energy (as urea) as well as the **energy expenditure** to synthesize it (2 ATP/N).

The theoretical energy expenditure for ATP synthesis from various substrates.

Source	**kJ mol^{-1} ATP**	**Source**	**kJ mol^{-1} ATP**
Glucose	74.0	Phenylalanine	124.0
Tri-stearin	75.7	Tyrosine	107.0
Acetate	87.4	Histidine	149.8
Propionate	85.4	Arginine	133.6

Source	kJ mol^{-1} ATP	Source	kJ mol^{-1} ATP
Butyrate	81.2	Serine	116.0
Lysine	102.2	Glycine	149.2
Methionine	129.3	Alanine	104.5
Cysteine	178.4	Glutamate	91.8
Threonine	100.0	Proline	92.5
Tryptophan	134.0	Aspartate	103.9
Isoleucine	88.4		
Leucine	90.6		
Valine	92.7		

The theoretical energetic efficiency of **protein synthesis** is approximately 85% but the actual efficiency is often lower, due to **protein turnover**. The efficiency of depositing protein in animal tissue appears to be considerably lower (~60%) than that of depositing protein in animal products such as milk or eggs (~75%). Part of this difference may be due to a difference in protein turnover between these types of production.

In ruminants, a major part of the energy supply is derived from the end-products of **fermentation** in the **rumen** and **large intestine**. The metabolic utilization of these end-products (and the associated cost of fermentation) results in lower efficiency than that observed in non-ruminant animals. As with the efficiency for ATP synthesis, the efficiency for **fat** deposition in non-ruminants

increases in the order protein, **carbohydrate**, **lipid**. (JAMcL; JvanM)

Further reading

Agricultural Research Council (1980) *The Nutrient Requirements of Ruminant Livestock*. Commonwealth Agricultural Bureaux, Farnham Royal, UK.

Agricultural Research Council (1981) *The Nutrient Requirements of Pigs*. Commonwealth Agricultural Bureaux, Farnham Royal, UK.

Janssen, W.M.M., Terpstra, K., Beeking, F.F.E. and Bisalsky, A.J.N. (1979) *Feeding Values for Poultry*. Spelderholt Institute for Poultry Research, Beekbergen, The Netherlands.

Energy value

The concentration of energy in a **feed**, usually expressed as **megajoule**s (MJ) per kg dry matter (DM). (JMW)

See also: Digestible energy; Gross energy; Metabolizable energy; Net energy

Englyst method

An *in vitro* procedure for the determination of **resistant starch**. The **sample** is treated with a combination of mammalian and bacterial amylolytic enzymes under controlled conditions for various periods of time to give estimates of **rapidly digestible starch** (RDS), slowly digestible starch (SDS) and total starch (TS). **Resistant starch** is calculated as TS – (RDS + SDS). (MFF)

Enrichment, feeding

In the wild, animals spend long periods foraging for appropriate food, whereas in captivity rations are usually provided so that the

animals have to spend minimum time searching for and consuming their food. They develop abnormal oral behaviours, which are often stereotyped in nature, which help to assuage the motivation for **feeding behaviour**. Feeding enrichment aims to make the feeding process more complex and time consuming to prevent these abnormal behaviours. It is especially common in zoos, where abnormal behaviours may deter visitors from viewing the exhibit. It is also common in laboratories, where natural behaviour is conducive to the effective testing of new treatments for animals. It does this by feeding live insects to insectivores, such as lizards, **scatter feeding**, providing whole or part carcasses to carnivores, making food hard to find by hiding it in puzzle boxes or in trees, varying the diet regularly, offering food in ice blocks, or requiring animals to use tools to get it. Such food provision should be monitored to ensure that intake is controlled. (CJCP)

Enrichment, isotopic
The concentration of a particular isotope in a sample of the element. Because each isotope has a certain natural abundance, enrichments are usually referred to as that value and expressed as 'atoms percent excess' (ape). For example, the natural abundance of ^{15}N, i.e. the proportion of all **nitrogen** on earth that is of mass 15, is about 0.36%. So a sample with an enrichment of 2.48% has ape 2.12. (MFF)

Ensiling:
see Silage

Enterocyte
A cell of the single layer of columnar cells on the surface of the **villi** of the **small intestine**. Enterocytes are in direct contact with the intestinal contents. They have a directional orientation toward the intestinal lumen. On their luminal surface are the microvilli (**brush border**) which dramatically expand the contact surface and contain some of the digestive enzymes (e.g. **lactase** and **sucrase**) and transporters. (NJB)

Enterokinase
A proteolytic enzyme (enteropeptidase: EC 3.4.21.9), secreted by epithelial cells of the **duodenum**, that specifically activates **trypsin** by the cleavage of a **lysine–isoleucine peptide** bond leading to the removal of an aspartyl-rich octapeptide from the NH_2-terminal of the inactive **zymogen**, **trypsinogen**. (SB)
See also: Protein digestion

Environment–nutrition interaction
Climate is not the only component of the environment that affects nutrition (lighting and social environment are also important) but it is the one that receives most attention. The underlying cause of climate–nutrition interactions is that mammals and birds are homeothermic (or endothermic), which means that they maintain a near-constant body temperature. This can occur only if **heat production** equals heat loss. Over a range of ambient temperature, known as the thermoneutral zone, or zone of minimal thermoregulatory effort, constant body temperature is maintained by physical means, with no change in **metabolic rate**. This zone is

narrow in poultry, intermediate in pigs and relatively broad in ruminants. Below the thermoneutral zone, **energy intake** usually increases as ambient temperature decreases. Above the thermoneutral zone, energy intake decreases. The rate of decrease above thermoneutrality usually shows two phases. Initially, intake decreases at a rate that reflects the decrease in metabolic rate and the consequent decrease in maintenance **energy requirement**. As temperature increases still further, there is often an increased rate of decline in energy intake, which may be a mechanism for reducing the **heat increment of feeding**. There is usually a further acceleration in the decline of food intake with the onset of **hyperthermia**. Farmed **fish** are poikilothermic (or ectothermic) and their body temperature is close to that of the surrounding water. Their metabolic rate and nutrient requirements therefore increase with ambient temperature, following the Q_{10} relationship (i.e. a temperature increase of 10°C caused a two- to threefold increase in rate from the initial level).

Intake of dietary energy is the nutritional variant most directly affected by ambient temperature. To maintain the required intakes of essential nutrients it may therefore be necessary to alter the ratio of nutrients to energy as temperature varies. This may be most practicable in the case of housed pigs and poultry, where there is good control of the composition of the diet. The most widely applied dietary alteration is to increase the ratio of essential amino acids to energy as temperature increases. This has some beneficial effect in allowing growth rates to be sustained at high ambient temperature. However, it is not always successful in preventing a

reduction in growth rate or production. There are clearly direct (physiological) effects of high temperature that cannot be prevented by dietary adjustment. It has sometimes been suggested that providing more energy in the form of fat rather than **carbohydrate** should be beneficial at high temperatures because of its lower heat increment, but this has not invariably been borne out in practice.

Increased dietary vitamin **supplementation** (especially with **vitamins** E and C) has been shown to alleviate some of the effects of **heat stress**. This is most likely to be due to their antioxidative effects, particularly in protecting the cell membranes of metabolically active tissues such as the **liver**.

Breeds indigenous to hot climates are generally better able to maintain their characteristic level of production at temperatures that severely limit the performance of imported 'modern' genotypes. However, their greater tolerance can be seen as a consequence of the lower metabolic intensity accompanying their lower rate of production. (MMacL)

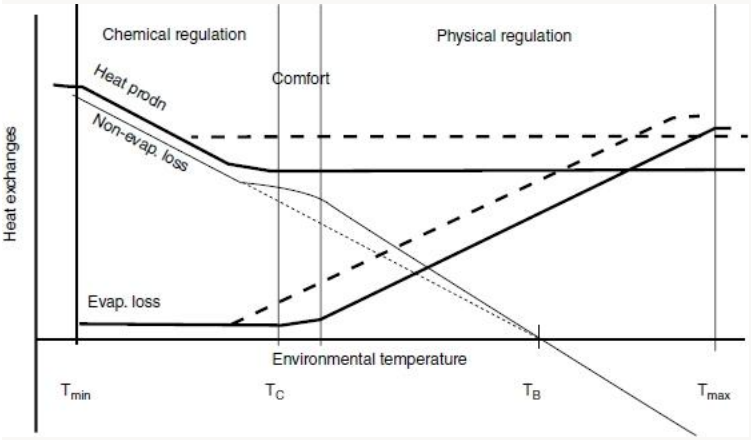
See also: Environmental temperature; Temperature, body; Thermoregulation

Environmental temperature

The effects of environmental temperature on heat exchanges of animals are illustrated in the figure, which is a model graph generally applicable to all homeothermic (warm-blooded) animals. Homeotherms maintain their deep-body **temperature** (T_B, usually measured as rectal temperature) close to a fixed normal level of around 38°C. T_B varies between species and tends to be

higher (up to 40°C) in small animals than in large ones.

Except in cold and extremely hot conditions, the rate of **heat production** is not affected by the environment but is determined largely by the levels of food intake and activity; it is shown in the model graph as a horizontal straight line between the two environmental temperatures, T_C (critical temperature) and T_{max}.



Effect of environmental temperature on heat exchange.

The heat exchange between an inanimate object and its surroundings is proportional to the temperature difference between them (Newton's law of cooling). It is obviously an over-simplification to apply this law to an animal – which is clearly not inanimate and has the ability to alter its rate of heat loss by various means, both reflex and behavioural, as well as to lose heat by evaporation – but for simple consideration of non-evaporative heat exchanges (i.e. convection, conduction and infrared radiation to the immediate surroundings) an animal may be thought of as two separate inanimate objects: one with minimal insulation for warm environments and the other with maximal insulation for cold ones. These are represented in the model as two straight lines of different slopes (insulation), both passing through or extrapolating

to the point of zero heat exchange at the environmental temperature that corresponds to T_B. The transition between these two lines is shown in the model graph as occurring over a short range of environmental temperature above T_C.

Since T_B remains near to a fixed level, it follows that **heat balance** is only maintained if **evaporative heat loss** is regulated at a level equal to the difference between heat production (which is constant) and non-evaporative heat loss. Evaporative heat loss thus decreases from a high level at T_{max} to near zero at T_C, and it is represented in the model by a straight line whose slope is equal but opposite to that of non-evaporative loss.

At environmental temperatures below T_C, evaporative loss is at a fixed minimal level consistent with minimal respiratory activity; it appears on the model as a horizontal line slightly above zero heat loss. In this cold region, heat balance is achieved by increasing heat production; it is shown as a straight line following the increased non-evaporative heat loss as the temperature falls. A limit occurs when the animal attains its so-called summit **metabolism** and is unable to increase heat production any further (at T_{min}).

Between T_{min} and T_{max}, which represent limiting environmental conditions for survival, lie the zones of chemical and physical body-temperature regulation. In the chemical zone, starting at the critical temperature (T_C is sometimes also known as the lower critical temperature), heat production is increased by increased voluntary activity or by shivering as the temperature falls. Above T_C, in the first part of the physical zone, reflex changes in **blood flow** just below the skin surface alter the thermal

insulation of the tissues, causing the transition between the lines of minimal and maximal non-evaporative heat loss. This is the comfort zone. As the temperature increases further (still within the physical zone), increased evaporation is caused by sweating or panting. The term 'thermoneutrality' is used by some authors to refer to the entire physical zone and by others just to the comfort zone; the 'zone of least thermoregulatory effort' has also been suggested to replace 'comfort zone' (Mount, 1974).

Among many deficiencies of this model is the fact that heat balance is only imperfectly achieved. T_B alters slightly and the temperatures of the limbs and of peripheral regions of the trunk alter considerably more. Periods of imbalance between heat production and heat loss give rise to temporary storage of heat in the body. The simple model also fails to take account of solar radiation. Solar heat load can be very considerable – even higher than the normal level of resting heat production. It can be included in the model by regarding it as an addition to heat production. To maintain heat balance, evaporative heat loss must be increased by a similar amount. These altered levels, consequent on solar radiation, are shown by dashed lines on the model graph. The net effect is a lowering of T_C and of temperatures in the comfort zone. Wind accelerates heat exchanges by reducing thermal insulation. The effect on the model is to make the slope of all lines steeper.

In addition to the reflex actions described above, animals (when free to do so) adopt behavioural patterns that influence heat exchanges. These include sheltering, huddling and curling up so as to limit heat losses in cold weather and standing in the wind or

seeking shade when the weather is warm.

For small animals the comfort zone is very narrow, perhaps better described as a comfort point; for large farm animals it is only a few degrees wide. The table gives approximate critical temperatures (°C) for some farm animals exposed to neither solar radiation nor wind. (JAMcL)

Critical temperatures (°C) for sheltered animals.

Species	Newborn	Mature	
		Maintenance fed	Lactating/laying
Cattle	14	7	−30
Sheep	29	−3	40
Pigs	32	23	14
Chickens	35	16	20

See also: Climate

Reference

Mount, L.R. (1974) The concept of thermal neutrality. In: Montieth, J.L. and Mount, L.E. (eds) *Heat Loss from Animals and Man*. Butterworths, London, pp. 426–439.

Enzootic ataxia

A **gait disorder** seen in young lambs, goat kids and deer, in Australasia and North America. It has also been seen in pigs. Swayback is a similar condition seen in lambs and goat kids in the UK: some breeds of sheep are much more susceptible than others.

Both conditions are caused by **copper** deficiency and are associated with demyelination of the cerebrum or spinal cord. (WRW)

Enzyme
A **protein** (or sometimes more than one protein) that has the ability to catalyse a specific chemical reaction. **Enzyme activity** requires specific conditions of temperature, pH, substrate and co-factor concentrations, etc. Since enzymes act as catalysts, they are not consumed while carrying out reactions. Enzyme activity can be reduced by **enzyme inhibitor**s. (NJB)

Enzyme activity
The potential of an enzyme, which may be one protein or a group of proteins, to carry out a reaction under idealized conditions. It can be measured using a purified protein or a sample of homogenized cells, tissue or organ. The system is optimized for pH, temperature, co-factor(s) and substrate concentration(s) and the reaction is assessed over a measured time. Results are expressed as a rate in relation to the amount of sample, e.g. μmol (min × mg protein)$^{-1}$. (NJB)

Enzyme inhibitors
A term applied to both inorganic and organic substances that have a negative effect on **enzyme activity**. Inhibitors compete with the normal substrate(s) or co-factor(s) for the enzyme and decrease the rate of reaction. The effectiveness of the inhibitor is described in many cases by the amount of the inhibitor required to suppress the

activity of the enzyme by 50%. This is referred to as the K_i and has units such as nmol l^{-1}. The smaller the value for the K_i, the more powerful is the inhibitor. Important examples of the role of enzyme inhibitors in nutrition are the **trypsin inhibitor**s found in many foods, especially **legume** seeds. (NJB)
See also: Feedback inhibition

Enzymes as feed additives
Enzymes are proteins that act as biological catalysts. They are produced by living cells and are intimately involved in essential transformations of substrates into products in biological systems. Many require non-protein co-factors. **Enzyme activity** depends on the co-factors present, the concentration and nature of substrate and enzyme as well as temperature and pH. The function of enzymes is critically dependent on their structure and they are therefore very susceptible to pH and temperature changes.

Enzymes are systematically named and each has an Enzyme Commission (EC) number which describes the reaction that it catalyses. The source of the enzyme (e.g. *Aspergillus niger*) is also frequently cited. Enzymes are often referred to as carbohydrases, proteases, **lipases**, **phytases**, etc., indicating that their major function is the degradation of **carbohydrates**, proteins, **lipids** and phytic acid esters, respectively.

Enzymes are produced commercially from microbes, fungi and yeasts in highly controlled conditions in **fermentation** plants. Their main uses are in the detergent and food industries but significant quantities are manufactured for use in animal diets. As

feed additives, enzymes are mainly used in the diets of non-ruminants but are also added to ruminant diets. Their main purpose is to improve the **nutritive value** of diets, especially when poor-quality, and usually less expensive, ingredients are incorporated. It has been estimated that about 95% of intensively fed poultry are now given diets containing supplementary enzymes. In some circumstances enzyme **supplementation** can improve performance and nutrient utilization by as much as 20%. The efficacy of a feed enzyme depends on the nature and quantity of its substrate in the diet, the specific ingredients, the age of the animal and its nutritional and disease status. Enzyme supplementation has the greatest effect on the young animal.

The feeds of plant origin used in poultry and pig diets are often **by-product**s of human food and of poor quality, with high concentrations of **non-starch polysaccharide**s (NSPs) and **oligosaccharide**s, as well as proteins that are resistant to **digestion**, and antinutrients such as **tannins**, **trypsin inhibitor**s, **lectins** and **phytates**. Such feeds cause physicochemical problems – increased **digesta** viscosity, water intake and moisture in the gut – that lead to reduced nutrient availability and increased endogenous losses. Nutrients are frequently enclosed in cells with indigestible cell walls, making them inaccessible to the animal's own digestive enzymes. Supplementation with the correct enzymes can increase the availability of nutrients and alleviate the adverse effects of antinutrients. In some instances, however, enzymes may actually release antinutrients.

Enzymes used as feed supplements are carbohydrases, proteases, phytases and, to a lesser extent, lipases. They may be used singly or in combination. The carbohydrases can be subdivided according to their substrate, whether **starch** or NSPs such as β-**glucans**, **cellulose**, **hemicellulose**, **xylan**s, galacturonans and **galactan**s. For use in the European Union, the enzyme preparations must be registered with the EU Scientific Committee on Animal Nutrition. The table gives a summary of the enzymes available and their sources.

Enzymes and the organisms from which they are obtained.

Enzyme	Main sources
Phytases	
3-phytase (EC 3.1.3.8)	*Aspergillus* spp., *Trichoderma* spp.
Phosphoric monoester hydrolase (EC 3.1.3.26)	*Aspergillus* spp.
Carbohydrases	
Endo 1→3 (4)-β glucanase (EC 3.2.1.6)	*Trichoderma* spp., *Aspergillus* spp., *Geosmithia* spp., *Penicillium* spp., *Humicola* spp., *Bacillus* spp.
Endo 1→4-β xylanase (EC 3.2.1.8)	*Trichoderma* spp., *Aspergillus* spp., *Geosmithia* spp., *Penicillium* spp., *Humicola* spp., *Bacillus* spp.

Enzyme	Main sources
Alpha galactosidase (EC 3.2.1.22)	*Aspergillus* spp.
Polygalacturonase (EC 3.2.1.15)	*Trichoderma* spp., *Aspergillus* spp.
Alpha amylase (EC 3.2.1.1)	*Bacillus* spp., *Humicola* spp., *Trichoderma* spp.
Proteases	
Subtilisin (EC 3.4.21.62)	*Bacillus* spp.
Bacyllolysin (EC 3.4.21.62)	*Bacillus* spp.

In poultry, the residence time of digesta in the **gastrointestinal tract** is relatively short (4–6 h); it is longer in the pig (6–8 h) and longer still in ruminants. Thus exogenous enzymes have greater opportunity to function effectively in ruminants and pigs than they do in poultry; however, this also depends on pH, buffering capacity and other conditions in the gastrointestinal tract. Generally, the enzymes required for ruminants are different from those needed in diets for pigs and poultry. For ruminants, **cellulase**s and hemicellulases are of particular interest, whereas the NSPs and phytases are especially useful in diets for non-ruminants.

Enzymes can be added to diets as powders, granules or liquids. The solid material is added during mixing while the liquid can be applied to pellets. The thermal stability of exogenous enzymes is extremely important in diets that are heated, either to reduce

transfer of pathogenic microorganisms or when the diets are pelleted. Overheating can denature supplemental enzymes, reducing their potencies.

A benefit of supplemental enzymes in diets for non-ruminants has been in reducing the occurrence of wet, sticky faeces. This tends to reduce the incidence of dirty animals, products and litter; it also tends to decrease contamination of the animals with dangerous bacteria such as *Clostridium* spp. Supplemental enzymes frequently reduce the **viscosity** of digesta in the gastrointestinal tract. (TA)

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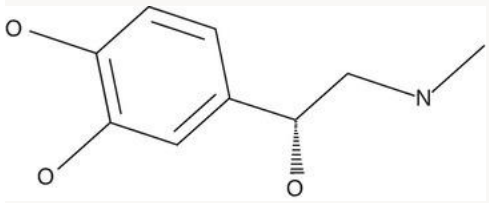
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Epinephrine

A catecholamine, also called **adrenaline**, produced in the **adrenal** medulla from the amino acid L-**tyrosine**. Epinephrine is released in response to both physical and physiological challenges. It causes the liver and muscle to increase the rate of **glycogen** breakdown, increases the release of **fatty acid**s from **adipose tissue** and increases circulating **lactate**. An increase in **metabolic rate** is often noted in response to epinephrine. (NJB)

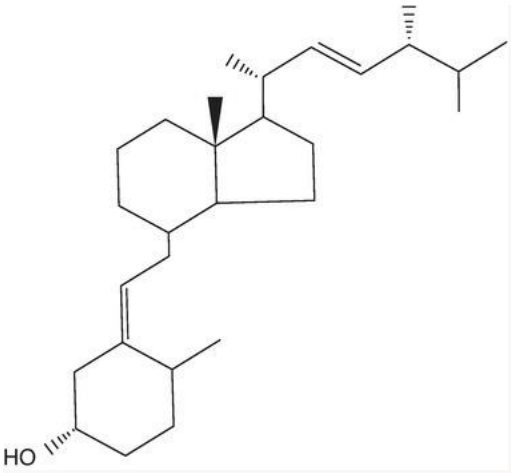


Epiphyses

Separate, enlarged, terminal ossifications of long bones attached to a growth plate, but growing separately from the shaft and covered by a layer of articular **cartilage**. (MMax)

Ergocalciferol

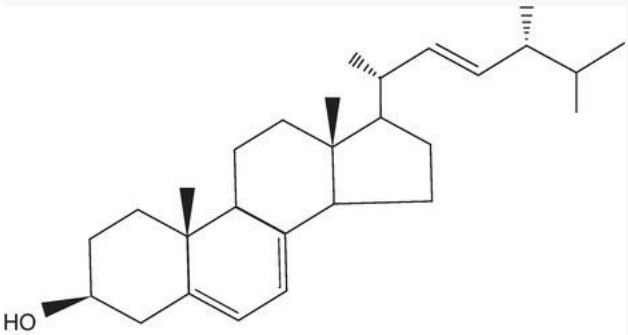
A trivial name for vitamin D_2 or a specific **vitamin D** compound that possesses the **ergosterol** side-chain. It is one of the two common nutritional forms of vitamin D, the other form being **cholecalciferol** or vitamin D_3. Unlike vitamin D_3, this compound is not formed in the body but is produced by ultraviolet irradiation of ergosterol. The structure of ergocalciferol is:



It can only be used in mammals. It has low biological activity in birds because it is rapidly metabolized. In mammals its activity is equal to that of vitamin D_3 or cholecalciferol. (HFDeL)

Ergosterol

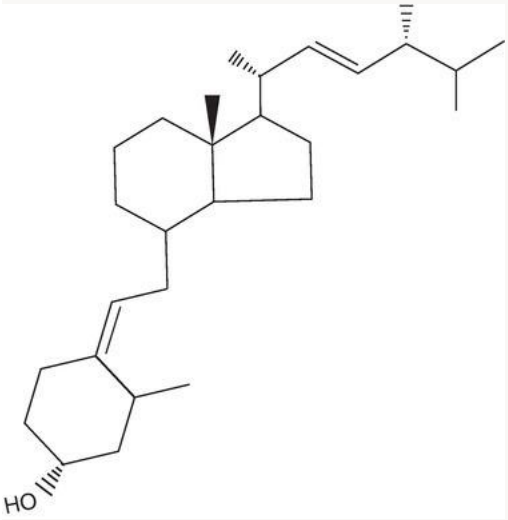
A **sterol** found in plants, **yeast** and moulds having the structure:



Upon irradiation with sunlight or ultraviolet light it is converted to **ergocalciferol** or vitamin D_2, having the structure:(HFDeL)

ErgotErgot alkaloids are produced by *Claviceps* fungi infecting grains and grass seeds, and by *Neotyphodium coenophialum* endophytic fungi infecting grasses such as tall fescue (*Festuca arundinacea*). *Claviceps purpurea*, *C. paspali* and *C. cinerea* are the three major fungal species. The fungus parasitizes the grass, attacking the ovary and replacing the developing seed with an enlarged, black structure in which fungal spores are contained in a

resin that eventually hardens, forming the sclerotium or ergot body. The ergot body may be harvested with the seed head or consumed by animals grazing an infected pasture.





Sclerotia of ergot of the species *Claviceps purpurea* (Fr.) Tul. growing on a spike of *Elymus repens*, one of the north-Italian wild graminaceous plants most infected by ergot. Photo courtesy of Giorgio Samorini. Licensed under CC BY-NC-SA 2.0.

The fungus produces toxic ergot alkaloids, including ergonovine, ergotamine and ergovaline, which are derivatives of lysergic acid. The hallucinogenic drug of abuse, lysergic acid diethylamide (LSD), is an ergot alkaloid. Symptoms of ergotism include **hyperthermia** (elevated body temperature), vasoconstriction and gangrene of extremities (e.g. fescue foot) and behavioural effects such as hyperexcitability, convulsions and poor

coordination. There are three main combinations of symptoms in livestock: the convulsive form, consisting of convulsions, laboured breathing, lack of coordination, excessive salivation and **diarrhoea**; the gangrenous form, producing dry gangrene of the nose, ears, legs and tail; and the reproductive form, consisting of **abortion**, agalactia and reduced neonatal survival. A major sign of tall fescue toxicity (summer fescue toxicosis) is ergot alkaloid-induced hyperthermia. Young poultry are also susceptible to ergotism, with the symptoms of severe toxicosis being poor feathering, nervousness, incoordination and gangrene of the foot and **beak**. Prevention of ergotism is only possible by removing animals from infected feed or removal of the ergots from the grain by screening. (DRG; PC)

Erucic acid

A long-chain monounsaturated fatty acid ($C_{22}\Delta^{13}$, $CH_3{\cdot}(CH_2)_7{\cdot}CH{=}CH{\cdot}(CH_2)_{11}{\cdot}COOH$). Diets in which erucic acid forms a major part of dietary fatty acids are associated with fatty infiltration of the heart, with subsequent permanent damage. Erucic acid has also been associated with **liver** damage in rats when fed at more than 5% of diet, resulting in slower mitochondrial **oxidation** of substrates.

Erucic acid is found in large amounts in some rapeseed oils, **mustard** seed oil and also **crambe**, meadow foam, nasturtium and lunaria seeds. The erucic acid content of rapeseed oil is controlled by two genes and zero-erucic acid rapes are now available. The EU has set maximum levels for erucic acid in human

foodstuffs at 2%. Erucic acid and its derivatives are used in industry, for example as lubricants. (EM)

Eructation

The release of gas from the **stomach**, or **rumen** in the case of ruminant animals, by passing it through the mouth. In this process first the lower and then the upper oesophageal sphincter is relaxed and then the gas is emitted with the aid of reverse **peristalsis**. This is a routine part of the **digestion** process in ruminants, which have large numbers of microorganisms in their rumen producing gaseous end-products. In humans it is associated with **aerophagia**, the consumption of air that happens when food is eaten too quickly. (CJCP)

***Escherichia coli* (*E. coli*)**

A Gram-negative bacterium which is a normal inhabitant of the gut of most mammals and birds. It is excreted in faeces and can survive in the environment for many weeks or even months. There are several different strains, most of which are not pathogenic. They can be distinguished and described by serotyping the O (cell wall), K (capsular), H (flagellar) and F (fimbral) **antigens**.

Pathogenic *E. coli* can cause enteritis or septicaemia in young animals, oedema disease in weaned pigs, mastitis, urogenital infections or toxaemia, depending on the strain and on the species of host animal.

Pathogenicity may depend on the presence of an antigen on the surface of the bacterium that allows adhesion to the intestinal wall or the ability to produce toxins. Toxins either act locally in the gut

or are absorbed and target other cells. Many strains of *E. coli* are secondary or opportunist pathogens. Those that are pathogenic for one host species may not be for others; for example, *E. coli* strain 0157, which has caused major food-**poisoning** incidents in humans, is carried undetected in the gut of a small proportion of cattle and other species. There may be variations in susceptibility within species to different genotypes, e.g. in piglets to *E. coli* strain K88.

Specific strains of *E. coli* can be controlled by vaccination, either of the dam to provide passive **immunity**, or directly of the susceptible animal. Vaccine–antisera combinations are available for enteric disease and there is also a vaccine to aid in the control of *E. coli* mastitis in cattle. (EM)

Essential fatty acids (EFAs)

18- to 20-carbon **unsaturated fatty acid**s having at least two double bonds. The term essential fatty acids indicates that they cannot be synthesized in the animal body and must be provided in the diet. EFAs are dietary essentials because animal systems do not have enzymes that can insert a double bond distal to n-9 carbon in a **fatty acid**. The EFAs are **linoleic acid** (18:2 n-6) and α-**linolenic acid** (18:3 n-3). **Arachidonic acid** (20:4 n-6), although essential, can be synthesized in the body from linoleic acid but with a low conversion efficiency. Like other polyunsaturated acids, these FAs form part of various membranes and play a role in **lipid** transport and certain **lipoprotein** enzymes. In addition they are the source materials for the synthesis of the **eicosanoid**s, including **prostaglandin**s, thromboxanes

and **leukotriene**s, **hormone**-like substances that play a key role in cell and tissue **metabolism**.

The classical symptoms of EFA deficiency are **growth** depression, decreased **reproduction**, decrease in skin integrity (more evaporative loss), tissue membrane degradation, and changes in fatty acid concentrations in blood and tissue lipids.

The **oilseed**s are generally good sources of linoleic acid and α-linolenic acid. Arachidonic acid is found predominantly in animal tissues. Pigs and poultry generally are fed diets containing a high content of oilseeds and meals, which are good sources of EFAs. **Ruminant animal**s receive an adequate supply of EFAs from grasses and forages. Requirements of pigs and poultry for EFAs are not well defined. Commercial diets are commonly formulated to contain 5–10 mg linoleic acid kg^{-1} to ensure adequacy. Poultry, pigs and cattle can be fed diets supplemented with feedstuffs such as flaxseed meal to provide eggs, meat and milk with enhanced contents of EFAs.

In common with other vertebrates, **fish** cannot synthesize either 18:2(n-6) or 18:3(n-3) de novo. Hence one or both of these fatty acids must be supplied preformed in the diet, depending on the EFA requirements. In addition, fish vary considerably in their ability to convert 18-carbon unsaturated fatty acids to longer-chain, more **highly unsaturated fatty acid**s (HDFAs) of the same series. The EFA requirement of the fish is thus related, to some extent, to their ability to exist between freshwater and stenohaline **marine fish**. In general, **freshwater fish** require either dietary linoleic acid, 18:2(n-6), or linolenic acid, 18:3(n-3), or both,

whereas stenohaline marine fish require dietary **eicosapentaenoic acid** (EPA), 20:5(n-3), and/or **docosahexaenoic acid** (DHA), 22:6(n-3).

According to the WHO, EFA deficiency is rare in humans although under certain conditions it does occur in infants, the elderly and people taking drugs that inhibit lipid absorption. This agency recommended that the acceptable range for total PUFA (n-6 and n-3 fatty acids) can range between 6% and 11% of dietary energy (FAO, 2010). An adequate intake to prevent deficiency was 2.5–3.5%. A **marker** of EFA deficiency is the triene:tetraene ratio in plasma, erythrocyte or tissue lipid. A ratio less than 0.4 suggests that the diet meets the EFA requirement. (RB; QS)

See also: Eicosanoids

Reference

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Ester

An **organic compound** in which the replaceable **hydrogen** of an acid can be replaced by an alkyl radical. Esters can be made on carboxyl carbons of **fatty acid**s, phosphate (PO_4^{2-}) in ATP, and **sulphate** (SO_4^{2-}) in heparin. Esters occur in neutral **fats,** the **fatty acid** binding to the alcohol group of **glycerol** ($\cdot R \cdot H_2CO \cdot OC \cdot (CH_2)_{14} \cdot CH_3$) and where a fatty acid binds to the alcohol group R·OH of **cholesterol** or α-**tocopherol**. The phosphate esters of ATP are R·O·P=O(OH)·O·R. The sulphate

esters of heparin are glucosamine·O·SO_3H. (NJB)

Esterification
The formation of **ester** bonds. For example, a carboxyl carbon $R{\cdot}COO^-$ reacts with an alcohol R·COH to produce an ester $R{\cdot}CO{\cdot}OCH_2{\cdot}R$. Examples are found in the **triacylglycerol** (triglyceride) molecule of a neutral fat when a **fatty acid** reacts with the alcohol group of **glycerol** or similar linkages in **phospholipid**s. Another example is **cholesterol** esters in which unsaturated or saturated fatty acids react with the alcohol group ^-OH of carbon 3 of cholesterol to form an ester bond. (NJB)

Ethanol
A monohydric primary alcohol (C_2H_5OH, molecular weight 46), most commonly produced by the **fermentation** of **carbohydrates** such as **molasses** and cereal **grain**s by *Saccharomyces* **yeast**. (JKM)

Ether extract
The residue obtained when a feed **sample**, or other material, is continuously extracted (4–16 h) with diethyl ether; in the **proximate analysis** of foods it is a measure of crude fat content. Water-soluble substances may first be removed from the sample by extraction with several portions of water; the sample is then dried and continuously extracted, in a Soxhlet apparatus, with anhydrous diethyl ether. The extract is weighed after evaporation of the ether. (CBC)

Ethoxyquin
An **antioxidant**, dihydro-6-ethoxy-2,2,4-trimethylquinoline, $C_{14}H_{19}NO$, boiling point 123–125°C. A light yellow to brown liquid with an unpleasant, mercaptan-like smell. It is combustible (flash point 107°C) and incompatible with oxidizing agents. It polymerizes if heated. (MG)

Ethylenediamine tetraacetic acid (EDTA)
$(HOOC{\cdot}CH_2)_2NCH_2{\cdot}CH_2N(CH_2{\cdot}COOH)_2$. An excellent chelating ligand molecule which is hexadentate. It forms strong complexes that wrap around **metal** cations, reducing their biological activity. **Chromium** EDTA has been used as an indigestible fluid **marker** in **digestibility** studies (*see* Feed evaluation). EDTA may also be used to strip toxic metals from the body and facilitate their excretion (chelation therapy). (IM)

EU regulations
Directives issued in Brussels by the European Commission regulate member states of the European Union on many issues. In the case of animal feeds these regulations include: target species; prohibition of feeds; feed processing requirements; feed **contamination**, composition and **labelling**; the marketing and management of animal foodstuffs; and licensing of **mineral supplement**s, pharmaceuticals and feed **additives**. (JKM)

European sea bass (*Dicentrarchus labrax*)
A eurythermal, euryhaline species living in coastal and **brackish water**s of the eastern Atlantic, ranging from Norway to the

Mediterranean and Senegal. It is grown in brackish lagoons and sea cages. Sea bass is spawned in full **sea water**, the larvae being fed initially on live prey organisms such as **rotifers** and artemia enriched with amino acids, vitamins and n-3/n-6 **polyunsaturated fatty acid**s, then switched to formulated micro-diets. A market size of 300–400 g is attained in 12–18 months at temperatures near 20°C. (RHP)

Evaluation, feed:
see Feed evaluation

Evaporative heat loss
Evaporation is a powerful means of dissipating heat from the animal's body to the environment, especially in warm climates. The heat required to convert liquid into vapour (the latent heat of vaporization of water) is approximately 2.2 kJ g^{-1}; this heat is drawn from the evaporating surface, which may be the skin, lungs or respiratory passages. There is a minimal rate of evaporation due to normal respiration and **diffusion** of water through the skin; these together normally amount to < 10% of the animal's resting rate of **heat production** and are unavoidable, even in cold weather. In hot weather, evaporative heat loss is increased reflexly as a result of sweating and panting and can rise to two or three times the resting **metabolic rate**. This is vitally important in hot environments where evaporation may be the only means of heat loss, especially if heat production is elevated due to work or by production of milk, eggs, etc., or by growth, and when the animal may additionally be subjected to solar radiation. To be effective as a

means of cooling, **sweat** must be evaporated from the skin surface; sweat that runs off the skin and drips to the ground as liquid provides no cooling. Some animals, e.g. pigs, voluntarily increase evaporation by wallowing to wet the skin surface when water, mud or damp bedding is available to them. (JAMcL)
See also: Climate; Environmental temperature; Thermoregulation

Ewe
A female sheep capable of breeding. Ewes are usually categorized by age. Those mated in their first year are referred to as ewe lambs; between 1 and 2 years of age they are called yearlings, shearlings or 'two-tooths', and thereafter adult or mature ewes. (JJR)

Ewe feeding
A priority in ewe feeding is to enable the ewe to achieve a predefined level of production with minimal risk to her well-being. In some sheep systems the aim of the feeding regimen is to promote full expression of the ewe's genetic potential for the production of specific products such as **meat**, **wool** or **milk**. In others the goal is lower levels of output commensurate with a reduced availability of food. The application of appropriate feeding regimes for specific systems is facilitated by setting targets for body weight and condition score during key stages of production. For example, **ewes** bred in their first year should have attained 60% of their estimated mature weight at mating. Thereafter their weight gains should be moderate (1–1.5 g kg^{-1} estimated mature weight per day) rather than excessive (three- to fourfold higher), as the latter leads to excessive partitioning of nutrients to the maternal

body at the expense of the placenta and fetus.

For the second and subsequent breeding cycles, practical guides for mating weights are 80% and 100% of estimated mature weights. The **body condition** of the ewe, which is often easier to estimate than weight, is also a valuable index in the implementation of feeding strategies. It has the added advantage that for many sheep breeds there is a positive correlation between the number of lambs born and the body condition of the ewe at mating. Thus the level of lamb production and therefore the feed requirements for pregnancy and **lactation** can be controlled by manipulating body condition at mating. The estimation of body condition involves palpation of the ewe over the lumbar region and ascribing a score (based on a 0–5 scale) for the degree of **fat** cover over the transverse processes of the vertebrae (Russel *et al*., 1969). For most breeds, maximum ovulation rate and therefore the potential for maximum lamb production occurs with a condition score at mating of 3–3.5. This level of body condition is characterized by transverse processes that have a smooth and rounded feeling; firm pressure is required to feel over their ends and the eye muscle areas are full with a moderate degree of fat cover. The ideal follow-up feeding strategy for ewes in this body condition at mating is one that maintains body weight and condition for the first month of pregnancy, followed by a gradual move to a mild energy deficit, equivalent to a loss of up to 0.5 units of condition score, from the end of the first to the end of the third month of pregnancy. In general this small energy deficit increases the size of the placenta, which is in its rapid growth phase at this

time. Provided that the **plane of nutrition** during the remainder of pregnancy is increased to meet the **nutrient requirement**s of the rapidly growing fetus or fetuses, the end result is slightly larger and more vigorous lambs at birth; the bigger placenta also enhances **mammary gland** development, thereby increasing the potential for milk production.

An important component of ewe feeding for the full expression of production potential relates to the adverse effects on ovulation rate of **undernutrition** approximately 6 months prior to mating. This corresponds to the time that ovarian follicles leave the primordial pool and become committed to growth. In many production systems it also corresponds with peak lactation and an associated negative **energy balance** in the ewe. Fortunately the adverse effect of this negative energy balance on ovulation rate can be avoided by a pre-mating increase in nutrition (**flushing**), which sustains ovulation rate by minimizing the number of **gonadotrophin**-responsive and -dependent follicles that are lost from the ovulatory pool through atresia.



The application of appropriate feeding regimes is facilitated by setting targets for body weight and condition score during key stages of production. Photo courtesy of Scottish Government. Sheep at Trough in Field | Scottish Government | Flickr

Some nutritional effects are irreversible. For example, undernutrition during early fetal life disrupts the normal development of oogonia in the fetal ovary, thus providing an explanation for the reduction in adult reproductive performance in ewe lambs conceived and born in harsh nutritional environments. Similarly, adverse effects on adult wool production have been recorded as a result of undernutrition during the last trimester of pregnancy in breeds such as the Merino, which has high genetic potential for **wool growth**. Secondary wool follicles (i.e. those that produce finer wool) are more affected. Other examples of nutritional effects *in utero* on later performance involve **trace element**s. **Enzootic ataxia** or 'swayback' arises from **copper** deficiency *in utero*, while subclinical **cobalt** deficiency during early pregnancy results in the birth of lambs that are slow to stand and suck; they also have a reduced acquisition of passive **immunity** as measured by their low serum IgG concentrations (Fisher and MacPherson, 1991). During the later stages of pregnancy an inadequate intake of **selenium** by the ewe results in the birth of lambs with reduced vigour and a suboptimal ability to generate heat from their **brown adipose tissue**. Many of the trace element deficiencies become more prevalent following the increase in pasture production that occurs after land drainage, additional fertilizer **nitrogen** usage and increases in soil pH. The

causal mechanisms are a reduced plant uptake of trace elements, the demise of pasture species rich in the elements and the higher trace element needs of ewes whose production potential has been stimulated by increased feed availability. Reduced maternal tissue mobilization arising from the general improvement in the energy and protein status of the ewe also contributes to the problem by inhibiting the release of essential mineral elements from the ewe's body reserves. Pre-lambing **calcium** deficiency (**hypocalcaemia**) provides another example of this phenomenon. Heavily pregnant ewes receiving adequate amounts of calcium in their diet are extremely susceptible to hypocalcaemia following a sudden drop in calcium intake. The reason for this is that the adjustments in gut **absorption** and mobilization of calcium from bone, which are needed to prevent a fall in blood calcium, do not occur quickly enough to maintain calcium **homeostasis** when dietary intake falls.

High-input systems maximize production potential with minimum dependence on body reserves; in contrast, low-input systems that are a feature of harsh nutritional environments involve major depletions of body **lipid** and mineral elements to sustain production. For these systems it is important that energy deficits in late pregnancy do not lead to excessive rates of body lipid mobilization and associated elevations in blood **ketone**s (3-**hydroxybutyrate** concentrations) above 0.8 nmol l^{-1} (Russel, 1984), otherwise there is a high risk of pregnancy toxaemia with the loss of both ewe and lambs. To prevent blood ketones rising above this threshold means restricting average daily energy deficits

to ~25 kJ ME kg^{-1} body weight or ~2 MJ for a 75 kg ewe bearing twins in which the daily **metabolizable energy requirement** 2 weeks before lambing is ~18 MJ (≅1.7 × **maintenance** needs of the ewe pre-mating). For ewes at the limits of their energy deficit during late pregnancy there are major nutritional benefits in feeding a small amount (1 g kg^{-1} ewe body weight per day) of a **protein supplement** such as fish meal. This **protein source** is rich in essential amino acids that escape degradation in the **rumen** and are therefore available for absorption in the **small intestine**. Its presence in the diet allows **body fat** reserves acquired prior to mating to be utilized more efficiently and safely for pregnancy; it also enhances colostrum production and the ewe's ability to combat gastrointestinal parasites (Donaldson *et al*., 2001).

Output from extensive systems is often dictated by available feed resources (natural plus **supplement**s) during late pregnancy and early lactation when nutrient demands are greatest. The magnitude of these demands is set by the plane of nutrition and **body condition** of the ewe at mating. Pre-mating improvements in nutrition (flushing) can increase the average **litter size** of ewes that are in poor body condition (score 1.5) from 1 to 1.3, while a one-unit increase in condition score to 2.5 can increase it to 1.6. Thus the post-**weaning** to pre-mating nutritional management of the flock plays a central role in its productivity. (JJR)

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Ewe lactation

The milk produced by lactating ewes may be used either for the production of lambs or, via milking, to provide milk and milk products (yoghurt, cheese and now pharmaceutical proteins) for human consumption. Milking usually follows a period (1–2 months) of **suckling** until the lambs can survive and grow on solid food alone. In some systems lambs are removed within 2 days of birth and ewes are milked for the next 6–7 months. Alternatively, following the first few days of suckling, ewes may be milked with the lambs restricted to daily sucking periods after milking until weaned at about 2 months of age, after which the ewes are milked for another 3–4 months. Durations of lactation therefore vary from approximately 3–4 months for lamb-rearing systems to 6–7 months for dairy systems, which use breeds such as the East Friesland and Awassi that are noted for their high milk yields.

In addition to ewe **genotype**, there are numerous other non-nutritional factors that affect milk yield. These include the positive effects of the number of lambs carried during pregnancy as well as the number reared. In the ewe, almost all of the udder's secretory

tissue is laid down during pregnancy. Thus the effect on milk production of **litter size** during pregnancy arises from the increase in the size of the placenta and the accompanying stimulatory effect on mammogenesis of its associated greater production of **hormone**s, notably placental lactogen. The effect on milk yield of the number of lambs reared is greatest between singletons and twins; milk intake by singletons is usually well below the ewe's production potential and thus ewes rearing twins produce about 40% more milk than those with singletons. Further increments in yield for triplets and higher multiples are generally much smaller (approximately 15–20%); they also occur early in lactation and gradually decrease so that by 12 weeks differences in yield due to the number of lambs suckled are negligible. At this point daily yields have declined from a peak of about 4 l to about 1 l. In contrast, for dairy breeds in which lamb suckling is replaced by twice-daily machine milking during the second month of lactation, the rate of decline is slower, with yields not falling to 1 l per day until 20–25 weeks of lactation.

Daily **nutrient requirement**s during early lactation are the highest experienced by the ewe in her lifetime and are met through a combination of increased **appetite** and the mobilization of body tissues. The extent of the appetite increase depends on the **body condition** of the ewe: fat ewes have smaller increases, and lose more **body fat** reserves, than their thinner counterparts.

Estimates of the **energy requirement**s for lactation can be obtained from the yields of milk constituents. For example, for meat-producing breeds, AFRC (1993) used the experimentally

derived relationship NE_l (MJ kg^{-1}) = 0.04194F + 0.01585P + 0.02141L, where NE_l = **net energy** requirement and F, P and L are the amounts (g kg^{-1}) of **fat**, **protein** and **lactose**, respectively. Typical values are 70 for F, 55 for P and 45 for L. CSIRO (1990) used the coefficients 0.0381, 0.0245 and 0.0165 for F, P and L, respectively, whereas INRA (1989) used the relationship NE_l (MJ per day) = 0.0588F + 0.265, in which F is in g l^{-1}. In converting net energy requirements for milk production to **metabolizable energy** (ME), all three feeding systems accept that the efficiency (k_l) of utilization of ME for milk energy production is influenced by the quality or **metabolizability** (q) of the diet, i.e. q = ME/GE where GE = **gross energy**. AFRC and CSIRO used the relationship $k_l = 0.35q + 0.420$ whereas INRA used $k_l = 0.24q + 0.463$, which gives slightly higher values for k_l than AFRC and CSIRO and therefore marginally lower estimates of the ME requirements for milk production.

With regard to the contribution that mobilized body tissue makes to energy needs for lactation, AFRC derived a dietary ME equivalent of 31.6 MJ kg^{-1} liveweight loss for a k_l of 0.63, i.e. a diet with an ME concentration of 11.5 MJ kg^{-1} dry matter (DM). The corresponding CSIRO value was 28 MJ kg^{-1} weight loss. In contrast, INRA linked the extent of body energy mobilization for milk production to a proportion of **maintenance** and adopted a value of approximately 70% of maintenance (equivalent to approximately 0.3 MJ of ME kg^{-1} $W^{0.75}$ per day) for early lactation, when the deficit between energy intake and requirements is at its

maximum.

Protein requirements for lactation are expressed in terms of **metabolizable protein** (MP). In the case of AFRC (1993) they were based on the assumption that ewe's milk contains 48.9 g **true protein** kg^{-1} and its production from MP is achieved with an efficiency of 68%. Although other systems use different efficiencies (CSIRO 70%, INRA 58%, NRC 65%), example calculations (Sinclair and Wilkinson, 2000) indicate that differences between systems in the estimates of **microbial protein** and the contribution of recycled **nitrogen** to the **rumen** lead to remarkably similar **crude protein** requirements. These are 169, 160, 167 and 154 g kg^{-1} dietary DM when the AFRC, CSIRO, INRA and NRC systems, respectively, are applied to a 70 kg **ewe** producing 2.0 kg of milk, consuming 2.1 kg DM and 23.1 MJ of ME daily and maintaining a constant body weight.

During periods of body tissue mobilization, which is the norm in early lactation, AFRC (1993) assumed that each kilogram of weight loss contributed approximately 120 g of milk protein (enough for about 2.4 kg of milk) whereas CSIRO used the slightly lower value of 108 g. In relation to the amount of milk (approximately 4.3 kg) that can be produced from the energy in 1 kg of weight loss, mobilized body tissue is clearly deficient in protein. Ewes in negative **energy balance** therefore respond, in terms of extra milk production, to increases in dietary protein. In fact, it can be argued that the aim should be to prevent body protein **catabolism** by ensuring that sufficient extra dietary protein (316 g MP kg^{-1} weight loss) is given to meet completely the

milk production contributed from mobilized body energy. This value is based on 1 kg of weight loss contributing enough energy for 4.3 kg of milk with a protein content of 5% and a 68% efficiency of use of MP for the synthesis of milk protein.

The requirements for the major **mineral** elements, **calcium** and **phosphorus**, are based on the same general principles as for energy and protein. Their respective concentrations in milk are 1.9 and 1.5 g kg^{-1} but conversion of these to dietary amounts, particularly in the case of calcium, is not straightforward in that there is an inverse relationship between intake and **absorption**; also mobilization of skeletal calcium and phosphorus is a normal occurrence during early lactation. AFRC (1991) provided a comprehensive set of dietary estimates for Ca and P in relation to ewe size, milk yield and the metabolizability (q) of the diet. For calcium, the recommended dietary concentrations for a 75 kg ewe consuming a diet for which q is 0.6 decrease from 0.38 to 0.27% in the DM as her daily milk yield declines from 3.0 to 1.0 kg and her associated daily losses in body weight decline from 100 g to zero. Corresponding recommendations for dietary phosphorus are 0.41% and 0.30%. Unlike calcium and phosphorus reserves, **magnesium** reserves in the ewe's body are trivial and there is little, if any, response in Mg absorption as requirements increase. The lactating ewe therefore requires a constant dietary supply, particularly in the first 6 weeks of lactation, when she is vulnerable to death from acute **hypomagnesaemia**, and particularly if she is grazing lush pastures that are high in **potassium** and low in **sodium**. A common dietary **supplement** is magnesium oxide given at a daily

rate of 7 g to ewes producing 3–3.5 kg milk per day. (JJR)

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Ewe pregnancy

Pregnancy in the ewe lasts from the time of fertilization of an **ovum** or ova in the oviduct until the resulting concepta leave the uterus. In a successful pregnancy, live lambs, with their associated placentas, are born approximately 5 months after fertilization. The gestation length is normally between 144 and 152 days but is to some extent dependent on breed, nutrition and the number of lambs in the uterus.

Ewes usually ovulate between one and four ova at each oestrous

period. The numbers vary according to the nutritional status of the ewe (*see* Flushing), age, season and breed. Some breeds commonly carry one or two lambs, whilst others, such as the Border Leicester, will often carry two or three lambs to term.

Immediately after fertilization, the ovum begins to divide, forming a solid cluster of cells or blastomeres known as a morula (from its mulberry shape). This process takes about 4 days, during which the embryo continues its passage down the oviduct and enters the uterus. From about day 5 after fertilization, the ovum hollows out to become a blastocyst, which consists of a single spherical layer of cells, the trophoblast, with a hollow centre and an inner cell mass at one edge. The inner cell mass is destined to form the embryo, whilst the trophoblast provides it with nutrients and will form the fetal component of the placenta. At about day 6 the blastocyst 'hatches' from its shell (the zona pellucida) and is elongating rapidly by about day 11. Meanwhile, the inner cell mass differentiates to form the germ layers, namely the ectoderm, mesoderm and endoderm. The ectoderm gives rise to the external structures such as skin, hair, hooves and **mammary gland**s and also the nervous system. The heart, muscles and bones are eventually formed from the mesoderm, whereas the other internal organs are derived from the endoderm layer. By day 45, formation of the primitive organs is complete.

The embryo is able to exist for a short time by absorbing nutrients from its own tissues and from the uterine fluids, but it ultimately becomes attached to the endometrium by means of its membranes, through which nutrients and **metabolite**s are

transferred from mother to fetus and vice versa. The ewe placenta, unlike that of the cow, allows the passage of **antibodies** from the mother to the fetus, so that lambs can acquire **immunity** from their dams *in utero*. The attachment process is known as implantation and may begin as early as day 10, but is not complete until around day 30. If the ewe is carrying more than one lamb, the placentas and their blood supplies remain separate. Thus, unlike the **cow**, there is little or no danger of sheep producing freemartins.

Fetal **growth** is exponential throughout gestation, the rate increasing as pregnancy progresses. **Fasting metabolism** during pregnancy is higher than that in non-pregnancy and increases throughout pregnancy. This, together with the **liveweight** increase that should occur, leads to a gradual rise in the maintenance **energy requirement**. Thus, the requirement for energy in pregnancy is increased by far more than the calculated requirements for the storage of energy in the uterus. The fetus has a high priority for energy and can draw specific nutrients from the ewe's body reserves even if she is being underfed. Fetal lambs can, for example, be adequately supplied with **iron** even when the mother is anaemic, and a ewe can lose up to 14 kg of her own body weight during pregnancy and still give birth to normal lambs. The fetus can maintain higher blood **sugar** levels than those of the ewe, which can thus succumb to a hypoglycaemic condition known as pregnancy toxaemia. Ewes carrying more than one lamb are more prone to the condition, which is also called **twin lamb disease**. The problem is exacerbated by the fact that voluntary **feed intake**

tends to be suppressed in late pregnancy when energy requirements are very high. It is good practice to scan **ewes** to detect the presence of more than one fetus, so that extra feed can be given during the last 2 months of pregnancy to ewes carrying multiple lambs as well as to those with lower **body condition** scores.

Severe underfeeding ultimately affects the unborn lambs as well as their mothers. The young may die *in utero* or have reduced viability after birth as a result of a lowered **birth weight** and a possible lowering of milk yield. Severe **malnutrition** in early pregnancy may simply reduce **litter size**. Protein, **vitamin A** and certain mineral and amino acid deficiencies can cause fetal death. In the case of vitamin A the lambs may be affected even though the ewe remains healthy. **Vitamin deficiency** may cause congenital deformities in fetal lambs that survive, while **copper** deficiency can cause 'swayback', which can severely affect the coordination of newborn lambs. Increasing the **energy intake** of the ewe in the last 6 weeks of pregnancy can increase the birth weight of lambs and ewe colostrum production and reduce ewe liveweight losses. (PJHB)

References and further reading

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Exercise:

see Activity, physical

Exopeptidase
A proteolytic enzyme that has the capability to hydrolyse the terminal **peptide** bonds in a protein. **Aminopeptidases** liberate amino acids consecutively from the N-terminus. In contrast, **carboxypeptidases** act from the C-terminus and may also liberate di- and tripeptides. (SB)

Exophthalmia
A common degenerative condition of the eye in which the globe is pushed out of the eye socket. In fish, it is typically related to the enlargement of the choroid gland of the posterior uvea or to degeneration of the ocular musculature. It has been linked to **niacin** deficiency. (DS)

Extensive livestock systems
Livestock systems, often based on natural **grazing** or **rangeland** in dry areas, in which inputs and outputs are low. In large livestock operations, breeding is often carried out extensively, followed by intensive finishing of progeny for marketing. Extensive systems are not suitable for profitable smallholder livestock production. (TS)

Extracellular waterBody water that is outside the cells, in contrast to intracellular water. Extracellular water includes that of blood, lymph, cerebrospinal and peritoneal fluids as well as interstitial water in the extravascular spaces within tissues. It can be estimated from the dilution of tracers that do not enter cells significantly during a short equilibration (e.g. bromide). **Total**

body water is the sum of extracellular and intracellular water. (MFF)

Extract, ether:
see Ether extract

Extraction, oil
Oil is extracted from oil-rich vegetable seeds, such as **soybean** (20% oil), **oilseed rape** (46%) and **linseed** (39%), by first dehulling and then **crushing** the seed between rollers or a screw press and collecting the resultant oil. This process is known as expelling. The remaining solids are known as expeller or 'cake' and have variable oil contents of around 10%. Many are sold and used as animal feed ingredients in this state. The oil is a useful component of the material but it is susceptible to **oxidation** and therefore poses potential storage problems. Further oil may be removed by organic solvent extraction, which reduces the oil content of the final meal to 2–3%. The solvent is finally evaporated from the meal using heat. The resulting **oilseed** meals are valuable vegetable **protein source**s for animals of all species. (MG)

Extrusion
A process in which conditioned meal is forced through an adjustable annular gap under high pressure. The high shear forces created rupture the cell structure, increase the temperature and gelatinize the **starch**. Extrusion takes place in a compression chamber of variable length, normally at least 2 m. The pressure is produced by feeding meal into the chamber at one end, whence it is

moved along the chamber by a revolving screw conveyor before being forced through a die with many holes at the other end. The flow of meal is adjusted to keep the conveyor running full and obtain maximum pressure at the die. Steam is normally injected along the length of the barrel to aid the extrusion process. Extrusion can be used to condition before **pelleting**, but is more commonly used as a manufacturing process in its own right. Extruded products are commonly used as fish food, as the modification of starch greatly improves the swelling properties in cold water. They are also used for diets for young mammals and poultry, due to the improved **digestibility** of the starch. Most dried pet foods now contain extruded chunks, since shapes can easily be made by changing the shape of the hole in the die. (MG)

Exudative diathesis

A disorder of poultry caused by **selenium** deficiency, usually as a result of consuming cereals with a low selenium concentration. It is characterized by a generalized oedema, which arises from abnormal permeability of the capillary walls. Usually the oedema first appears on the breast, wing and neck, with the greatest accumulation of fluid eventually forming under the ventral skin. Broilers are usually affected between 3 and 6 weeks of age, when they will lose weight, develop **leg weakness**es and may die. Supplementary selenium or **vitamin E** will prevent the disorder. (CJCP)

Eye diseases

The eye is well protected from variation in nutritional status but

there are disorders of the eye that have nutritional connections. **Vitamin A** deficiency causes a dryness of the conjunctiva (**xerophthalmia**) and can lead to **night blindness** or complete **blindness**. Eyes are susceptible to cancer during excessive exposure to ultraviolet **light**, and foods with high levels of **antioxidant**s protect against this. **Diabetes** mellitus, arising from chronic **hypoglycaemia**, can result in retinopathy, **cataract**s and glaucoma. In grazing animals, eye inflammation, or conjunctivitis, can arise from irritation from seeds, chaff, awns, etc. (CJCP)

F

Factorial method (for estimating nutrient requirements) A method by which the requirement for a nutrient is estimated as the sum of its components. Depending on the animal and the nutrient in question, these components may include **growth**, activity, gestation, **lactation**, **egg production**, **wool growth**, etc. Dietary nutrients are used with varying efficiency to meet these needs, and these efficiencies must be included in the assessment. For example, the **energy requirement** (R) of a growing animal is commonly considered to be the sum of its requirements for

maintenance (M), **protein** accretion (P) and **fat** (**lipid**) deposition (F). Thus,

$$R=M/km+P/kp+F/kf$$

where k_m, k_p and k_f are the efficiencies with which dietary energy (usually **metabolizable energy**) is used for each process. It will be seen that the equation is used to derive a requirement for particular rates of protein and fat deposition; when these rates are inserted into the equation, an estimate of the intake required to support those rates is generated, though at some intake the animal's potential for protein or fat deposition will be reached and the linear responses will no longer apply.

Such a simple model implies that efficiency is constant at all intakes, which is often demonstrably untrue. More complex models allow for diminishing efficiency at higher intakes. The simple model also applies only to an individual, whereas in practice the need is usually to derive the response of a population (herd or flock) that comprises individuals with varying values for each of the terms. This requires a more complex set of equations. (MFF)

Faecal flora:

see Gastrointestinal microflora

Faeces

Waste matter discharged from the intestines through the anus. Also called stool. The amount and composition of faeces vary between species and according to the diet consumed. Faeces originate from undigested feed and endogenous losses (gastrointestinal secretions and sloughed epithelial cells from the **gastrointestinal tract**)

that have not been reabsorbed. A considerable portion of these may be transformed into microbial matter. A large part of the **electrolytes** present in the faeces are of metabolic origin.

Faeces of non-ruminant animals are dominated by bacterial cells, which may contribute up to 85%. **Starch** in faeces is indicative of inefficient **milling** of cereals or of retrogradation. Faeces of ruminants consuming mainly **roughages** are mainly cell wall components. The colour of faeces is derived from plant pigments and bacterially degraded **bile** pigments.

The water content varies considerably within a species but is generally higher in the faeces of cattle (75–85%) than that of pigs (65–75%) or even hens (70–75%), which secrete urine together with faeces via the **cloaca**. The pH varies with the composition of the diet and is generally below 7 in cattle and horses but above 7 in pigs, sheep and hens.

An abnormal water content of faeces is indicative of **digestive disorders**, in particular **diarrhoea**. **Steatorrhoea** is the excretion of fatty, bulky, clay-coloured stools resulting from impaired **digestion** and absorption of fat. (SB)
See also: Defecation

Faeces collection
Faeces are collected for many purposes, most commonly for measuring **nutrient digestibility** or for investigating effects on the microflora. Total collections are made by confining the animal in a metabolic cage or by a container fixed around the anus or **cloaca**, usually with a harness. Simple 'grab' sampling of the faeces can be used to measure digestibility if a **marker** is added to the

diet and if faeces samples are collected systematically for a suitable period. Faeces are often collected from fish by stripping, i.e. pressing out the contents of the lateral intestine. In all digestibility studies a sufficiently long preliminary period, which depends on the **transit time** in the particular animal species, is essential. (SB)

Fasting metabolism
Measurement of an animal's fasting **metabolic rate** is commonly used as an estimate of its **basal metabolism**. The animal must be pre-trained to the **calorimeter** and the actual measurement takes place over a prolonged period during which the animal is free to move within the confines of the chamber. The fasting period before the measurement begins should exceed that over which there is an observable heat increment following the last feed; in ruminant animals this is 48 h or more. (JAMcL)
See also: Heat increment of feeding

Fat metabolism:
see Lipid metabolism

Fat-soluble vitamins
There are four fat-soluble vitamins: A, E, D and K. A deficiency of **vitamin A** results in defective night vision and keratinization of epithelial tissues, e.g. in the eye (**xerophthalmia**) which can lead to **blindness**. The lungs and **gastrointestinal tract** are also affected. A deficiency of **vitamin D** results in rickets and osteomalacia, which involve a derangement of **calcium** and

phosphorus metabolism. A deficiency of **vitamin E** (an **antioxidant**) leads to tissue damage by reactive oxygen species produced during aerobic metabolism. A deficiency of **vitamin K** results in haemorrhage, because vitamin K is involved in the synthesis of the blood-clotting factors. (NJB)

Fats

Esters of **fatty acid**s with **glycerol**. Simple fats are called **triacylglycerol**s or triglycerides. Triacylglycerols with three **saturated fatty acid**s of ten or more carbons are solid at room temperature. Those with fatty acids of less than ten carbons or fatty acids with one or more double fat bonds (unsaturated) are often liquid at room temperature and are called **oils**. Thus, fats and oils are similar in structure but are either solid or liquid at room temperature. Processed fat derived from pigs is called **lard**. Processed fat from cattle, sheep and horses is called tallow. Both of these are solid at room temperature.

To estimate the amount of fat in a feed or food, a sample is extracted for a specified time with a solvent such as ether. In some cases, where total fat in a tissue is required, a system based on a mixture of chloroform/methanol is used. In the Weende system of feed analysis, the fat component is defined as the ether-extractable material. The weight of material extracted from a known amount of sample is used to calculate the percentage of the sample weight that is made up of 'fat'. However, not all ether-extractable material is fat as defined above, because other **lipid**-soluble materials are extracted by ether. Fats used as food or feeds come both from animals and plants. Animal products generally contain more

saturated fats while plant products contain more unsaturated fats. Fat is a significant source of food energy. The **gross energy** content of fat is 37.7–39.7 kJ g^{-1} (9.0–9.5 kcal g^{-1}), 2.5 times that of **glucose**.

Fats used for animal feeding are extracted either from animal carcasses, e.g. tallow, or from plant seeds, e.g. palm oil. **Beef** tallow is no longer used since the occurrence of BSE. **Coconut** oil and palm kernel oil are rich in **lauric acid** (C12:0) and are sometimes referred to as the lauric acid oils. Palm oil and tallow are composed mainly of palmitic (C16:0), stearic (C18:0) and oleic (C18:1) acids. The melting point of fats is determined mainly by the chain length of the fatty acids and their saturation. Fats with **short-chain fatty acid**s or **unsaturated fatty acid**s have lower melting points than those with long-chain saturated fatty acids. **Saponification** value is an indicator of the chain length of fatty acids in a fat or oil. High values indicate shorter chain lengths. **Iodine** value is an indicator of the degree of unsaturation of a fat or oil; high values are associated with a high proportion of unsaturated fatty acids. (NJB; JRS)

Fattening

The term fattening (or 'finishing') is used to describe the process of bringing animals to an appropriate stage of **body condition** prior to slaughter for meat consumption. As the animal grows towards maturity the parts of the musculature that provide the most desirable cuts of meat tend to be late developing and the subcutaneous and visceral fat deposits increase more rapidly. The

desired state of fatness (or 'cover') will vary with the culture and consumer demand. Furthermore, as the rate of protein deposition decreases and the rate of fat deposition increases, the **feed efficiency** declines to a point where it becomes uneconomic to grow the animal to a higher weight. In developed economies, where the consumption of **animal fat** is generally regarded as detrimental to health, there are usually grading systems in place with financial penalties for animals that are considered to be too fat. In the case of pigs, grading is usually based on one or more measurements of subcutaneous fat depth at specified points on the carcass. Systems for cattle and sheep relate to visual inspection of the extent and depth of subcutaneous fat cover on the carcass. With poultry there is little external fat and even the fat content of the meat tends to be low; the main source of fat is the abdominal fat pad, which is usually left in the eviscerated bird. (KJMcC)
See also: Carcass; Finishing; Meat composition; Meat production

Fatty acid composition (%) and physicochemical properties of common fats.

Lipid	Beef tallow	Lard	Coconut oil	Maize oil	Rapeseed oil	Palm oil
10:0			7			
12:0			47			
14:0	3	2	17			1
16:0	26	26	8	11	4	48

Lipid	Beef tallow	Lard	Coconut oil	Maize oil	Rapeseed oil	Palm oil
16:1	6	4				
18:0	17	14	4	2	2	4
18:1	43	43	5	24	56	38
18:2	4	10	2	58	20	9
Melting point (°C)	40–50	28–48	23–26			38–45
S/U ratio	0.85	0.72	13.29			1.13
Saponification value	190–200	193–200	251–264			196–202
Iodine value	32–47	46–66	7–10			48–56

S/U ratio = ratio of saturated to unsaturated fatty acids.

Fatty acid synthase

A multi-enzyme complex of seven enzyme activities responsible for the *de novo* synthesis of fatty acids in mammals, birds, fish and yeast. In bacteria, the individual enzymes of the fatty acid synthetase system are separate proteins. In biosynthesis of longer-chain fatty acids, two carbon units derived mainly from the **catabolism** of **glucose** and amino acids are added two by two

(i.e. via malonyl CoA to acetyl CoA) to make palmitate, which is a 16-carbon **saturated fatty acid**, $CH_3{\cdot}(CH_2)_{14}{\cdot}COO^-$. In ruminants the source of the two carbon units is **acetate** from fermentative digestion in the rumen. The major site of fatty acid biosynthesis depends on the animal. In humans and adult rats, it is in the **liver**; in young rats, liver and adipose; in pigs and ruminants, white **adipose tissue**; and in birds it is only in the liver. (NJB; GW)

Fatty acid synthesis

The process whereby fatty acids (for example, palmitate, $CH_3{\cdot}(CH_2)_{14}{\cdot}\ COO^-$) are synthesized, mostly from non-fat sources (**carbohydrate** and **amino acid**s). Synthesis of fat is a means whereby excess energy from a meal can be stored in the body for later use. The *de novo* synthesis of fatty acids occurs in the cytoplasm of **liver** or **adipocyte**s, depending on the species. Acetyl-CoA ($CH_3{\cdot}CO{\cdot}SCoA$), derived from carbohydrate or fat **catabolism** or from activation of **acetate** formed in intestinal **fermentation**, is the starting two-carbon unit for **long-chain fatty acid** biosynthesis. Another acetyl-CoA is converted to malonyl-CoA by acetyl-CoA **carboxylase**, $CH_3{\cdot}CO{\cdot}SCoA + CO_2 \rightarrow HOOC{\cdot}CH_2{\cdot}CO{\cdot}SCoA$, and added to the growing acyl-CoA chain as a three-carbon unit. After loss of CO_2 from the added malonyl-CoA a two-carbon unit has been added. To complete the process of adding a two-carbon unit to a growing fatty acid chain, two molecules of NADPH are used to reduce the unsaturated double bonds created in the biosynthetic process. The reducing equivalents

(i.e. NADPH) are produced in the catabolism of **glucose** in the **pentose** cycle. The overall stoichiometry of the reaction is: 1 acetyl-CoA + 7 malonyl-CoA + 14 NADPH + $14H^+ \rightarrow CH_3{\cdot}(CH_2)_{14}{\cdot}COOH + 7CO_2 + 6H_2O$ + 8 CoASH + 14 $NADP^+$. (NJB)

Key reference

Mayes, P.A. (2021) Biosynthesis of fatty acids. In: Kennelly, P.J., Botham, K.M., McGuinness, O., Rodwell, V.R. and Weil, P.A. (eds) *Harper's Biochemistry,* 32nd edn. Appleton and Lange, Stamford, Connecticut.

Fatty acids

Compounds of carbon, hydrogen and oxygen with a functional group, a carboxyl carbon, $CH_3{\cdot}(CH_2)_n{\cdot}COOH$. They are either saturated or unsaturated (see table 'Fatty acid composition (%) and physicochemical properties of common fats' in entry for 'Fats'). **Unsaturated fatty acid**s, which have at least one double bond, belong to one of three families. The 18-carbon n-9 (Δ^9) oleic family has at least one double bond between carbons 9 and 10. The 18-carbon n-6 ($\Delta^{9,12}$) linoleic family has at least two double bonds, one at 9–10 and one at 12–13. The 18-carbon n-3 ($\Delta^{9,12,15}$) linolenic family has at least three double bonds, one at 9–10, one at 12–13 and one at 15–16. When fatty acids are synthesized by an animal, the initial fatty acid unit may be either a two- or three-carbon fatty acid. When a two-carbon unit (**acetate**) is the starting unit, the fatty acids are even-chained because the fatty acid chain is elongated by two carbon units. If the starting unit is a three-carbon unit (**propionate**), the fatty acid will be an **odd-chain fatty acid**. All combinations of saturated, unsaturated, even- and odd-chain

fatty acids would be expected in nature.

A unique series of fatty acids is the **medium-chain fatty acid**s, C-6, C-7, C-8, C-9, C-10. In animal nutrition they play a important role in meeting the energy needs of newborn mammals. These fatty acids are usually located in the *sn*3 position of milk triglyceride. Fatty acids in this position are released by lingual **lipase** or pre-gastric esterase and are absorbed directly into the bloodstream, where they are transported as **free fatty acid**s. After being taken up by cells, these fatty acids do not require **carnitine** to be transported across the inner mitochondrial membrane to the matrix, their site of **catabolism**. Since their rate of **metabolism** is not controlled by transport, these fatty acids can be metabolized rapidly. In the mitochondrial matrix they are activated by one or more of the acyl-CoA synthases, which convert them to fatty acyl-CoA, which can be degraded to two carbon units of acetyl-CoA and used as a source of energy. Because these medium-chain fatty acids (as **triacylglycerol**s) can be taken up rapidly, they may be selected as a fuel when normal digestive processes have been compromised.

Long-chain fatty acids, with 30 or more carbons, are released from dietary triacylglycerols in the lumen of the intestine by pancreatic lipase. In the presence of **bile** salts they diffuse into the mucosal cells as free fatty acids and monoglycerides, where they are re-esterified into triglycerides (triacylglycerols) combined with cholesteryl esters, some **phospholipid** and protein. They are packaged into **chylomicron**s and delivered to the body via the lymphatic system. After being taken up by cells, the fatty acids are

activated by one or more of the acyl-CoA synthases in the cytoplasm to acyl-CoA. In the cytoplasm these long-chain fatty acids and the acyl-CoA derivative must be converted to acylcarnitine before they can be transported across the inner mitochondrial membrane by carnitine palmitoyltransferase. Once in the mitochondrial matrix, fatty acids are reconverted to fatty acyl-CoA, which can be degraded to two carbon units of acetyl-CoA and used as a source of energy for ATP production. (NJB)

Feather meal

A high-protein by-product from the marketing of meat birds and spent layers, obtained by hydrolysing, drying and grinding the feathers.

Feathers amount to about 3–7% weight of the live bird and contain about 80–90% **keratin**. This highly polymerized protein contains about 8% cysteine, a sulphur amino acid that makes strong disulphur bonds between each other within the primary structure and contributes to the folding of the chain into secondary structures. While this makes feathers light and durable, it also makes raw feather keratin undigestible. Steam **hydrolysis** under pressure for 30–45 min at a temperature of about 145°C renders the proteins soluble. This process disrupts the disulphide, **peptide**, and hydrogen bonds of the keratin protein, allowing the protein to become more readily digested. In addition, the process alleviates the risk of contamination with organisms such as *Salmonella*.

Feather meal is used mainly as a feed ingredient or fertilizer. Commercial batches for use in animal feeding are tested to ensure

that the product has been processed properly (**crude protein** (CP) at least 75% digestible using a **pepsin** digestibility assay). Composition depends on the type and age of fowl processed.

According to the European INRAE-CIRAD-AFZ feed tables, feather meal has the following average nutrient profile (as-fed basis, main nutrients): dry matter (DM) 92%, CP 78.9%, crude fibre 1.3%, crude fat 8.5%, ash 5.1%, neutral detergent fibre (NDF) 6.7%, acid detergent fibre (ADF) 5.1%, lysine 18 g kg^{-1}, methionine 5.5 g kg^{-1}, calcium (Ca) 11.7 g kg^{-1}, phosphorus (P) 7.7 g kg^{-1}, phytate phosphorus 0, net energy for lactation (NEL) 1940 kcal kg^{-1}, net energy for gain (NEG) 1840 kcal kg^{-1}, N degradability ruminants 34%, metabolizable energy (ME) pigs 3640 kcal kg^{-1}, ME poultry 2720 kcal kg^{-1}. This reference contains a more detailed nutritional profile.

The **protein quality** of feather meal is low because it is deficient in important amino acids for poultry and pigs, notably **lysine**, **methionine**, histidine and **tryptophan**. In addition the availability of the protein is only about 50%, although this feature is of benefit in dairy cattle feeding since the protein can be considered as a by-pass protein. Maximum dietary inclusion rates of feather meal are commonly 7% for beef cattle, 3% for lamb and 2.5% for ewe, goat and dairy cattle diets. The meal is of low **palatability** and must be introduced into the diet gradually.

Since 2001, feather meal (and other processed animal proteins such as meat meal) have been banned for animal feeding in the European Union and several other countries, following the outbreak of bovine spongiform encephalopathy (BSE). (RB)

Reference

INRAE-CIRAD-AFZ (2017–2021) Feather meal. Available at https://www.feedtables.com/content/feather-meal, accessed 9 September, 2022

Feather pecking

Pecking at and removal of the feathers of one bird, usually by another bird. Self-plucking is also known. A form of **cannibalism** in intensively housed poultry, which can lead to complete denudation of birds. Each feather removal by another bird is painful and defeathered birds are fearful and stress-susceptible. It occurs primarily due to birds being unable to forage naturally, therefore provision of a range of palatable forage materials can prevent the behaviour.



Chickens in battery cage that have been feather pecked. Photo courtesy of Animal RIghts Advocates Inc. Licensed under CC BY-NC-SA 2.0.

In the wild, junglefowl spend about 60% of their time foraging; laying hens fed a mash and given access to long straw on the floor spend 52% of their time and laying hens fed pellets and without access to straw spend just 29% of their time, less than half of that in the wild. Feather-pecking birds prefer high-fibre diets and they often eat the feathers, suggesting that a shortage of fibre in the diet is responsible for the condition. Feathers speed up the digestion in the same way that fibre does, and it is likely that there is an innate appetite for the fibre to stimulate digestion. **Supplementation** with a **roughage** source, such as **maize** or **barley–pea silage**, **oat** hulls or **carrot**s, reduces feather pecking. At the same time as increasing the fibre content, the energy content should be reduced. Birds fed pelleted diets are more likely to become feather peckers than those fed a mash diet. Scoring systems have been developed to quantify the loss of feathers and degree of cannibalism in poultry flocks. Feather pecking is often controlled by **beak** trimming, which is itself associated with both acute and chronic pain. (CJCP)

Feed

A source of nutrients for animals and an ingredient of diets. Feeds include grazed pasture, conserved forage crops, grains and seeds, crop residues and by-products. The word 'feed' usually refers to animal diets and the word 'food' to human diets. (JMW)

Feed additive:

see Additive, feed

Feed blocks

These are designed to provide supplementary **nitrogen**, **phosphorus** and other minerals, vitamins and medications in situations where animals graze pasture that is deficient in these nutrients, or where animals are at risk from **bloat** or other disorders. Feed blocks use either **salt** or **molasses** as a carrier, with other ingredients to provide the required nutrients or medications. Raw materials in feed blocks include cereal **grain**s, cereal **by-product**s, distillery by-products, molasses, salt, **urea** (in blocks for ruminants), di- and mono-di-**calcium phosphate** (or other phosphorus sources), other mineral sources and vitamins. Blocks may be medicated; for example, they may include anti-bloat agents. Feed blocks are usually made by grinding the raw materials, mixing with molasses or salt and compressing with a hydraulic press in a mould to form a dense block. Molasses blocks may also include calcium oxide or calcium carbonate: the exothermic reaction between these and the molasses sets the material into a hard block. The block must be hard enough to avoid excessive intakes but not so hard that animals, particularly those with less secure teeth, cannot access the supplement. The block should be resistant to rain and dew, and to heat.

Feed blocks are mainly used for animals grazing pasture that is deficient in nitrogen and/or phosphorus, and where there will be a positive and economic production response. Blocks vary in weight from 20 kg to 500 kg, and are fairly easy to transport and feed out. They are designed for relatively low daily intakes, for example 175 g per head for sheep or 500 g per head for cattle. They may also be

used to relieve the boredom of stalled animals such as pigs and horses. In addition, they have innovatively been used to administer medication to wild game birds, e.g. moorland grouse. (MG; GMcLD)

Further reading

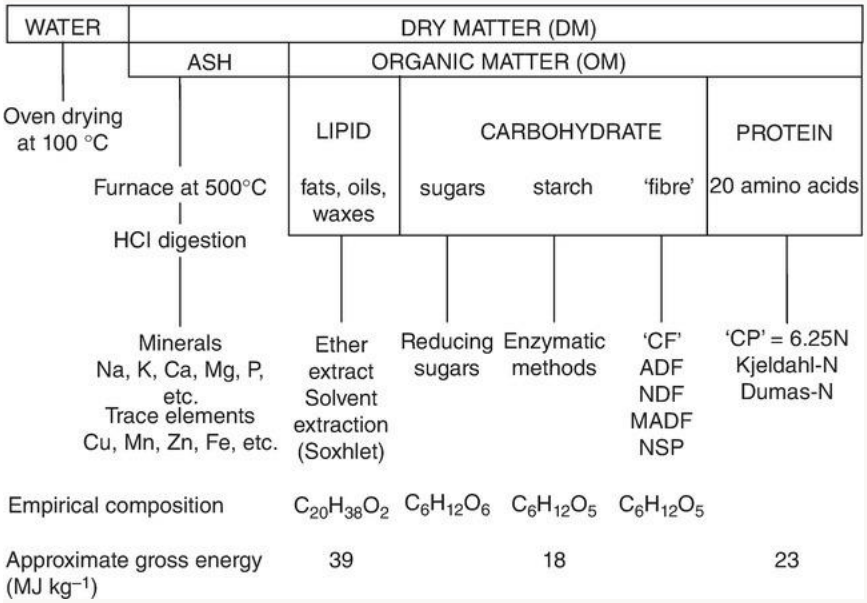
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Feed composition and analysis

Descriptions of the **chemical composition** of foods (and of plant and animal tissues) are largely based on the **proximate analysis** scheme introduced by Henneberg and Stohman at the Weende Institute in Germany in about 1840. In this scheme (see figure) food is considered to be composed of water and dry matter. The dry matter consists of an inorganic fraction (minerals and **trace element**s), represented practically as **ash**, and an **organic matter** fraction represented by the mass lost on combustion. The organic matter in turn is composed of three main classes of chemical compounds: **lipids**, **carbohydrates** and **proteins**, although **lignin**, **vitamins**, secondary substances (e.g. **tannins**, **gossypol**), etc. are also part of the organic matter.

The lipid consists of **fats**, **oils** and waxes, which are mainly long-hydrocarbon-chain **glycerol** triesters $(\text{-}CH_2\text{-})_n$. They are hydrophobic and insoluble in water but soluble in non-polar organic solvents. Total lipid can be determined by a percolating extraction with solvent in a Soxhlet extractor. Originally, diethyl ether was used and total lipid was therefore described as **ether extract** (EE). The lipid components can be further characterized

by determining individual **fatty acid**s from gas **chromatography** of their methyl esters (FAME-GC: fatty acid methyl esters) or by high-performance liquid chromatography (HPLC) of intact triglycerides.



The proximate analysis scheme for plant and animal tissues.

The protein content of foods can be estimated from the **nitrogen** content. Proteins contain, on average, 160 g N kg^{-1}; hence **crude protein** (CP) is defined as N × 1000/160, or N × 6.25, although other factors can be used, for example 6.38 for **milk** protein. Total nitrogen has traditionally been determined by the **Kjeldahl** procedure (1883) but the **Dumas method** is also used. Methods of estimating protein from nitrogen determination do not distinguish between protein and **non-protein nitrogen** (NPN). Amino acid composition can be determined on hydrolysates by ion exchange or HPLC methods.

The carbohydrate fraction of foods consists of soluble **sugars** (mainly **monosaccharide**s and disaccharides), **starch** and **non-starch polysaccharide**s (NSPs). NSPs are mainly the cell wall

polysaccharides – **cellulose**, **hemicellulose**s, pectins, **fructans** and β-**glucans** – but because some are water-soluble, NSP is not synonymous with 'fibre' (*see* Dietary fibre). The term 'fibre' is not well defined; it is used for a complex range of plant cell wall constituents that may or may not include lignin, which is not a carbohydrate but a complex aromatic polymer of phenylpropane subunits. Many methods for determining and characterizing fibre have been developed but they all have some inadequacies. Many either do not remove non-fibre components adequately or fail to recover completely material that is a part of the dietary fibre complex, and all methods are labour intensive and require considerable analytical expertise to obtain accurate or even reproducible results on a variety of samples.

In the **Weende** system the carbohydrate fraction was considered to consist of **crude fibre** and **nitrogen-free extract**s (mainly starch and simple sugars, but because it was estimated by difference rather than by chemical analysis, it also included vitamins, secondary substances, etc.). Crude fibre was determined by a sequential acid–alkali extraction, but the method did not isolate all of the cell wall **polysaccharide**s, and its composition varied between different foods – the acid–alkali extraction can remove up to 60% of the cellulose, 80% of hemicellulose, and a highly variable proportion of lignin. These inaccuracies led to the development of chemical methods that better identified the carbohydrate fraction of foods, especially the fibre content.

The detergent analyses (**acid detergent fibre** (ADF) and **neutral detergent fibre** (NDF)) were developed to better

characterize the fibrous cell wall constituents of plant foods fed to ruminants. The NDF procedure (Van Soest and Wine, 1967) is a gravimetric method that is widely applied to animal feeds. It was designed to recover plant cell wall material and does not recover storage or soluble fibre components, though a modification of the NDF method allows recovery of a soluble fibre fraction (Mongeau and Brassard, 1993). The NDF method measures all cellulose, variable amounts of the hemicelluloses and essentially no pectins or β-**glucans**. Enzymatic treatment with **amylase** is necessary to remove starch from the NDF residue (Robertson and Van Soest, 1981). Nitrogen also is incompletely removed by conventional NDF analysis. In the Association of Official Analytical Chemists (AOAC) method, a dry sample is defatted (if it contains more than 5% by weight of fat), treated with proteases and amylases, dried and weighed. Then one aliquot of the remaining fibre residue is ashed; Kjeldahl nitrogen is measured in the duplicate aliquot and converted to crude protein (× 6.25). The weights of ash and crude protein are subtracted from the residue weight to give total fibre. The AOAC method is not without potential error – firstly because starch is not always removed completely and secondly because, during the **ethanol** precipitation step, simple sugars co-precipitate with the fibre residue when they are present in high concentrations, such as in fruits or feeds containing sugar products. Both sources of error produce an inflated **dietary fibre** value. The most accurate method of measuring dietary fibre is to obtain a residue free from simple sugars and starch, acid-hydrolyse it with **sulphuric acid** to generate the constituent monosaccharides and

individually quantitate these, usually by either HPLC or GLC. Colorimetric quantitation of these mixtures of monosaccharides is not accurate, because the mixture contains essentially unknown amounts of different monosaccharides that absorb at different wavelengths. In starchy foods the Englyst non-starch polysaccharide (NSP) enzymatic procedure is more appropriate for non-ruminant animals and humans. Enzymatic or chromatographic methods can be used to measure individual monosaccharides, disaccharides and starch.

Major minerals (Na, K, Ca, Mg, P) and trace elements (Fe, Cu, Mn, Zn, Co, Mo, etc.) can be determined by flame emission spectroscopy (FES), atomic absorption spectroscopy (AAS), or inductively coupled plasma spectroscopy (ICP) conducted on **hydrochloric acid** solutions of the ash from feeds. Modern ICP spectrometers can measure as many as 26 elements simultaneously on one **ash** solution.

The **gross energy** (GE) value of foods is determined by combustion in an adiabatic **bomb calorimeter**. It may also be approximated from the lipid, nitrogen and carbohydrate determination, using average heats of combustion of those components. It will be appreciated that a full characterization of the **chemical composition** of a food is a lengthy, complex and costly procedure that can never be complete. Gross composition is 'operationally defined' and overlap between the classes of lipid, carbohydrate and protein (e.g. **glycolipid**s, **lipoprotein**s) means that measured constituents may not sum to 100% in any given food.

Because of the many costly analyses required to determine the composition of foods, a newer method of analysis, **near-infrared spectroscopy** (NIRS), attempts to characterize the composition of food from its spectral signature in the near-infrared. Instrumental methods of food analysis have now largely replaced extractive wet chemical methods for food analysis. (IM; JAM; GMcLD)

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Feed composition tables

Nutritionists require feed composition tables for research purposes, computerized diet formulation, the monitoring of variability in key nutrients in feed ingredients and to assist in making purchasing decisions. The data are also of value to crop scientists and to farm advisory personnel in making decisions on crop development, crop introductions and rotations. Two major up-to-date, on-line data sets of feed composition are available internationally.

The first is the Feed Composition Database produced and maintained by the National Animal Nutrition Program of the US Department of Agriculture, which supersedes the US–Canadian Tables of Feed Composition published previously by the US National Research Council in 1982. This database includes nutrient composition data for feedstuffs commonly fed to animal species. Currently 121 ingredients and 129 nutrients are represented in the database. Users are required to establish an account in order to access the data.

The second is the INRAE-CIRAD-AFZ set of feed tables produced by a European consortium comprising INRAE (the French National Institute for Agriculture, Food and Environment); CIRAD (the French Agricultural Research Centre for International

Development, an organization working for the sustainable development of tropical and Mediterranean regions) and AFZ (the French Association for Animal Production), supported by the EAAP (European Association of Animal Production) and the feed industry (Ajinomoto Animal Nutrition Europe). These tables update the tables of composition and nutritional values of feed materials published by INRA in 2002–2004, and provide chemical, nutritional and environmental data on feeds for ruminants, pigs, poultry, rabbits, horses and fish (salmonids). More than 200 feeds of plant and animal origin and 100 mineral sources are included. Separate feed composition values are available for organically produced feeds (e.g. Kyntäjä *et al*., 2014).

The nutrients listed in these databases include main constituents, as well as proteins and amino acids, carbohydrates, lipids, minerals, vitamins, digestibility, protein rumen degradability and metabolizable energy values. (CJCP; RB)

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Feed conversion:
see Efficiency of feed conversion (FCE); Feed conversion ratio (FCR)

Feed conversion ratio (FCR)
The ratio of the weight of feed eaten by an animal to the weight of its productive output. The productive output of a growing pig or calf is its weight gain; the productive output of a laying hen is the weight of eggs produced; and that of a dairy cow is the weight of milk produced. The cost of feed is the major cost in animal production and so the feed conversion ratio (FCR) has importance in describing the efficiency of an animal production system or enterprise.

Differences between animals affect the FCR on a standard feed. The proportion of nutrients required for body **maintenance** in relation to the amount then available for productive output can differ between species and strains, and between individuals within a strain. Higher FCRs result if a greater proportion of the nutrients is used for maintenance of body tissues and **metabolism**. Maintenance requirements are affected primarily by the body weight of the individual, the ambient **temperature** and the extent of physical activity. The composition of the productive output also

affects the FCR. Productive outputs with high water contents (e.g. lean meat) result in a lower FCR (water intake is not considered part of the **feed intake**). The energy density of **body fat** is greater than the energy density of lean tissue and so the **energy cost** of depositing 1 kg of body fat is greater than that of depositing 1 kg of body lean. Body weight gains that have a high proportion of fat thus result in higher FCRs.

Differences in the composition of the feed can affect the FCR of a given population of animals. FCRs decrease with increasing nutrient density. Nutrient density can differ between feeds because of the water content of the feed, the types of nutrients supplied in the feed (high-fat feeds are more energy dense) or the availability of the nutrients. Many practical feedstuffs contain high proportions of **non-starch polysaccharide**s (**dietary fibre**). These are largely unavailable to non-ruminants, especially poultry, and so increase the FCR of the feed. The availability of other nutrients, such as protein, may be reduced in practical feedstuffs and also give similar effects on FCR. The apparent FCR of a feed may also be increased if there is a large amount of feed wastage that results in feed being spilt on the floor and not being eaten.

Some people prefer to consider the ratio between feed intakes and productive output as an efficiency and so they express the relationship as a ratio of weight of productive output to weight of food intake. This is called feed conversion efficiency (FCE). (SPR; DB; CJCP)

See also: Efficiency of feed conversion; Feed:gain ratio

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Feed dispensers:
see **Automatic feeding**

Feed evaluation
The process of determining the nutritional value of a feed. Feed evaluation can be conducted in a number of different ways. Practical feeding trials remain the best way to investigate any given feed, providing information not only on **nutrient availability** but also on voluntary intake or **palatability** of a feed when fed to the animal species of interest at the relevant stage of development. In these *in vivo* feeding trials, nutrients are evaluated in terms of the proportion that is retained in the animal body or secreted as **milk**, and the proportion that is excreted in faeces, urine and, in some

cases, gas. Such trials are energy or mass balance trials in which all of the feed inputs and excretory outputs are measured over a trial period and the mass (or energy) not lost in excreta is divided by the input to give the **apparent digestibility**. The partitioning of **gross energy** fed to an animal is conceptualized as shown in Fig. 1. An example of an *in vivo* feeding trial might involve six animals in **metabolism** cages that allow total collection of excreta. After a 2-week preconditioning period the animals are fed at **maintenance** level for an 8-day period during which total feed input and the outputs of faeces and urine are measured according to a defined protocol. Some energy is also lost as **methane** and **hydrogen**: to measure these losses it is necessary to enclose the animal in a **respiration chamber** equipped with gas analysers. Energy lost as urine and methane in ruminants can often be assumed to be relatively constant for most practical purposes. Weighed pellets of dry feed and faeces are combusted in an adiabatic **bomb calorimeter**. The apparently **digestible energy** (DE) is obtained from the difference between feed energy input and faecal energy output. **Metabolizable energy** (ME) may be estimated from DE using assumed or measured values for energy lost as urine (UE) or methane (CH_4 E) in ruminants, or simply by assuming that ME = 0.81 DE. ME is the energy absorbed by the animal and available for metabolism (anabolism and **catabolism**). Some of the ME is lost as heat in the form of the **heat increment of feeding** (HI) and the remaining fraction is described as **net energy** (NE). Part of the net energy is used in maintenance, which merely serves to keep the animal alive with no change in body

mass, while the remainder of the net energy is used in production.

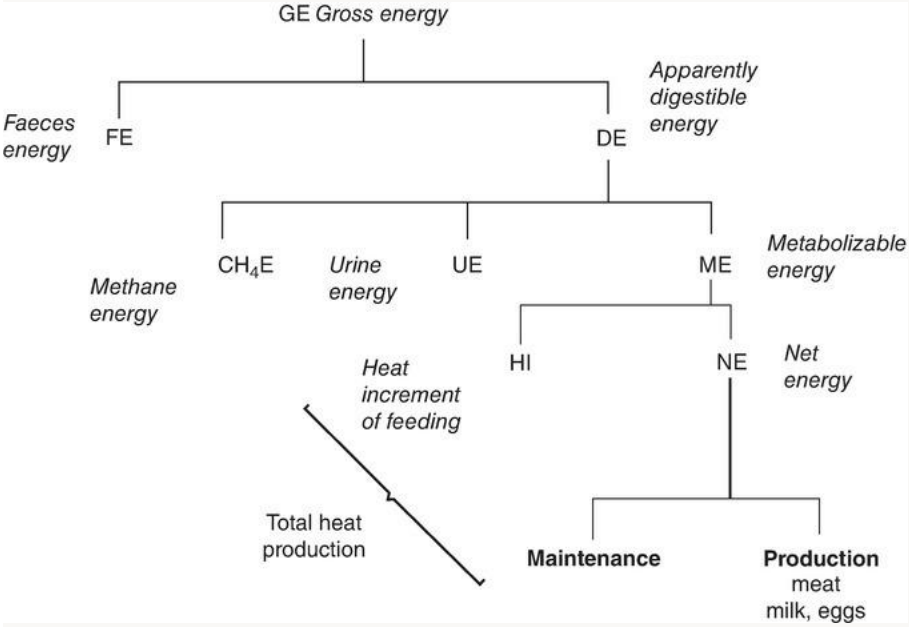


Fig. 1. Partitioning of food energy in animals.

By using indigestible **markers** it is possible to evaluate feeds *in vivo* without total faecal collection. For this, the feed includes a known concentration of an inert marker substance such as **chromium** trioxide (Cr_2O_3). The concentration of the marker in 'grab' samples of faeces is determined by chemical analysis and the **dry matter digestibility** (DMD) can be determined from:

DMD %=100–(100×concentration of marker in feed DMconcent

Similar marker methods have been devised using endogenous substances naturally present in forage feeds, such as acid-insoluble ash, or cuticle wax *n*-alkanes (Mayes *et al*., 1986). This method uses the ratio of naturally occurring odd-chain-length *n*-alkanes to dosed synthetic even-chain *n*-alkanes to estimate herbage intake and diet herbage composition.

So-called *in vitro* methods for the evaluation of feeds attempt to mimic digestion in the animal. These methods were devised mainly

for forage evaluation for ruminants using the two-stage rumen-**pepsin** digestion devised by Tilley and Terry (1963) and subsequent modifications including replacement of **rumen fluid** by **cellulase** from *Trichoderma viride* (Jones and Hayward, 1975), or liquor from homogenized sheep faeces.

A more recent development of the *in vitro* rumen technique involves the gasometric technique (Menke *et al*., 1979) in which a feed sample is digested in buffered rumen fluid in a 100 ml gas syringe. The rate of **gas production** vs. time gives a curve which can be interpreted to give the kinetics of degradation in a similar but more accessible way to the ***in sacco*** technique. The *in sacco*, or nylon bag technique, isolates a small aliquot of feed in a porous nylon bag which can be suspended in the rumen of an animal and removed at intervals to monitor the rate of digestion. Alternatively, nylon bags may be allowed to pass through the whole digestive tract to be recovered from excreta. The gasometric and nylon bag techniques permit study of the kinetics of degradation of cell wall material or protein by fitting equations to the observed degradation curve (Ørskov and McDonald, 1979). Both the rate and extent of digestion have a bearing on the nutritional value of feedstuffs, especially in ruminants. The degradation curve for a food (Fig. 2) shows that the soluble material is immediately lost from the nylon bag. This component is represented by **a** in the equation below. Initially the most readily degraded fraction is hydrolysed rapidly with rate decreasing with time until a plateau in the degradation curve is reached, where the curve becomes asymptotic, reaching the maximum extent of degradation represented by **a+b**. As the

degradation progresses the slope of the curve **c** decreases. Such curves can be described by an equation of the form:

$$p=a+b(1-e-ct)$$

where **p** is the per cent degradation at time **t**, and **a**, **b** and **c** are constants.

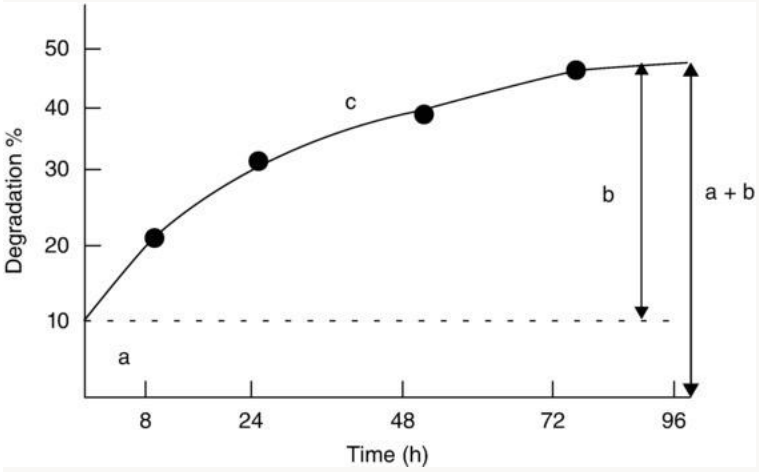


Fig. 2. Degradation of fibrous feeds derived from intra-ruminal **incubations**.

Laboratory methods of feed evaluation based on chemical analysis attempt to measure nutritional attributes and predict animal performance (*see* Feed composition table and analysis). Prediction equations that use laboratory chemical measurements as explanatory variables to predict animal performance have been devised for forages and compounded feeds. With the advent of computer-assisted near-infrared (NIR) reflectance spectroscopy (Norris *et al.*, 1976), the prediction of **chemical composition** and animal performance can be done rapidly using NIR. (IM)

See also: Digestibility measurement

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Feed formulation

Traditionally, **compound feed**s were manufactured using standard formulae that were tried, tested and seldom varied. These feeds provided an excellent ration for livestock, although the balance of nutrients supplied fluctuated with natural variations in the quality of ingredients. These formulae could not be easily changed to take account of changes in the market prices of raw materials or to make best economic use of the resources available.

In recent decades, the number of available raw materials has increased greatly. Given such a range of raw materials, there can potentially be thousands of combinations that will satisfy the **nutrient requirement**s defined in a feed specification. One of those combinations of raw materials will be the cheapest. The development of computing and particularly the introduction of **linear programming** allowed such least-cost solutions to diet formulation to be calculated. The first electromechanical machines, introduced in the 1950s, took up to an hour to calculate a single diet but today microcomputers can do the calculations in fractions of a second. Software can now provide least-cost solutions for raw material use and allocation not just for a single feed product but also across multiple products, manufacturing sites and periods of time.

To formulate an individual feed product the input data required are the price and nutrient values of each available ingredient, a product specification that defines the minimum and maximum concentrations of each nutrient and the minimum and maximum permitted inclusion of each available ingredient. The least-cost solution generated for a single feed product is dependent on the relative price and nutrient content of each available ingredient. It takes no account of the amounts of ingredients required to manufacture other feed products. However, it is not always possible to purchase enough of an ingredient to satisfy the demand created by a number of feed products that have been formulated independently of each other. Equally, an excess stock of an ingredient may have been purchased which it is necessary to use

up. In these situations, linear programming can optimize multiple specifications and allocate ingredients most economically. The additional data required to build this economic model are maximum levels of scarce ingredients, minimum levels of surplus ingredients and the amount of each product which is to be manufactured. In a similar way, linear programming can also be used to optimize the distribution of ingredients across multiple manufacturing sites and periods of time. Decisions can then be taken on when and where to buy, sell or use ingredients.

Linear programming is based on providing exact values for the input data. In practice, the nutrient contents of the feed ingredient are not known with certainty but are laboratory analytical mean values with standard deviations. Such values are stochastic rather than discrete. As a result the calculated nutrients in a formula are not known with certainty. Using average values, linear solutions will only meet nutrient requirements 50% of the time. When formulae need to be produced with a high probability of meeting nutrient levels, calculations must take into account the uncertainty in the nutrient content of each ingredient. For this purpose, stochastic formulation systems, using non-linear programming techniques, can be used. (AMo)

Feed:gain ratio

A measure of the efficiency of converting feed inputs into productive output. It is also called **feed conversion ratio** (FCR) In growing animals, it is the feed consumed per unit of body weight gain. It may also be used in other situations; for example, with laying hens, as feed consumed per unit of egg mass output; or in

milk production, as feed consumed per litre (or gallon) of milk produced. (SPR)
See also: Efficiency of feed conversion (FCE)

Feed grains The cereal **grains** used for feeding livestock. They include **wheat**, **maize**, **sorghum**, **millet**, **barley**, **oats**, **rye** and **triticale**. Livestock consume 6 billion tonnes of feed (dry matter) annually – including one-third of global cereal production from 40% of all arable land – of which 86% is made of materials that are currently not normally eaten by humans. Typically about 2.8 kg of human-edible feed are used to produce 1 kg of meat from ruminant animals, compared with 3.2 kg for meat from monogastric animals. (ED; DB; CJCP)

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Feed intake

In broad terms, feed consumption is the amount of food required to provide the nutrients to allow the animal to fulfil its genetic programme. When food availability is unlimited (i.e. more food is provided than is required), the amount of food eaten is referred to as **voluntary food intake**. When food availability is limited, as during routine quantitative food restriction, feed intake is usually equal to the ration provided, because animals are chronically hungry and eat it all.

In general terms, food is consumed voluntarily in that amount which most closely meets the animal's needs, i.e. supplies the nutrients that allow it to fulfil its genetic programme. There are several reasons why animals might eat more or less than would be predicted from a knowledge of their 'requirements'.

1. The 'requirements' specified by a particular feeding system might not be the same as the animal's needs. For example, a lactating cow's requirements for nutrients are conventionally calculated from the needs for maintenance and those for milk production; in fact the cow may be programmed to regain body reserves and/or to produce more milk than it is currently producing. In this case it will be driven to eat more than predicted from a 'knowledge of its requirements'.
2. There might be a physical restriction on intake, such as slow rate of eating or limited capacity for fibre in the stomach. For example, intakes of forages are likely to provide less nutrients than 'required' by either the feeding system in use or the animal's programme.
3. There might be metabolic imbalance. For example, if a food provides a lower ratio of protein to energy than required, the animal might increase its daily intake of that food in order to obtain sufficient protein. This would increase **energy intake** which, through various mechanisms, counteracts the drive to eat more food. Depending on the exact situation, nutrient imbalance can result in a higher (but usually lower) intake than predicted from **nutrient requirement**s.

4. The animal might be suffering from an infectious or metabolic illness. This might change its 'requirement' for nutrients. For example, parasitic infection might increase protein requirements, which would stimulate intake, but in practice food intake might be reduced due to abdominal discomfort. Fever usually reduces food intake, while **lameness** can restrict the extent to which the animal is prepared to walk when grazing. A good stock-person is very aware of a reduction in voluntary food intake as an early sign of disease.

In practice, voluntary food intake is best predicted from observations of food intake in similar situations to those of current interest. Typical intakes of the major types of farm animal are outlined in the following paragraphs.

Growing broiler chickens

Intake increases steadily from hatching, to reach a plateau of around 160 g dry matter (DM) per day at about 6 weeks, under thermoneutral conditions. A major limitation to intake is high **environmental temperature**, especially at high stocking densities with heavy birds.

Laying hens

Food intake varies according to energy density of the diet, environmental temperature, rate of egg laying and body weight, and is around 120 g DM per day under many commercial conditions. Changes in the **metabolizable energy** content of the food cause compensatory changes in voluntary intake, but such compensation is not complete, resulting in higher weight gain and, sometimes, higher egg production in hens given more energy-

dense foods.

Growing pigs

Before weaning, piglets are often given access to 'creep' feed. Their intake of this is not usually more than a few grams per day. After weaning it can be expected that voluntary intake will be such as to meet the animal's **energy requirement**s and therefore to be proportional to body weight and weight gain, and to be affected by the **digestible energy** concentration of the food. Under UK conditions the relationship between digestible **energy intake** (DEI, kJ per day) and body weight (LW) of growing pigs between 30 and 100 kg was found to be: $DEI = 4000\ LW^{0.5}$. Thus, a pig of 50 kg is predicted to eat 29.4 MJ per day or, for a typical diet containing 13 MJ DE kg^{-1} DM, 2.26 kg DM per day. However, this is a simplification, as intake is influenced by potential to grow and fatten, amongst many other factors. In particular, during the first few days after weaning, intakes of both food and water increase slowly and weight gain does not normally resume until up to a week after weaning.

Pigs, pregnant and lactating

Pregnant sows will voluntarily eat about 6 kg of a concentrate feed per day, which results in extreme fatness. This is normally prevented by feeding about 2.5 kg per day. During lactation, intake increases up to about day 17 but then declines. A typical intake at the peak is 7.5 kg per day but this is influenced by environmental temperature, litter size and diet quality.

Growing cattle

The voluntary food intake of ruminants fed indoors varies over a

wide range according to the quality of forage on offer (particularly its **particle size**, rate of digestion and **crude protein** content), the level (if any) of concentrate **supplementation**, and the genetic potential for **growth** and/or milk production. Under **grazing** conditions it is even more difficult to predict, complicated by effects of sward conditions, weather and social factors. Most of the equations for predicting the voluntary intake of food by ruminants are complex and outside the scope of this entry. A simple equation is: DMI (kg per day) = $0.172 \times LW^{0.61}$.

Lactating cows

The following simple equation has been widely used in the UK:

DMI=0.025 LW+0.1 MY

where LW is body weight (kg) and MY is milk yield (kg per day); for a cow weighing 650 kg and producing 30 kg milk per day, a total intake of 19.3 kg DM per day is predicted. However, forage intake is depressed by concentrate supplements and there is typically a reduction of 0.4 kg forage DM intake kg^{-1} concentrate DM allowance. In addition, intake usually increases more slowly than milk yield after calving, leading to loss of body weight. This is replaced later in lactation, when intake remains high as yield falls.

Sheep

Intake of growing lambs depends to a great extent on the quality of the food available, as well as on their potential to grow and fatten. As with other classes of ruminants, prediction of intake is difficult and equations can only be used in situations close to those in which the data were collected from which the equation was derived. A lamb of a fast-growing breed at the point of inflexion of its growth

curve would be likely to eat 2 kg DM per day of a pelleted food made from concentrates and **dried grass**.

During pregnancy, there is sometimes a slight increase in intake but often a marked decline in late pregnancy, especially in the last few days. A ewe of a hill breed weighing 50 kg might eat 1.5 kg forage DM per day, declining to 1.2 kg per week before lambing and to almost zero on the day of parturition. Intake increases in early lactation, reaching about 2.5 kg per day in the small hill ewe; suckling of twin lambs tends to increase the ewe's intake but also results in loss of more body reserves than in a similar ewe rearing a single lamb. (JMF)

See also: Voluntary intake

Feed mixing

Feed is mixed primarily in order to provide a homogeneous composition to ensure that animals receive the intended quantity of each constituent ingredient. Failure to mix ingredients accurately can have a number of detrimental effects. Firstly, **palatability** may be adversely affected if one or more ingredients has a strong **taint** that would be masked if it was correctly mixed. This would almost definitely lead to large quantities of feed being rejected, which is not only wasteful but will also affect the animal's performance. Secondly, if the animal's intake of micro-minerals, vitamins and medication is variable due to inconsistent mixing, deficiency or toxicity symptoms may arise. Lastly, feed that is to undergo pellet pressing will have variable physical quality characteristics unless the raw materials are equally dispersed. Raw materials that have little or no **starch** and are not very pliable (e.g. mineral

supplements) are difficult to press into a pellet capable of withstanding further handling and storage. A well-compounded mixed meal will bind these materials, forming a hard pellet, as opposed to a poorly mixed meal in which some material will not bind, resulting in a high and unacceptable proportion of dust.

Mixing is generally achieved with a mechanical mixer. Mixers fall into a number of different types, either horizontal or vertical, and mix a constant mass of material for a specific period of time. Vertical mixers have a central, vertical auger inside a cylinder. Material is taken from the bottom of the cylinder, transported up the centre of the drum inside the screw conveyor and dropped on the top. Horizontal mixers either rely on a spinning drum with internal bars to retain material, similar to a domestic washing machine, or use a rotating ribbon inside a fixed hopper. The ribbon is usually in the form of a double helix. Mixing times depend on the material being mixed and the equipment used but are generally between 30 s and 300 s. A third mixer design is based on a chain and flight conveyor mounted at an angle of approximately 45°. Material is continuously fed into the bottom of a hopper and carried very slowly to the top, where it is then dropped back down to the bottom, mixed material being taken away from the top. (MG)

See also: Compound feed; Pelleted feed; Quality control in feed mills

Feed preferences:

see Choice feeding

Feed roots:
see Carrot; Cassava; Fodder beet; Jerusalem artichoke; Potato; Sugarbeet; Swede; Sweet potato; Turnip; Yam

Feed selection
There are many situations in which animals show a preference for certain feeds, or feed constituents. **Grazing** animals may select particular pasture species and reject others; they may also avoid **forage** that is contaminated. **Browsing** animals may select leafy material. Stall-fed animals may reject hard stemmy material in **hay** and most animals reject mouldy feed. Poultry given mixed rations may select certain parts over others. Animals given a free choice between alternative feeds may select a mixture that reflects their nutritional needs. (MFF)
See also: Choice feeding

Feed supplements:
see Supplement

Feed trough
A trough, by definition, is a narrow, open container in which food or water for animals may be placed. With cattle and sheep, a feed trough can be a large wooden or metal construction, usually of U- or V-shaped profile, on legs, which is kept permanently outside and is filled manually. In the case of pigs, the trough is usually sited at a low level along one wall of the housing. As it needs to be very robust, it is often built in and lined with half-round glazed pipe. It can be filled manually, or mechanically by an auger or automated

liquid feeding system. A variety of designs have been developed, such as single-space hoppers, wet-and-dry feeders (in which a nipple **drinker** is incorporated) or multi-space feeders where several animals can feed simultaneously. The most sophisticated systems are those used for cattle or pigs in which each animal carries an electronic tag that opens a gate to permit only one animal access to the trough. Trough feeding is less common today with poultry farmers than in the past, due to the need for greater automation and to avoid feed wastage. However, it is still used with adult birds such as breeding stock, or with extensively housed laying hens. Older mechanical systems used a chain to drag the feed from a large hopper at one end of the house along a continuous trough that ran all through the house. This was adequate for birds fed *ad libitum*, but not for restricted-feeding systems for breeders. This problem has been overcome by the use of an auger in the bottom of the trough to give high-speed feed distribution. (KF)

Feedback inhibition

The inhibition of the activity of an enzyme early in a metabolic pathway by the end-product of the pathway. This is in contrast to product inhibition, in which the accumulation of a product inhibits its own production. (NJB)

Feeding behaviour

Most animals are not born with an innate ability to recognize food (apart from a young mammal's innate knowledge of where to seek milk) but have to learn this through experience. Parents, usually

mothers, guide the food choice of their offspring and young animals stay close to their mothers for the first days and weeks of life. In the absence of a mentor, the young have to learn from post-ingestion consequences which items that are swallowed provide positive feedback and which ones do not. For example, in the absence of their mothers, it took 3–4 days for chicks to learn to distinguish mash food from sand. In commercial conditions, the positioning of food, drinkers, lighting and heating in the first 2–3 days after hatching or weaning is intended to stimulate eating. Even so, observed variation in growth rate between individual animals in the first days and weeks of life may well reflect variation in development of feeding behaviour.

Feeding behaviour can be monitored by eye but it is very time-consuming to collect comprehensive data. Time-lapse video recording is useful but still requires time to analyse the recordings. Automation of meal monitoring is possible by fitting a transponder to each animal's collar or ear tag, to be detected when the animal puts its head into the feeder. If the weight of the feed container is also monitored by the computer connected to the identity system, comprehensive data on meal timing and weight can be collected.

It must be emphasized that food-directed activity (e.g. duration of feeding) and weight of food consumed at a meal are not always closely correlated, i.e. food intake cannot be predicted directly from time spent eating. This is because feeding efficiency (g food eaten min^{-1} feeding) varies greatly, not only with different food **particle size**s but also between individuals, genetic lines, times of day, environments and even within meals. For example, animals in

individual pens spend much more time eating than those in groups, because individuals spend more time playing with food without eating it, whereas those in groups have more distractions; both may eat the same amount of food per day. A possible explanation is that eating per se may be separately reinforcing from food ingestion and that, depending on environmental constraints, feeding is sometimes expressed in apparently inappropriate ways in response to a specific deficit in reinforcement. Another environmental influence on feeding is social facilitation (mutual stimulation of behaviour in groups of animals), which has been shown to act more on food-directed activity than food consumption.

Information about processes underlying short- and longer-term control of feeding can be obtained by studying ways in which feeding activity and/or food intake vary from minute to minute, hour to hour and day to day.

Minute-to-minute variation (meal eating)

Animals with free access to food generally concentrate their feeding in discrete meals, which can be defined by identifying a criterion for distinguishing interruptions within meals from inter-meal intervals. Frequencies of different-length gaps in feeding are usually distributed in a bimodal way, with many short pauses within meals and many long gaps between meals, with relatively few inter-meal intervals of intermediate length; the inter-meal interval at the nadir of this frequency distribution is used to define the critical inter-meal interval. By calculating correlation coefficients between the size of meals and either succeeding (post-prandial) or preceding (pre-prandial) adjacent intervals, clues can

be obtained about degrees of control that **hunger** and **satiety** mechanisms have over initiation and termination of meals. Both types of correlation are weak in farm animals, consistent with the randomness in spontaneous meal occurrence.

However, when meal sizes are manipulated artificially there can be close relationships, verifying the existence of short-term hunger and satiety mechanisms. Because such mechanisms appear to have only loose control over meal eating, it seems appropriate to think in terms of degrees of hunger and satiety, rather than 'set points', determining probabilities of feeding starting and stopping.

Although meal and interval lengths are usually distributed exponentially within animals, mean meal-eating variables tend to be distributed normally between animals. Thus, in any population, some habitually eat many small meals while others consume the same amount per day in fewer larger ones. Furthermore, short- and longer-term regulation of food intake can be considered in terms of adjustments in mean meal size, **meal frequency**, or both.

Hour-to-hour variation (diurnal rhythms)

There is usually a diurnal rhythm of feeding. Most domesticated species of mammal take more frequent and larger meals during the day than at night. In both birds and mammals there is more intensive feeding after dawn, as a result of hunger due to lower intake at night, and before dusk, in anticipation of a period of low intake. While chickens do not normally eat in the absence of **light** they will do so if the dark period is very long. In continuous light, domestic animals show periodicity in food intake if there are

regular phase-setting stimuli for them to cue into, or if they have been kept previously on a cycle of light and dark. There is evidence that regulation of feeding behaviour from hour to hour depends more on changes in meal frequency than in mean meal size.

Longer-term variation

Generally, longer-term adjustments in feeding behaviour and food intake, over days or weeks, depend more on changes in mean meal size than in meal frequency. Such adjustments may be in response to changes in diet or physiological requirement. Changes in mean meal size are usually gradual, and may be associated with gradual changes in capacity of the part(s) of the alimentary tract where meal eating is controlled (*see* Voluntary food intake).

There is surprisingly large variation in the weight of food eaten on consecutive days by individual animals. Over a period of several days the highest intake can be as much as double the lowest intake. As progressively more days are averaged a plateau in variability is reached, at about 3 days in chickens, 4 days in lactating cows, and 6 days in growing cattle. This suggests that the control of intake is on a time scale of several days rather than meal-by-meal, or even day-by-day. (JMF; JSav)

Feeding standards

Recommendations, published mostly by expert committees, that describe acceptable nutrient contents of diets to be fed to different types and species of animals. The recommendations are guidelines for good practice and do not necessarily describe the most economically or biologically efficient nutrient composition of a diet for a particular animal or population of animals. (SPR)

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Feeding stimulants:

see Palatability enhancers

Feedlot

An enclosed area on a farm or ranch where livestock, especially **beef cattle**, are fed intensively prior to slaughter for meat. In hot climates the areas may be partially roofed to provide shade. Systems of mechanical feeding are generally employed. The high density of cattle on a dirt substrate can lead to respiratory problems, unless mitigating action, such as dampening the substrate regularly, is taken. It can also lead to behaviour problems, such as excessive riding and penis damage in males. Other behaviour problems, such as **tongue rolling** (tonguing), are associated with a high **grain** diet and insufficient fibre consumption. (AJFR; CJCP)



Feeding cattle in a feedlot in the USA. Photo courtesy of Loco Steve. Licensed under CC BY 2.0.

See also: Beef cattle production systems

Fermentation

The decomposition of organic substances by microorganisms, including the conversion of **carbohydrates** to alcohol by **yeasts** and to **organic acid**s by (mainly) bacteria. Anaerobic fermentation occurs in the digestive tract of animals and in the preservation of crops by ensilage. Essentially, dietary carbohydrates, proteins and some **fats** are reduced to **short-chain fatty acid**s with the production of **carbon dioxide**, **methane** and ATP. The short-chain fatty acids produced in the digestive tract are principally acetic, propionic and butyric acids, though occasionally **lactic acid** is also produced. The main **fermentation product** in **silage** is lactic acid.

The most important fermentation in the digestive tract of ruminants occurs in the **rumen** and **reticulum**, which account

for more than half the total volume of the digestive tract. In other animals, fermentation occurs mainly in the **large intestine**. This is of significance in all species, but especially in **herbivore**s such as the rabbit and the horse. The ruminant has a considerable advantage over other herbivores because it has effectively two separate **digestion** processes and two sites of **absorption** of the end-products of digestion – through the wall of the rumen, and through the wall of the large intestine.

The fermentation of plant cell walls is very important in the nutrition of herbivorous vertebrates, because the animals themselves do not produce enzymes capable of breaking down **cellulose** and **hemicellulose**, which are the main components of most plant cell walls. The end-products of fermentation in the rumen account for about 75% of the energy supply to the ruminant animal.

The most important bacteria involved in these fermentations are the cell-wall digesting or **cellulolytic** microorganisms. The concentration of bacteria in the parts of the digestive tract where fermentations occur is usually very high. For example, **rumen fluid** has about 10^{10} to 10^{11} bacteria ml^{-1}, most of which are attached to particles of food. The predominant species of bacterium varies with the type of fermentation, which depends on the principal **substrates** in the diet. Thus the major species of bacteria in the rumen of animals given a diet of **grass** are those that digest cellulose and hemicellulose, such as *Ruminococcus albus*, *R. flavefasciens* and *Bacteriodes succinogenes*. Other species, such as *Streptococcus bovis*, ferment **starch** to acetic acid

and **ethanol**. This species, along with other *Streptococcus* spp., can produce lactic acid and is more tolerant of acid conditions than other species of rumen bacteria. Acidosis can occur if the diet of the animal is changed abruptly from cellulose to starch or **sucrose**. The population of bacteria in the rumen changes from cellulolytic to amylolytic as the pH falls. Lactic acid accumulates and accelerates the fall in pH. Even a small fall in the pH of the rumen from pH 7 to pH 6 is reflected in a reduction in cellulose digestion and a change in the population of the bacteria towards the more acid-tolerant species.

Proteins are degraded to a varying extent during the fermentation to their constituent amino acids. Some amino acids are used directly by bacteria and protozoa, but most are used as a source of energy and are broken down further to **ammonia** and **volatile fatty acid**s. Ammonia is used as a substrate for the production of **microbial protein**, with the excess being absorbed into the animal's portal **blood** and converted to **urea** in the **liver**. The extent to which proteins are degraded during the fermentation in the rumen depends on their **solubility**, which is generally relatively high except in feeds that have been subjected to **heat treatment** during processing. Thus the degradation of protein in fish meal is only about 0.4, compared with 0.9 for fresh herbage. **Protein degradation** also depends on the time the material spends in the rumen, and is lower for diets that pass rapidly through the rumen (concentrates and feeds of small **particle size**) than for long forages, which are digested slowly.

Protozoa and fungi are also involved in fermentations in the

digestive tract of animals. These organisms can digest cellulose, starch, sugars and fats to produce acetic acid, butyric acid, lactic acid, hydrogen and carbon dioxide.

The predominance of the weak acids (acetic, propionic and butyric) in the end-products of fermentation in the digestive tract highlights the importance of buffering agents to maintain the pH of the environment close to neutrality. **Saliva**, containing **sodium** and **potassium bicarbonate** and **urea**, is the most important buffering agent in the rumen, and the amount of saliva produced during eating and **rumination** is therefore crucial to the neutralization of the fermentation acids in the rumen. Long fibre is often included as a **supplement** to diets high in concentrates to stimulate **chewing** and rumination. The constant flow of saliva into and the outflow of **digesta** from the rumen, as well as the absorption of digested nutrients into the portal **blood**, ensure that in most nutritional circumstances the environment for fermentation remains relatively constant. However, digestive disorders can arise to disrupt the equilibrium. Toxins, produced by undesirable bacteria and from moulds present in foods, can damage the sensitive lining of the wall of the rumen and intestines and reduce the absorption of nutrients. Parasitic infections can also interfere with both fermentation and the absorption of nutrients. Sudden changes in diet can change the microbial population and result in the production of lactic acid in the rumen, with a consequent reduction in **rumen pH**. If the pH of the rumen falls below pH 5 and remains low, there is a risk of rumen stasis that can result in **bloat**, because the animal can no longer eructate the gases

produced by the fermentation.

Methane loss from the rumen is estimated to account for about 8% of the total **gross energy** eaten. Methane is also produced by fermentation in the **large intestine**, as well as some hydrogen. **Methanogenesis** can be reduced by **ionophore**s and by changing the pattern of fermentation to increase the proportion of **propionate** and reduce the proportion of **acetate**. Reduced total **gas production** is desirable in hindgut-fermenting animals, such as the horse, because excessive gas production is associated with digestive disorders, including **colic**. Fermentation rate can be reduced by including in the diet a source of slowly digested or indigestible fibre, such as hay or straw. (JMW)
See also: Rumen digestion

Fermentation products
The end-products of fermentation by bacteria, protozoa and yeasts. Fermentations occur in the production of alcohol, in making **silage**, in the rumen of ruminant livestock, and in the **large intestine** of most animals. The major fermentation product in silage is **lactic acid**, which is produced from the fermentation of **fructans** and **glucose** by lactic acid bacteria that either are present in the crop at harvest or are added in an inoculant additive (*see* Preservative). Other fermentation products in silage include acetic acid, **propionic acid**, butyric acid, **ammonia** and **amine**s. The concentration of individual fermentation products in silage reflects both the extent and the pattern of fermentation in the silo. The extent of fermentation is determined mainly by the

concentration of moisture in the crop at the time of ensiling. The wetter the crop, the greater is the amount of fermentation. The pattern of fermentation is determined by the concentration of fermentable **carbohydrate** in the crop and the buffering capacity of the crop. The lower the amount of fermentable carbohydrate and the higher the buffering capacity, the greater is the likelihood of an unstable fermentation, with the production of mixed fermentation acids and degradation of **amino acid**s to amines and ammonia. The extent of fermentation can be reduced by **wilting** to remove water before the crop is harvested. The pattern of fermentation can be controlled by the use of preservatives, such as **formic acid**, and inoculants designed to accelerate the production of lactic acid in the early stages of the fermentation in the silo.

The major products of fermentation in the rumen and large intestine are acetic acid, propionic acid, butyric acid and ammonia. (JMW)

See also: Acetate; Butyrate; Fermentation; Rumen digestion

Ferredoxin

A family of low-molecular-weight soluble proteins involved in electron transfer (**oxidation**/reduction) reactions. These highly evolutionarily conserved proteins are found in bacterial, plant and animal cells. Ferredoxins are **iron–sulphur** (Fe–S) proteins that function in photosynthesis and other reactions in bacteria, plants and animals. Fe–S proteins contain iron and acid labile (released) sulphide, which together act as the co-factor for the protein. Ferredoxins are involved in the formation of Fe–S proteins in mitochondria, where they donate electrons involved in formation

of Fe–S clusters. (RSE)

Ferritin
Iron-storage protein of animals and plants. Ferritin-like proteins are also found in bacteria. In animals it has been found in all tissues examined. Ferritin stores **iron** in a relatively safe and metabolically available form and also serves to sequester iron, reducing its toxic effects. Ferritin has 24 protein subunits of two types, H (heavy) and L (light), that form a hollow sphere with channels in its wall. The ferritin macromolecule can store up to 4500 iron atoms but is usually found with 2000–2500 iron atoms *in vivo*. Liver and spleen contain the highest amounts of ferritin and serve as an important reserve of iron for red cell formation when dietary intake is insufficient. An iron-poor serum form of ferritin can be a useful indicator of body iron stores and its abundance is directly related to body iron stores in many situations in humans. Serum ferritin is artificially elevated in inflammatory situations and is not a good indicator of iron stores in this case. (RSE)
See also: Haemosiderin

Fertility
The ability to produce offspring. In the male, this signifies the ability to produce a sufficient quantity of normal, fertile semen, to be physically capable of depositing it in a natural or artificial vagina and to possess sufficient libido to be willing and able to do so. In the female, fertility depends on the efficient functioning of a series of processes: (i) the ovulation of viable ova; (ii) the efficient

transport of the ova to the site of fertilization in the oviduct; (iii) the display of oestrous behaviour at the appropriate time; (iv) efficient sperm transport and fertilization of the ova; (v) timely transport of the fertilized ova to the uterus; (vi) implantation; and (vii) carrying the products of conception to the point of birth of one or more live young. All of these processes can be affected by extremes or imbalances of nutrition.

In males and females, the reproductive processes are controlled by the secretion of **gonadotrophin**-releasing hormone from the **hypothalamus**, which in turn controls the release of **luteinizing hormone** and follicle-stimulating hormone from the anterior pituitary. Severe underfeeding interferes with this control mechanism. In males, prolonged underfeeding with a sub-maintenance ration will eventually give rise to some reduction in fertility as a result of decreased output of spermatozoa or accessory secretions. Libido is also likely to be adversely affected by chronic **starvation**. In females, continued underfeeding suppresses ovarian function. This is a particular problem in high-yielding post-partum dairy cows. Negative **energy balance** leading to loss of condition can cause a considerable delay to the resumption of ovarian cycles or, less commonly, a cessation of cycles. Underfed females are less likely to display oestrus, even if they are cycling regularly. Acute energy deficiency has been shown to cause embryo mortality in farm animals. Underfeeding of young males and females can delay the onset of **puberty**.

Overfeeding can also cause reproductive problems. Obese males are less inclined to mount oestrous females and are more likely to

cause injury to them if they do. Overweight females are likely to have difficulty in giving birth. This can lead to damage to the reproductive tract and subsequent infection and infertility. In ruminant animals, **obesity** can restrict the intake of feed when energy demands are at their highest. This can lead to rapid mobilization of body reserves with consequent metabolic disfunctions such as pregnancy toxaemia in sheep or **ketosis** in high-yielding dairy cows.

Nutritional imbalances can also cause infertility. Specific deficiencies of vitamins and minerals have frequently been blamed for fertility problems, although in many experiments their effects have been confounded with those of inadequate **energy intake**. Protein insufficiency can cause infertility but, in cows at least, there is also evidence that high concentrations of **crude protein** can cause infertility. A variety of factors, including **nitrate** or **ammonia** toxicity in the reproductive tract, a depression of **carbohydrate** content of the grass and nitrate effects on rumen microflora, have been blamed for poor fertility when cows are turned out to spring grass heavily fertilized with **nitrogen**. (PJHB)

Fertilizers for animal nutrition

Fertilizers are primarily administered to crops, including forages for animals, to enhance plant growth rate. Plant growth is limited by the supply of nutrients, although temperature and water may have over-riding effects. By supplying just one limiting nutrient, often **nitrogen**, but also **potassium**, **phosphorus** and a range of **trace element**s, the plant composition is affected, which may

impact animal production. For example, supplying potassium annually to grass pasture limits the plants' uptake of **sodium**, which may potentially create a deficiency in the consuming animal. Furthermore, potassium in the rumen of herbivores such as cattle and sheep can restrict the uptake of **magnesium**, to cause a magnesium deficiency known as grass staggers. The solution is to use fertilizers containing sodium, and a major portion of the action of potassium in the plant can be replaced by sodium. Fertilizers can also be used to enhance the content of **micronutrient**s in crops used in products for direct human consumption; for example, selenate or **macronutrient** fertilizers fortified with **selenium** applied to **wheat** crops can biofortify **bakery product**s and thereby enhance selenium intake of human consumers. (CJCP)

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Fetal growth

The growth of the conceptus in the uterus from the end of differentiation until the time of birth. Each cell of the early embryo, formed by mitotic division after fertilization, is capable of forming any of the body tissues. Over the next few days or weeks, the cells differentiate, becoming specialized so that in future development

they can only form specific tissues and organs. Once this process is complete and the rudimentary organs are formed, the embryonic phase gives way to the fetal phase. Thereafter, fetal growth in all viviparous animals is exponential, the rate increasing as pregnancy progresses. The size and weight of the fetus, and thus its requirements for energy, protein and minerals, increase rapidly, especially during the last third of gestation. As the fetus grows, its associated placenta increases greatly in size and the uterus also enlarges to many times its non-gravid weight and size in order to accommodate the physical bulk of the fetus and placenta and to provide the large surface area necessary for nutrient and waste exchange between the fetal and maternal circulatory systems.

The mother's own **maintenance** requirements also increase during pregnancy, so that her overall requirements increase by more than simply the nutrients required for deposition in the uterus. Furthermore, the uptake of nutrients by the fetus and placenta is less efficient than that of the mother's body, further increasing requirements. The fetus takes precedence over its mother for most nutrients and, once the pregnancy is firmly established (at about 60 days in cows and 40 days in sheep), it is able to maintain higher **sugar** levels than in the maternal bloodstream and generally does not suffer from underfeeding of the mother unless this is chronic or severe. On the other hand, feeding the mother at levels above maintenance requirements, especially in late lactation, can increase the **birth weight** of the young.

Severe long-term underfeeding of the mother in earlier

pregnancy may result in the death of one or more fetuses. In later pregnancy, severe **malnutrition** may result in the death of the young *in utero* or to reduced birth weights and reduced viability. There may also be congenital abnormalities, particularly as a result of specific nutritional deficiencies. Non-ruminants, such as pigs, have specific amino acid requirements for the development of the fetus. (PJHB)

Fibre:
see Dietary fibre

Fibrin
The single protein monomer resulting from the blood clotting process whereby the soluble plasma protein **fibrinogen** is converted into fibrin by the action of the plasma protease thrombin. The released fibrin monomers polymerize, cross-link and form an insoluble clot. (NJB)

Fibrinogen
A soluble plasma protein that is cleaved by the protease thrombin to produce a single molecule of **fibrin** which polymerizes with other fibrin molecules to become a clot. (NJB)

Fig
A member of the genus *Ficus* of the Moraceae (**mulberry** family). The common fig (*Ficus carica*) is grown for its valuable fruit. The seeds have laxative properties that limit the inclusion of fig seeds in animal diets. The leaves of the fig can be fed to cattle when harvested directly following fruiting and before the onset of

senescence (see table). (JKM)

Typical composition of figs and fig leaves (g kg^{-1} dry matter).

	Dry matter (g kg^{-1})	**Crude protein**	**Crude fibre**	**Ether extract**	**Starch and sugar**	**Ash**
Fresh figs	120	13	22	2	6	–
Fresh leaves	340–350	140–145	170–175	55–60	–	160–170

Finishing
The process of bringing **meat** animals to a desired state of **body condition** prior to slaughter. For cattle this may be a period of some months. Non-ruminants are usually given a diet of lower protein content than that required for the earlier grower period. Normally for broilers, finishing represents the last one-third of life and is the time when the vast majority of the feed (often known as finisher feed) is consumed. For pigs the period from around 40 kg to slaughter is generally known as the finishing period. (KF)
See also: Fattening

Fish
In the general vernacular, a fish can be almost any exclusively aquatic vertebrate or invertebrate (e.g. '**shellfish**', 'finfish' and 'jellyfish'). Scientifically, the word is restricted to aquatic, cold-

blooded, water-breathing, craniate vertebrates and includes three major groups: (i) the Agnatha (primitive jawless fish, for example lampreys and hagfish); (ii) the Chondrichthyes morphs (jawed fish with cartilaginous skeletons, for example sharks, rays, rat-fishes); and (iii) the Teleostomi (jawed fish with bony skeletons, for example **catfish**, **trout**, bass, perch, salmon). This group contains by far the greatest diversity of living fish.

There are about 28,000 species of living fish, which accounts for slightly more than half the total number of living vertebrate species. There are 482 fish families with known living species, of which eight families comprise one-third of all species. These are, in descending order: the Cyprinidae (minnows and carps); Gobiidae (gobies); Cichlidae (cichlids, such as **tilapia**); Characidae (such as the tetras of the aquarium fish trade); Loricariidae (armoured catfish); Labridae (wrasses, such as the 'cleaning wrasses'); Balitoridae (river loaches); and Serranidae (sea basses).

At least eight orders of ray-finned fish contain species that have received some attention for commercial culture as food, and the number is considerably greater if fish cultured for the pet trade are included. These include: Acipenseriformes (**sturgeon**s); Anguilliformes (freshwater **eels**); Perciformes (perches, sea basses, cichlids, etc); Salmoniformes (salmon, trout, whitefish); Gadiformes (cods); Pleuronectiformes (**flatfish**); Siluriformes (catfish); and Gonorhynchiformes (**milkfish**). (RHP)

Fish culture:
see Aquaculture

Fish farming:
see Aquaculture

Fish feeding
On the basis of their feeding habits, fish are broadly classified as herbivores, omnivores or carnivores. Feeding habits are also associated with particular body forms and functional morphologies of skull, jaws and alimentary tract. **Herbivores** do not have teeth but instead possess fine gill rakers that sieve **phytoplankton** from water. They also lack a true stomach. **Carnivores** have well-developed teeth and possess stomachs and a shorter intestine. The alimentary system of omnivores is intermediate in form between herbivores and carnivores. Many herbivores lack the ability to ingest and digest materials other than plants and they consume large quantities of food and extract nutrients in their elongated guts (e.g. **grass carp**). Carnivores have a specialized gut which is related to the size of their prey, being larger in those that consume small aquatic animals.

Feeds and feeding of fish depend upon the type of farming system used: extensive, semi-intensive, or intensive. In the first two systems, fish derive all or a substantial part of their nutrients from natural food organisms in culture ponds. Fish and **shrimp** maintained in intensive fish culture systems (tanks, raceways and cages) are totally dependent on the provision of nutritionally complete diets produced in either a dry or a semi-moist form. Formulated feeds are produced either by steam or cold pressure **pelleting** or by an **extrusion** process in various physical forms and shape and of different buoyancies (floating, slow- or fast-

sinking). For example, **catfish**, salmon and shrimp require floating, slow-sinking and fast-sinking feeds, respectively. Proper feed distribution is necessary to achieve a better feed efficiency.



Feeding fish in aquacultural system. Photo courtesy of Averain. Licensed under CC BY 2.0.

The body **temperature** and **metabolic rate** of cold-blooded fish are commensurate with the **water temperature**. The amount of feed offered to fish per day has been based on feeding tables developed on the basis of a percentage of body weight and water temperature. Small fish, often called fry or fingerlings, require feed at a greater percentage of their body weight (> 5%) per day than large fish. Demand or *ad libitum* feeding is commonly used in hatcheries where demand feeders dispense small quantities of feed when activated by the fish. Automatic feeders or hand feeding are used to feed fish in tanks or sea cages and their **feeding behaviour** may be monitored by video cameras. Frequency of feeding is important: larval fish and fry are offered a small amount of feed more than 12 times per day and the frequency is gradually decreased to one to three times per day. More time is required to feed fish at low temperatures.

Since fish live in water, **water quality** affects their feed consumption, **growth**, survival and health. **Overfeeding** results in feed wastage and deterioration in water quality, particularly an increase in suspended particles and lower dissolved **oxygen** levels, which directly affects respiration. In pond culture, on days with little sunlight when there is no photosynthesis, coupled with an increased water temperature, less feed must be offered, even though fish eat avidly, because in these circumstances excessive feeding would deplete the dissolved oxygen. Generally, undigested protein or **carbohydrate** increases the suspended solids in the water and increases biological oxygen demand. The principal excretory end-products of protein **catabolism**, ionized and non-ionized **ammonia**, are excreted through the gills. The latter product is toxic to fish. **Fat** not properly retained in the feed may leach out, producing a thin film on the surface of the water and causing respiration problems.

Fish locate food either by their sensory characteristics or by sight, but the **taste** of the food determines whether it will be swallowed or rejected. Species-specific taste receptors for chemical cues have been identified in several farmed fish species. Feeding stimulants include amino acids, **betaine**, inosine, dipeptides and **organic acid**s. Generally, carnivores show a positive response to alkaline and neutral substances such as **glycine**, **proline**, **taurine**, **valine** and betaine, whereas herbivores prefer acidic substances such as aspartic and glutamic acid. Appearance (size, shape and colour) and feel (hard or soft, moist or dry) of the feed also influence the feeding behaviour and food intake.

Feeding of larval fish requires special consideration, because their **digestive system** is not fully developed after hatching. Currently larviculture depends upon feeding live feed organisms, such as brine shrimp (*Artemia*), **rotifers** and other planktonic organisms, that have been enriched with specific nutrients (**essential fatty acid**s, vitamins, amino acids, etc.) to improve their nutritional value. Larvae are gradually weaned onto highly digestible water-stable micro-diets of appropriate **particle size** (~0.1–0.6 mm), colour and organoleptic properties. (SPL)

See also: Aquaculture; Fish; Fish larvae; Salmon culture; Zooplankton

Key references

Houlihan, D., Bouiard, T. and Jobling, M. (2001) *Food Intake in Fish*. Blackwell Science, London.

National Research Council (1993) *Nutrient Requirements of Fish*. National Academic Press, Washington, DC.

Fish fingerling

The fish fingerling stage is when the fish's body looks like human fingers. The alimentary tract is completely developed, and the feeding habits are very similar to those of yearlings or adults. They usually accept most feeds at this stage, except for filter feeders, such as **silver carp** and **bighead carp**. (QS)

Fish juveniles

This includes the growth stage from fingerling to yearling, encompassing the main period when the fish grows to maturity. The fish in this stage generally grow faster compared with later

stages in their growth and are often in better health, hence they are often used for conducting nutrition trials to test effects on growth. (QS)

Fish larvae

The development of most fish species passes through four general stages: egg, larva, juvenile and adult. The larval stage begins at hatch and ends with metamorphosis, when body length is often about 10 mm. Fish larvae are usually transparent, with only scattered pigment cells or patches. The notochord and myotomes are visible, the blood is frequently without **haemoglobin**, and the full complement of fins is rarely present. The mouth and jaws may or may not have appeared. The alimentary tract is developing and, from a nutrition perspective, the larval stage may be subdivided into a period of endogenous yolk utilization (yolk-sac or pre-feeding larva) and a period of exogenous feeding prior to metamorphosis (post-feeding larva) often by preying on **phytoplankton** and **zooplankton** as filter feeders. The larval stage is frequently a difficult one for culturists, particularly the transition from yolk utilization to exogenous feeding. Metamorphosis to the juvenile stage is associated with generation of scales and skin pigmentation. The swim bladder and lateral line may develop at this time. The minimum adult fin ray complement has developed. With **flatfish**, the optic region of the skull rotates at metamorphosis so that both eyes lie on the same side. Transition from juvenile to adult stage is primarily concerned with development of sexual maturity (gonad maturation and acquisition of sexual characters such as heightened colour). (RHP; QS).



King salmon fish larva. Photo courtesy of NOAA Great Lakes Environmental Research Laboratory. Licensed under CC BY-SA 2.0.

Fish meal:
see Fish products

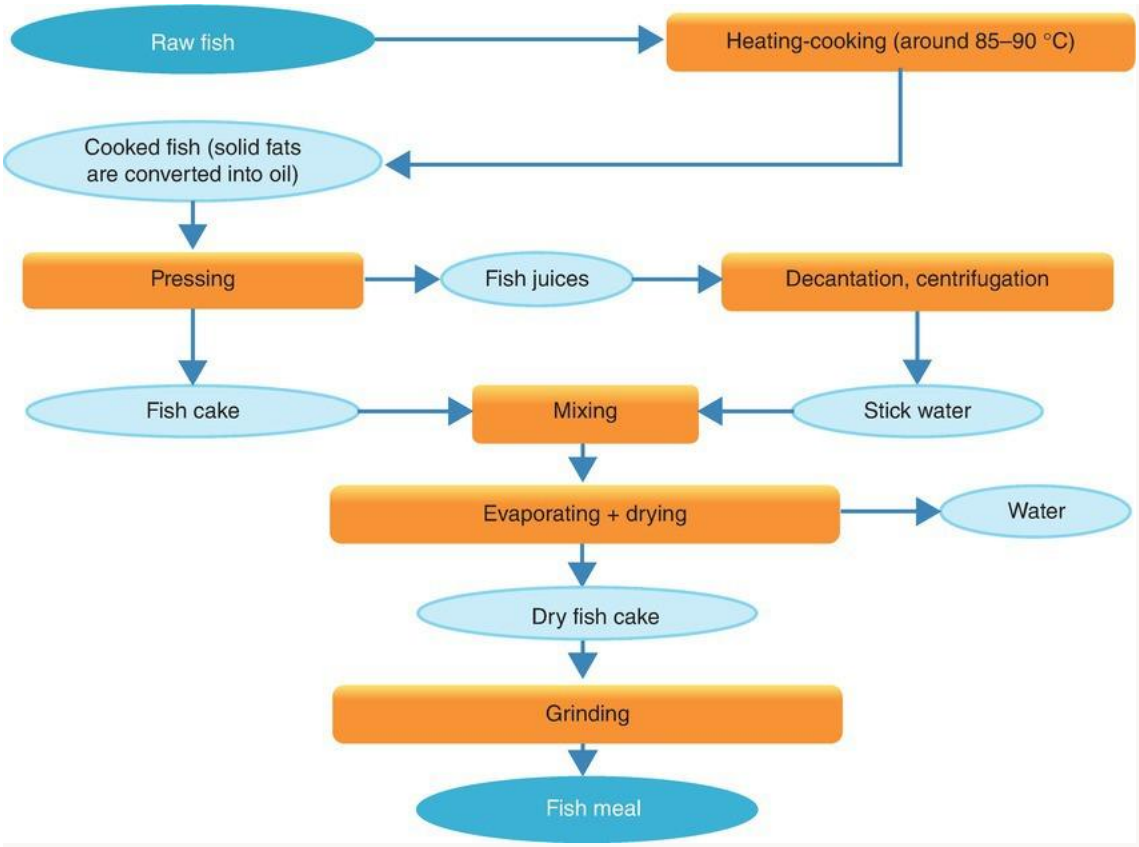
Fish oil:
see Marine oils

Fish pond
A natural or artificial body of water used to culture fish. It may be up to 50 ha in expanse and generally at least 1 m in depth and may have a sump for facilitating harvesting and cleaning. A number of fish ponds may be linked in series or in parallel, ideally gravity fed and easily drained. Fish ponds may be earthen, concreted or lined. Earthen fish-pond culture is most commonly found in developing countries, often integrated with agriculture or animal enterprises such as duck and pig farming. (RMG)

Fish products
The annual world catch of fish was about 179 million tonnes in

2018, of which about one-third was not used for direct human consumption and may be considered as raw material for fishery **by-product**s. Fish meal is the predominant product; probably about 95% of all raw material not used for direct human consumption is processed into fish meal, because it is a stable, high-protein **concentrate** that may be transported around the world without deterioration. Of world fish meal production, about 90% is produced from oily species such as **anchovy**, capelin and menhaden, and less than 10% from white fish such as **cod** and haddock. Only about 1% of meal is produced from other sources such as whales and **shellfish**.

Almost all fish meal is produced by the wet reduction method in which the principal operations are cooking, pressing, separation of the **oil** and **water** emulsion with recovery of oil, drying of the residual protein material and grinding (see figure). This is accomplished in machinery designed for this purpose. During the pressing operation the aqueous portion (stickwater) and the largest portion of the **lipid** component are removed from the raw material. The remaining portion is known as the press cake. The oil-and-water emulsion is then separated and the water portion partially condensed. It may or may not be returned to the press cake to make a whole fish meal. The oil is collected and may be further processed into specific products.



Fish meal processing. Courtesy of Phu Thinh Co. Licensed under CC BY-SA 2.0.

Fish meal is usually a brown powder that normally contains a high level of protein and appreciable quantities of fat and minerals. It contains a higher level of **lysine** and **sulphur** amino acids than **oilseed** meals. White fish meal has a lower oil content and slightly higher mineral content than other types.

There are fishery by-products other than fish meal but their commercial production is limited. Crab process residue meal (or crab meal) consists of the undecomposed ground dried waste of crab and contains the shell, viscera and part or all of the flesh. Condensed fish solubles and dehydrated fish solubles are obtained by condensing or dehydrating the stickwater. Condensed fish autolysate (fish **silage**) is the condensed enzymatic digest of clean undecomposed whole fish or fish cuttings, or both, using an

enzymic autolysis process. **Shrimp** process residue meal (or shrimp meal) consists of the whole undecomposed ground dried waste of shrimp and contains parts of shrimp or whole shrimp. **Krill** meal consists of the whole undecomposed ground dried parts of krill.

The tables give the **chemical composition** of various fish products. (JSA)

Chemical composition of various fish products.

Ingredient	**International feed number**	**Dry matter** %	**Crude protein** %	**Ether extract** %	**Crude fibre** %	**Ca** %	**Total P** %	**Ash** %
Crab meal	5–01–663	95.0	30.0	2.2	10.5	18.0	1.5	31.0
Fish meal, AAFCO	5–01–977	88.4	59.0	5.6	1.0	5.5	3.3	20.2

Ingredient	International feed number	Dry matter %	Crude protein %	Ether extract %	Crude fibre %	Ca %	Total P %	Ash %
Fish meal, herring, Atlantic	5–02–000	93.0	72.0	10.0	1.0	2.0	1.0	10.0
Fish meal, menhaden	5–02–009	92.0	62.0	10.0	1.0	5.0	3.0	19.0

Ingredient	International feed number	Dry matter %	Crude protein %	Ether extract %	Crude fibre %	Ca %	Total P %	Ash %
Fish meal, anchovy, Peruvian	5–01–985	91.0	65.0	10.0	1.0	4.0	2.9	15.0
Fish meal, sardine	5–02–015	92.0	65.0	6.0	1.0	4.5	2.7	20.0
Fish meal, white	5–02–025	91.0	61.0	5.0	1.0	7.0	3.5	24.0

Ingredient	International feed number	Dry matter %	Crude protein %	Ether extract %	Crude fibre %	Ca %	Total P %	Ash %
Fish solubles, condensed	5–01–969	52.0	37.0	4.0	1.0	0.1	0.5	10.0
Fish soubles, dehydrated	5–01–971	93.0	40.0	6.0	5.5	0.4	1.2	12.5
Krill meal	——	91.0	57.0	11.0	8.0	4.0	2.0	15.0
Shrimp meal	5–04–226	88.0	39.9	3.2	12.8	7.9	1.8	27.2

Ingredient	International feed number	Dry matter %	Crude protein %	Ether extract %	Crude fibre %	Ca %	Total P %	Ash %
Fish silage	——	29.0	15.5	10.0	1.0	1.0	0.5	2.5

Ingredient	International feed number	Met %	Cys %	Lys %	Trp %	Thr %	Isl%	His %	Val %	Leu %	Arg %	Phy %
Crab meal	5–01–663	0.50	0.20	1.40	0.30	1.20	1.20	0.50	1.50	1.60	1.70	1.20

Ingredient	International feed number	Met %	Cys %	Lys %	Trp %	Thr %	Isl%	His %	Val %	Leu %	Arg %	Phy %
Fish meal, AAFCO	5–01–977	1.72	0.57	5.17	0.67	2.49	3.64	1.53	3.26	4.69	3.73	2.68

Ingredient	International feed number	Met %	Cys %	Lys %	Trp %	Thr %	Isl%	His %	Val %	Leu %	Arg %	Phy %
Fish meal, herring, Atlan	5–02–000	2.20	0.72	5.70	0.80	2.88	3.00	1.91	5.70	5.10	5.64	2.56

Ingredient	International feed number	Met %	Cys %	Lys %	Trp %	Thr %	Isl %	His %	Val %	Leu %	Arg %	Phy %
Fish meal, anchovy, Peruvian	1.90	0.60	4.90	0.75	2.70	3.00	1.50	3.40	5.00	3.38	2.39

Ingredient	International feed number	Met %	Cys %	Lys %	Trp %	Thr %	Isl%	His %	Val %	Leu %	Arg %	Phy %
Fish meal, sardine	5–02–015	2.00	0.80	5.90	0.50	2.60	3.30	1.80	3.40	3.80	2.70	2.00

Ingredient	International feed number	Met %	Cys %	Lys %	Trp %	Thr %	Isl%	His %	Val %	Leu %	Arg %	Phy %
Fish meal, white	5–02–025	1.65	0.75	4.30	0.70	2.60	3.10	1.93	3.25	4.50	4.20	2.80

Ingredient	International feed number	Met %	Cys %	Lys %	Trp %	Thr %	Isl%	His %	Val %	Leu %	Arg %	Phy %
Fish solubles, condensed	5–01–969	0.45	0.19	1.46	0.11	0.70	0.70	1.09	1.00	1.60	1.37	0.70

Ingredient	International feed number	Met %	Cys %	Lys %	Trp %	Thr %	Isl%	His %	Val %	Leu %	Arg %	Phy %
Fish solubles, dehydrated	5–01–971	0.64	0.50	2.60	2.30	1.10	1.20	0.90	1.60	2.60	1.80	1.30

Ingredient	International feed number	Met %	Cys %	Lys %	Trp %	Thr %	Isl%	His %	Val %	Leu %	Arg %	Phy %
Krill meal	——	1.54	0.68	3.93	0.74	4.10	2.62	1.25	2.68	4.10	3.19	2.39
Shrimp meal	5–04–226	0.82	0.59	2.17	0.42	1.42	1.46	0.90	1.83	2.60	2.35	1.59

Ingredient	International feed number	Met %	Cys %	Lys %	Trp %	Thr %	Isl%	His %	Val %	Leu %	Arg %	Phy %
Fish silage	— —	0.53	0.27	2.74	— —	1.55	1.29	0.89	1.61	2.59	1.80	1.54

Ingredient	International feed number	A IU g^{-1}	E ppm	Thiamine ppm	Ribo ppm	Pantoto ppm	Biotin µg kg^{-1}	Folic µg kg^{-1}	Choline ppm	B_{12} µg kg^{-1}	Niacin ppm
Crab meal	5–01–663	— — —	— — —	—	7.5	6.6	— — —	— —	2024	448	44
Fish meal, AAFCO	5–01–977	— —	18.5	1.3	6.5	8.7	— — —	— —	3510	250	60.8

Ingredient	International feed number	A IU g^{-1}	E ppm	Thiamine ppm	Ribo ppm	Panto ppm	Biotin µg kg^{-1}	Folic µg kg^{-1}	Choline ppm	B_{12} µg kg^{-1}	Niacin ppm
Fish meal, herring, Atlantic	5–02–000	— —	16.8	0.1	8.7	21.7	200	520	5240	588	141.6

Ingredient	International feed number	A IU g^{-1}	E ppm	Thiamine ppm	Ribo ppm	Pantoo ppm	Biotin µg kg^{-1}	Folic µg kg^{-1}	Choline ppm	B_{12} µg kg^{-1}	Niacin ppm
Fish meal, menhaden	5–02–009	—	5.7	0.2	4.8	8.8	150	1000	3080	150	55

Ingredient	**International feed number**	**A** IU g^{-1}	**E** ppm	**Thiamine** ppm	**Ribo** ppm	**Panto** ppm	**Biotin** µg kg^{-1}	**Folic** µg kg^{-1}	**Choline** ppm	**B_{12}** µg kg^{-1}	**Niacin** ppm
Fish meal, anchovy, Peruvian	5–01–985	—	5.6	0.1	7.5	20.3	200	220	5100	600	135

Ingredient	International feed number	A IU g^{-1}	E ppm	Thiamine ppm	Ribo ppm	Panto ppm	Biotin µg kg^{-1}	Folic µg kg^{-1}	Choline ppm	B_{12} µg kg^{-1}	Niacin ppm
Fish meal, sardine	5–02–015	—	5.6	0.08	4.4	14.3	100		3880	300	100
Fish meal, white	5–02–025	—	5.6	1.51	4.6	4.7	—	—	4050	71	38

Ingredient	International feed number	A IU g^{-1}	E ppm	Thiamine ppm	Riboflavin ppm	Pantothenic acid ppm	Biotin µg kg^{-1}	Folic acid µg kg^{-1}	Choline chloride ppm	B_{12} µg kg^{-1}	Niacin ppm
Fish solubles, condensed	5–01–969	2.2	— —	5.5	14.5	35.4	200		4028	350	169

Ingredient	International feed number	A IU g^{-1}	E ppm	Thiamine ppm	Riboflavin ppm	Pantothenic acid ppm	Biotin µg kg^{-1}	Folic acid µg kg^{-1}	Choline ppm	B_{12} µg kg^{-1}	Niacin ppm
Fish solubles, dehydrated	5–01–971	—	—	6.8	16.5	48.4	490	726	3960	308	209
Krill meal	—	12	—	3	1	7	100	—	—	100	23

Ingredient	International feed number	A IU g^{-1}	E ppm	Thiamine ppm	Riboflavin ppm	Pantothenic acid ppm	Biotin µg kg^{-1}	Folic acid µg kg^{-1}	Choline chloride ppm	B_{12} µg kg^{-1}	Niacin ppm
Shrimp meal	5–04–226	—	—	—	—	—	—	—	5500	—	—
Fish silage	—	—	—	—	—	—	—	—	—	—	—

Ingredient	International feed number	Na %	K %	Mg %	S %	Mn ppm	Fe ppm	Cu ppm	Zn ppm	Se ppm
Crab meal	5–01–663	0.85	0.45	0.88	0.04	133.0	440	32.8	102	3.8
Fish meal, AAFCO	5–01–977	1.07	0.39	0.21	0.24	22.8	360	14.6	100	1.8

Ingredient	International feed number	Na %	K %	Mg %	S %	Mn ppm	Fe ppm	Cu ppm	Zn ppm	Se ppm
Fish meal, herring, Atlantic	5–02–000	0.73	1.50	0.18	0.62	3.8	82	4.5	100	2.0

Ingredient	International feed number	Na %	K %	Mg %	S %	Mn ppm	Fe ppm	Cu ppm	Zn ppm	Se ppm
Fish meal, menhaden	5–02–009	0.34	0.72	0.14	0.45	35.6	438	11.4	151	2.2

Ingredient	International feed number	Na %	K %	Mg %	S %	Mn ppm	Fe ppm	Cu ppm	Zn ppm	Se ppm
Fish meal, anchovy, Peruvian	5–01–985	0.88	0.90	0.27	0.54	9.3	226	9.2	100	2.0

Ingredient	International feed number	Na %	K %	Mg %	S %	Mn ppm	Fe ppm	Cu ppm	Zn ppm	Se ppm
Fish meal, sardine	5–02–015	0.18	0.30	0.10	0.30	24.9	300	20.0	105	1.8
Fish meal, white	5–02–025	0.97	1.10	0.22	—	9.7	80	8.0	80	1.8

Ingredient	International feed number	Na %	K %	Mg %	S %	Mn ppm	Fe ppm	Cu ppm	Zn ppm	Se ppm
Fish solubles, condensed	5–01–969	3.10	1.75	0.02	0.13	11.9	300	48.2	38	2.0

Ingredient	International feed number	Na %	K %	Mg %	S %	Mn ppm	Fe ppm	Cu ppm	Zn ppm	Se ppm
Fish solubles, dehydrated	5–01–971	0.40	2.50	0.27	0.45	10.0	948	20.0	76	2.7
Krill meal	— —	1.80	0.40	0.80	— —	7.4	280	70.0	74	——

Ingredient	International feed number	Na %	K %	Mg %	S %	Mn ppm	Fe ppm	Cu ppm	Zn ppm	Se ppm
Shrimp meal	5–04–226	1.50	0.80	0.50	—	29.0	102	—	28	——
Fish silage	— —	0.15	0.20	0.05	—	—	—	—	——	——

Fistulation

Establishment by surgery, under general anaesthesia, of an opening (fistula) into some part of the digestive tract. Fistulae into the lumen of the gut (oesophagus, **stomach** or intestine) are normally fitted at surgery with a **cannula**, usually made of plastic, which is

closed by a screw cap or plug. Within a few weeks the fistula heals by formation of an epidermis-to-epithelium junction. The procedure allows sampling of gut contents or introduction of materials into the gut in the conscious, normally fed animal. Re-entrant cannulas may be fitted into the intestine to allow sampling and direct measurement of the flow of intestinal content: the intestine is transected, each end is sewn up and cannulas are fitted into each end, passed through the body wall and connected externally so as to re-establish the flow of intestinal content. (RNBK)



Steer with rumen fistula, giving access for sampling (for nutrition research) via the plastic cannula. Photo courtesy of minicooper93402. Licensed under CC BY 2.0.

Flaking

The rolling of grains and seeds using wet heat. The steam process causes gelatinization of grain **starch** and is carried out either at atmospheric pressure or under pressure (pressure cooking). The cooked grains are then rolled between close-fitting steel cylinders. Flaking increases **palatability** and **digestibility**, and modifies

starch and protein **digestion** characteristics. It results in a high proportion of starch being digested in the reticulorumen (e.g. 93% in **wheat**) and also improves **microbial protein synthesis** through reduced **protein solubility** in the rumen. The process is commonly applied to cereal grains such as wheat, **maize** and **oats**, and to seed **legumes** such as **peas**, **beans** and **lupin**s. Because of the cost of processing, its use is generally confined to feeds for weaners and young growing stock and horses. (ED)

Further reading

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Flatfish

Farmed flatfish species include Senegal sole (*Solea senegalensis*), **turbot** (*Scophthalmus maximus*), **halibut** (*Hippoglossus hippoglossus*) and Japanese halibut (*Paralichthys olivaceus*), while farming of other species is still at the initial stages (lemon sole, *Microstomus kitt*; and **plaice**, *Pleuronectes platessa*). These species have highly compressed bodies with symmetrical pelvic and pectoral fins, elongated dorsal and anal fins extending to the base of the caudal fin, asymmetrical pigmentation and cranial asymmetry with an ocular side. The flatfish with sinistral (left) eye migration are the right-eye flounders (Pleuronectidae), including soles, halibut, turbot and plaice; the left-eye flounders (Bothidae) include Japanese halibut. All right-eye flounders and most left-eye flounders are marine species. All have the common feature of

hatching as bilaterally symmetric pelagic larvae and undergoing a true metamorphosis before settlement as compressed asymmetric benthic juveniles.



Flounder, dab, turbot, megrim and common sole. Photo courtesy of Peter van der Sluijs. Licensed under CC BY-SA 3.0.

The farmed flatfish spawn or are manually stripped for their pelagic **eggs**, which hatch to release small pelagic larvae; these live on their yolk reserves until they commence exogenous feeding or 'first feeding' on **phytoplankton** or **zooplankton**. The small size of the larvae and their relatively primitive development at first feeding initially necessitated commercial use of intensively cultured microalgae, small cultivated **rotifers** or *Artemia* (intensive culture) or filtered wild zooplankon (extensive culture) rather than inert formulated diets. The 'green water technique', using **algae** as a direct source of nutrition and other zootechnical benefits for rotifers, *Artemia* and **fish larva**e, has become common.

There is general agreement on the importance of the **essential fatty acid**s, **eicosapentaenoic acid** (20:5 n-3), arachidonoic acid (20:4 n-6) and **docosahexaenoic acid** (22:6 n-3), the latter having an undisputed importance for correct neural development in larvae. **Marine fish** larvae generally have a requirement for vitamins C and A, which impact on skeletal and retinal development, and stress and disease resistance. Flatfish may have additional special needs for correct metamorphosis.

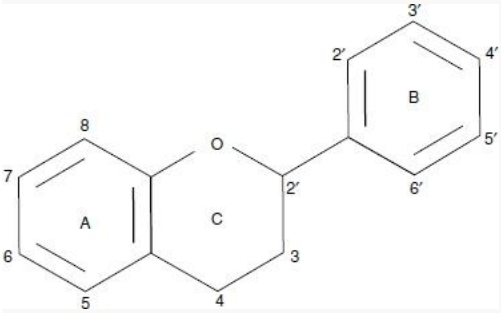
A special feature of flatfish farming is the need for volume prior to settlement (hatcheries for egg and larva stages) and the need for area after settlement. Common hatchery densities are 30 turbot larvae l^{-1} and < 10 halibut larvae l^{-1}. Rigorous hygiene is necessary and attention must be paid to **water quality** and renewal, as disease commonly strikes in intensive cultivation systems. The use of **probiotic**s and microbial manipulation has potential, and most juveniles are vaccinated using commercially available vaccines against common bacterial diseases. Various technical systems have been employed for grow-out, such as raceways, circular flat-bottomed tanks, submerged mesocosms and entire enclosed seawater ponds. Some refinements are subject to commercial confidentiality.

There is general agreement that brood-stock management is essential to egg quality, though neither has been rigorously defined. Appropriate lighting (**photoperiod**, shading, intensity), temperature, **oxygen** and salinity, nutrition and husbandry affect brood-stock physiology and thereby affect allocation of nutrients to eggs, **spawning** time or duration, fecundity and egg viability.

Information on brood-stock nutritional needs is sparse but commercial pelleted brood-stock diets are available. (KP)
See also: Aquatic organisms; Live fish food; Prey size

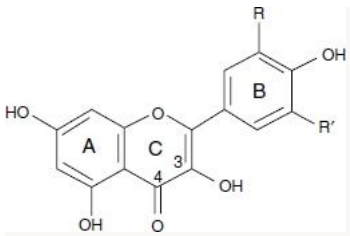
Flatus:
see Gas production

Flavonoids
A group of secondary plant **metabolite**s based on substituted ring structures of the parent compound, flavan.



The subclasses of flavonoids are based on the substitution and state of **oxidation** of the C ring. There are at least 16 subclasses of flavonoids but **flavonol**s, anthocyanidins and proanthocyanidins are the most abundant. The flavonoids are pigments in fruit, flowers and leaves. Their content in the leaves of higher land plants is highly variable, but in some species may account for more than half the **organic matter**. (JDR)

Flavonols
A subclass of flavonoids that are substituted with a **ketone** group at position 4, a hydroxyl group at position 3 and a double bond between positions 2 and 3 of the flavan C ring. The common flavonols are hydroxylated as shown here:



The three most common flavonols are kaempferol (R and R′ = H), quercetin (R = OH, R′ = H), and myricetin (R and R′ = OH). Naturally occurring flavonols in plants are glycosylated. (JDR)
See also: Flavonoids

Flavour compounds
Although birds have few **taste** buds compared with mammals, there is plenty of evidence that all have a good sense of taste. The **domestic fowl** has, on average, 340 taste buds located mainly in the palate and floor of the mouth, while most mammals have hundreds of thousands. Flavour compounds are factors detected by taste buds, which can modify consumption of food or water, especially in the short term. Domesticated animals are sensitive to bitter, sweet, salt and acid flavours and they have an innate preference for sweet flavours. However, any flavour that is consistently associated with a food whose intake generates favourable metabolic consequences will become preferred, while sweet flavours can become aversive if paired with toxic or imbalanced foods. Foods can be flavoured in order to mask changes in the taste of their ingredients; for example, dairy cows exhibit neophobia for concentrate **supplement**s with a novel flavour but this can be prevented by including a masking flavour in all supplements.

Flavours in common use in animal foods include aniseed, talin

and plant **oils**. While saccharin is used as a sweetening agent in foods for young mammals, it is strongly aversive to chickens. (JSav; JMF)

Flexitarian

A person who eats primarily **vegetarian** food, but occasionally eats **meat** and other animal products. The term was created by Dawn Jackson Blatner in her book *The Flexitarian Diet*. Within its vegetarian focus, it emphasizes whole grains, fruit, vegetables and legumes, rather than processed food. (CJCP)

Flour

The product arising from the fine grinding of cereal **grain** or other **starch**-rich plant fractions. Flour is an important commodity in the manufacture of a wide range of food products worldwide, particularly baked products such as bread. Flour made from certain types of **wheat** grains is the one most closely associated with bread making. The production of flour involves the **milling** of refined grains in order to separate the starch-rich **endosperm** from the remaining fractions of the grain (kernel). The **gluten** of wheat flour has elastic properties that are utilized in baking and which help to trap air in the dough during bread making. Soft wheats (80–120 g **crude protein** kg^{-1} dry matter (DM)) produce flours that are suitable for products requiring minimal structure (e.g. cakes, biscuits, crackers), while hard wheats (120–150 g crude protein kg^{-1} DM) are more suitable for products requiring a stronger structure (e.g. breads). Wheat may be processed to produce a range of flours, including: (i) whole-wheat (Graham)

flour made from the entire wheat kernel and often unbleached; (ii) gluten flour, a starch-free, high-protein, whole-wheat flour; (iii) all-purpose flour, refined (separated from the **bran** and germ), bleached or unbleached; (iv) cake flour, refined and bleached, with very fine texture; (v) self-raising flour, refined and bleached, with added raising agent and **salt**; (vi) enriched flour, refined and bleached, with added nutrients; and (vii) durum wheat flour, used for pasta manufacture.

Some **by-product**s of the milling process are suitable for animal feeding, including wheat bran, wheat middlings and **wheat feed**, which comprises fragments of the outer skins and broken particles of grains to which some **endosperm** is still attached(ED)
See also: Milling by-products

Fluid therapy
Replacement of fluids lost by a clinical condition, e.g. haemorrhage, or by overuse of normal routes, e.g. sweating, vomiting and **diarrhoea**, or arising from insufficient fluid intake. Fluid therapy may also be used to maintain a high rate of fluid throughput to wash out a toxin or noxious agent from the circulation; it may also provide a convenient route for the administration of a therapeutic agent over a prolonged period. The solutions used are isotonic, e.g. 0.9% **sodium chloride**, and may also include dextrose as a source of rapidly available carbohydrate. The acid–base status of the animal may be corrected by the addition of **sodium bicarbonate** in the case of an acidosis or ammonium chloride in the case of an **alkalosis**. The replacement of specific **electrolytes**, e.g. **potassium** ions lost during excessive diarrhoea, may be achieved

in this way. (ADC)

Fluoride

In very small amounts, fluoride increases the strength of bones and **teeth**. However, fluoride is generally regarded as toxic to domestic livestock, because in high amounts it accumulates in bone to an extent that actually weakens it, leading to **lameness** and increased wear of teeth. The teeth of fluoride-intoxicated cattle become mottled and stained and are eroded or pitted. Rock phosphates (fluorapatite, $Ca_{10}F_2(PO_4)_6$) can affect cattle when used in feed or when applied as a fertilizer without first being defluorinated. To qualify as defluorinated, feed-grade phosphates can contain no more than one part of **fluorine** to 100 parts of **phosphorus**. Other potential sources of fluoride include **bone meal**, deep-well water, and soil near volcanoes or **aluminium**-processing plants. Soluble forms of fluoride, such as **sodium** fluoride, are rapidly and almost completely absorbed by cattle. Minor morphological lesions can occur in young cattle receiving as little as 20 ppm fluorine in their diets when their teeth are developing rapidly, but the relationship between these minor lesions and animal performance is unknown. (JPG)

Fluorine

A halogen with an atomic mass of 19.00. Fluorine is found in nature as **fluoride** salts of various mineral elements. Excessive intake of fluorides from water, phosphate sources, or industrial pollution causes a disease called fluorosis. The syndrome is characterized by skeletal lesions and damage to developing

dentition. (JS)

Fluorine toxicity

Fluorine (F) is a chemical element. In its molecular form of F_2, which is composed of two fluorine atoms, fluorine is a highly toxic, reactive, yellowish-green gas with a pungent odour. Fluorine gas exists naturally, as reported for being trapped inside a dark purple rock called antozonite. The **fluoride** ion (F^-) is the negative ion of fluorine and is present in some compounds, such as **hydrogen** fluoride (HF, a colourless gas), **calcium** fluoride (CaF_2) and **sodium** fluoride (NaF). When hydrogen fluoride is dissolved in water, it is called hydrofluoric acid. Fluoride (F^-) is widely present in plant- and animal-source feedstuffs, as well as ground-surface water. Naturally occurring fluoride concentrations in surface waters are generally low (< 0.5 ppm), but a wide range of fluoride (0.1–6 ppm) has been reported in groundwater depending on the locations (EFSA, 2013). Sea water contains fluoride at concentrations of 1.2–1.5 ppm.

An adequate intake of fluoride from all sources (including non-dietary sources) is 0.05 mg kg^{-1} body weight per day for both children and adults, including pregnant and lactating women (EFSA, 2013). Humans can tolerate the intake of 0.2 mg fluoride kg^{-1} body weight per day (Baines *et al.*, 2017). Depending on species and age, farm animals tolerate different amounts of fluoride in their diets (ppm): cattle, 40 (young) to 100 (finishing); sheep, 60 (breeding) to 150 (finishing); swine, 150; turkeys, 150; chickens, 200; rabbits, 40; and horses, 40 (Wu, 2018). At elevated

levels, fluoride is extremely toxic and often fatal.

Mechanisms for the toxicity of fluorine/fluoride are clearly understood. Fluorine gas is a powerful oxidizing agent; therefore, it is extremely toxic and often fatal by inhalation and skin **absorption**. In addition, fluoride is an inhibitor of many metal-dependent and independent enzymes such as enolase, aconitase, pyrophosphatases, the membrane-bound, proton-pumping H^+-ATPase, acid phosphatase, acetylcholinesterase, catalase, **cytochrome** c oxidase, **glucose**-6-phosphatase, **glutathione peroxidase**, **lactate dehydrogenase**, **protein** phosphatase and **superoxide** dismutase (Whitford, 1996; Strunecka and Strunecky, 2020). These enzymes are involved in **glycolysis**, the Krebs cycle, the mitochondrial electron transport system, **gluconeogenesis**, antioxidative defence, the **hydrolysis** of pyrophosphate, neurotransmission and redox balance. Thus, excess fluoride enhances the production of reactive oxygen species by cells and reduces the intracellular concentrations of glutathione, leading to oxidative stress and cell death (Barbier *et al*., 2010).

Acute and chronic fluorine/fluoride **poisoning** occur when animals (including humans) are exposed to indoor or outdoor air with excess fluorine/fluoride due to the burning of coal that contains high fluorine levels, or when they drink water (including groundwater) and consume food that contain elevated levels of fluoride. Chronic exposure to high levels of fluoride (e.g. > 93 ppm fluoride in diets for dairy cows) affects: (i) the formation of enamel (the outer covering of the tooth), leading to dental fluorosis that is characterized by mottled, discoloured and porous enamel; and (ii)

osteoblast growth and structure, causing osteoporosis in bones. Endemic fluorosis in teeth and bones in lactating cows, beef cattle, sheep and dogs may be due to their chronic exposure to fluorine and fluoride in the neighbourhood of fluorine industries (Krishnamachari, 1987). In humans, symptoms of fluoride toxicity may appear with the intake of 3 mg fluoride kg^{-1} body weight, including tooth discoloration, tooth decay, physical weakness, neurological disorders, high blood pressure, acne, seizures, nausea, vomiting, **diarrhoea** and abdominal pain (Kabir *et al*., 2020). Death may result from the ingestion of 32 and 16 mg fluoride kg^{-1} body weight in an adult and a child, respectively. In animals (including humans), the toxicity of fluoride can be treated by: (i) oral administration of dilute calcium hydroxide or calcium chloride to prevent intestinal fluoride absorption; and (ii) intramuscular injection of calcium gluconate to increase plasma calcium concentrations, which in turn block fluoride uptake by bones and other tissues.

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Fluorosis:

see Fluorine

Flushing

A feeding strategy consisting of an increasing **plane of nutrition** in animals, usually applied before mating. It is particularly common in sheep, in which there is normally a period of several months between the end of **lactation** and the beginning of the breeding season, during which feeding levels provide for little more than **maintenance** requirements. Ewes that have been better fed during this period, and are thus in better **body condition** at the beginning of the breeding season, are more inclined to have multiple ovulations and hence to bear twins or triplets. The same effect can be achieved more economically by flushing, i.e. changing ewes from a maintenance ration to one that promotes liveweight

gain 2–3 weeks before breeding begins. This can increase the lambing percentage (the number of lambs born per 100 ewes) by 10% or more.

Female pigs are commonly mated during and shortly after lactation, when their plane of nutrition is well above maintenance, so that flushing is superfluous. It may, however, be valuable in gilts at first mating.

It was once common to increase nutritional levels in order to promote liveweight gain in dairy cattle in the few weeks prior to calving, but it is now generally accepted that growth should be restricted, rather than encouraged, at this time in order to avoid the problems of calving too fat (*see* Fertility). (PJHB)

Foal

A young horse of either sex up to 1 year of chronological age, or registered age. Registered Thoroughbred (TB) foals are conventionally aged from 1 January of the year in which they are born (in the southern hemisphere TBs are aged from 1 August in the 12 months of their birth) and other breeds from 1 May, irrespective of their actual foaling date. Thus foals born just prior to 1 January (or 1 August) become 1 year of registered age immediately after those dates. Male foals are termed colt foals and females are filly foals. (A hinny is the offspring from a **stallion** and a female ass, whereas a mule is the offspring from a male ass and a horse **mare**.)

Under natural environmental conditions in the northern hemisphere most foals are born between March and June, but with the use of artificial **light** and increased nutrition for the breeding

mare the dates of conception and birth can be brought forward, so that foaling occurs in January. Foals are conventionally weaned from their dams at from 4 to 6 months of age, but for weaker foals **weaning** may be delayed. Healthy, strong foals commence eating significant amounts of grass at 3–5 weeks of age and it is possible, but not normally practicable, to wean foals with appropriate supplementary feed soon after they have received **colostrum**.

It is essential that the mare provides colostrum for her foal during the first 24 h following birth, before the foal receives other energy-containing feed. In the absence of this the foal should receive colostrum from another mare managed in the same environment, or, in the absence of both, a colostrum substitute. The foal receives γ-**globulin** from these sources, giving it some passive, or acquired, **immunity** to infection. The foal's active production of γ-globulin is detectable in the **blood** by 4 weeks of age in normally reared animals.

The **large intestine** of the foal is relatively small at birth and significant **roughage** consumption depends on the development of this region of the intestinal tract, though its development and expansion will be stimulated by roughage intake.

The foal gains rapidly in body weight during the first 6 months of life. A foal with a mature body weight of 500 kg may gain initially at the rate of 1.2–1.4 kg per day, the rate falling to 0.8 kg per day at 6 months and to 0.5 kg per day at 12 months. The weight increase is principally muscle and bone, hence the requirements for protein, **calcium** and **phosphorus** are high during the first 12 months. These needs are met by provision of mare's **milk**, but

weaned foals need a high-protein cereal-based diet in order to achieve a normal growth rate. Alternatively, vegetatively growing spring grass will meet the energy, protein and calcium needs of foals weaned at a normal age.



Foals gain weight rapidly in the first 6 months of life. Their high requirements for protein, calcium and phosphorus are met by the mare's milk. Photo courtesy of Kvetina-Marie. Licensed under CC BY 2.0.

The normal neonatal foal has adequate **iron** reserves at birth to meet its requirements for this element until grazing commences, and **supplement**s of **trace elements** will be required only if foals are weaned early and healthy pasture is unavailable. If the grazed pasture is deficient in **copper**, then copper supplementation of the pregnant mare is essential to ensure control of articular **cartilage** lesions in the young foal. Pasture deficiencies of **iodine** and **selenium**, and possibly of certain other trace elements, must be rectified by supplementation during pregnancy. For the minimum nutritional requirements of the foal,

see Horse feeding. (DLF)

Fodder
Crops and crop residues used as animal feeds. (JMW)

Fodder beet (*Beta vulgaris* L.)
A member of the Chenopodiaceae. It is sown from late March to June in the UK and October/November in New Zealand. In the UK the grey-white fleshy beet-like roots are harvested from October to December and are often washed and chopped before feeding. Tops and roots can be used either fresh (grazed) or as **silage**. Fodder beet crops in New Zealand are used for feeding dairy cattle; they are grazed in May/June, and cattle eat the tops and roots. Fodder beet produces high yields of digestible nutrients. It is high in energy but low in protein, vitamins and minerals. Tops and roots can be used either fresh or as silage. Fodder beet tops contain **oxalates** and nitrates that can cause scour but **wilting** reduces this effect. Levels of **calcium** and **phosphorus** are low and cattle can be deficient in these nutrients. Because of the overall low fibre content, and the high **sugar** content (400–650 g kg^{-1}) in the root, the inclusion of high levels of fodder beet in the diets of unadapted cattle can cause rumen acidosis and **hypocalcaemia**, and transitioning from grazing grass pasture to fodder beet requires careful management (Gibbs, undated). When animals are hand fed, dietary inclusion may be limited in large ewes to 20% of the diet or < 2.5 kg per day, in beef cattle 20% of the diet or < 3.5 kg 100 kg^{-1} liveweight and in dairy cattle to < 1.7 kg 100 kg^{-1} liveweight in early **lactation** and < 3.0 kg 100 kg^{-1} liveweight in late lactation.

Fodder beet can be fed to lambs at 15% and calves at 10% of the diet. Fodder beets are about 20–25% leaf and 75–80% root (on a dry matter (DM) basis). The leaf has 180 g DM kg^{-1}, more than 150 g protein kg^{-1} and 250–300 g neutral detergent fibre (NDF) kg^{-1}. The typical (DM) content of fodder beet is 160–180 g kg^{-1} and the nutrient composition (g kg^{-1} DM) is **crude protein** 63–70, **crude fibre** 60–65, **ash** 55–60, **starch** 20–22 and **sugars** 620–650, with ME 12–12.5 and DE 2.3 MJ kg^{-1} DM. (JKM; GMcLD)



Feeding fodder beet to sheep in the UK. Photo courtesy of Eirian Evans. Licensed under CC BY-SA 2.0

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Foetal growth:
see Fetal growth

Foie grasForce feeding geese and ducks large quantities of high-energy food enlarges their **liver**, which can be made into a fat-rich pâté popular with the French and in some Francophone regions. The food has been consumed since the 18th century in France, conferring a culinary cultural heritage that was enshrined in French law in 2008. About 25 tonnes are produced globally each year, 80% of that in France. However, because the production of foie gras usually involves 'forced feeding' to increase fat stored in the liver, several countries have now banned its production. High-energy feeds are forced into the **gastrointestinal tract** of ducks and geese by inserting a gavage, or metal tube, into their throats. The oversupply of energy-rich food causes fatty deposits in their liver, which swells to several times its normal size. The forced feeding causes the birds to experience pain, an urge to vomit, a scarred oesophagus, reduced mobility and a deliberate avoidance of the person doing the feeding. Birds are usually housed in a small space. Supporters of foie gras production assert that their cultural heritage is being eroded by multinational organizations, in particular the EU and WTO (Gille, 2011). (CJCP)

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Food transportation

Food transportation is the process of moving food products from the place of production to storage, distribution outlets or consumers. Food preservation and safety are main concerns during food transportation. Different modes of transportation can be used, such as by air, rail, road and water. They are associated with various times and costs as well as with different environmental footprints, with sea transport being the preferred option in relation to **carbon dioxide** emissions. In some cases, food is transported as primary commodities, such as grains or live exports, while in others it is firstly processed. During food transportation, infestation with insects or pests, spoilage, **contamination** and damage should be avoided. Refrigeration is often used to maintain the quality of some foods, such as perishable fruit and vegetables, meat or dairy products. The packaging of food during transportation is important from the point of view of safety but it can also contribute towards plastics pollution and generation of greenhouse gas emissions.

The concept of food miles was introduced in the 1990s to measure the distance between the place of cultivation and processing to the consumer at the point of sale or consumption. It measures how far food travels before it reaches the consumer's plate with the assumption that the fewer food miles are needed, the lower is the food's carbon emissions. Although these are legitimate considerations, estimates show that food transportation contributes between 5% (for individual food items) and 20% (including the

transportation of all ingredients) of the total greenhouse gas emissions associated with food production. (DM)

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Food waste

Food is wasted at all sections in the human food supply chain, starting with unharvested crops and harvesting losses and pervading every activity of transport and storage to the products that were never sold or were thrown away before reaching the dinner table, right up to the consumers' waste from their plates. Technically speaking, food waste refers only to unused food products in retail and consumption while food loss describes wastage during the production and supply chain. However, it is common to refer to any wastage or loss of edible material as food waste. Food loss and waste differ significantly across the world, with wealthier countries throwing away much more at the consumption stage.

There are numerous reasons for food waste. Industrial crop

production incurs major food losses associated with the various stages in the process due to inability to fully harvest or store. Spoilage occurs because of bacteria, mould, insects, rodents and bird damage. Viruses and other diseases affect livestock animals, generating significant losses and health emergencies. Food gets discarded because it is not seen as perfect in appearance or because of people buying or ordering higher quantities than they can consume. The hospitality and retail sectors also make a major contribution. In the long road from the farm to the fork, one-third of the world's food does not reach the consumer, or 1.3 billion tonnes of food yearly that could feed about 3 billion people are wasted.

Much of the food waste ends up in landfill. **Methanogenesis** from food waste in landfills contributes approximately 20% of global warming. The management methods for food waste include animal feed, fertilizing crops, biochemical processing, anaerobic digestion, composting/aerobic processes, generating energy, controlled combustion, donation, land application, landfill and sewer/wastewater treatment (EPA, 2020). Of these, landfill represents by far the largest currently used option. Packaging also contributes to the complexity of food waste, particularly when plastic and other decomposable materials are used.

Food waste is an anthropogenic concept. If food waste is to be eliminated, human production and consumption processes should imitate nature, where nothing is lost. Biomimicry and ecomimicry offer a myriad of new solutions, from the use of cyanobacteria for closed-loop hydroponics, sustainable edible packaging to food

preservation methods that do not rely on electricity but use natural defence mechanisms. Digital apps can also assist farmers and consumers to improve their practices to reduce food waste. (CJCP; DM)

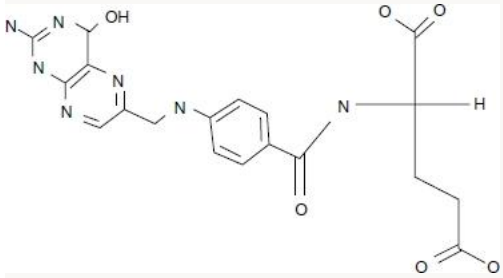
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Folate

The B vitamin called folic acid, $C_{19}H_{19}N_7O_6$. The term folacin is used to describe the multiple metabolically active forms of folate. The vitamin is made of three components, having a pteridine linked to a *p*-aminobenzoic acid (PABA) linked to a **glutamate**. In its metabolically active form, folate is involved in the **metabolism** of one-carbon units that have **oxidation** levels from the methyl, methylene, methenyl, formyl to the formimino forms. The vitamin has two **nitrogen** atoms that are intimately involved in its function in one-carbon metabolism. These are N^5 and N^{10} to which the one-carbon units are either linked one-to-one, such as N^5-methyl, or bridged across the two, as $N^{5\text{-}10}$-methylene. In order for folate to function in metabolism it must be reduced in two separate steps to **tetrahydrofolate**. In this form it is designated as tetrahydrofolate monoglutamate. The vitamin will function in this form but it is required in concentrations 70 times that of the pentaglutamate, which is the most abundant cellular form. The glutamate residues

are added as the γ-glutamate. Cellular folates contain from one to seven γ-glutamyl residues attached to the tetrahydrofolate. The dietary form of folate is the tetrahydrofolate with multiple γ-glutamyl residues that must be hydrolysed before the vitamin can be absorbed as tetrahydrofolate monoglutamate. In metabolism, tetrahydrofolate **polyglutamate** is involved in **catabolism** of **serine**, **glycine**, the methyl carbons of **choline**, **betaine**, etc., as well as the single carbons of **formaldehyde** or **formic acid**. Folate intermediates (N^5-methyl, $N^{5\text{-}10}$-methylene, $N^{5\text{-}10}$-methenyl and N^{10}-formyl) provide one-carbon units critical to methyl-carbon metabolism via their role in **methylation** of **homocysteine** to form **methionine** (*see* Methylation). This methylation step provides a system by which methionine is regenerated. This methylation is critical to folate metabolism because of the production of tetrahydrofolate, which can again participate in one-carbon metabolism. The intermediate forms of tetrahydrofolate ($N^{5\text{-}10}$-methylene, $N^{5\text{-}10}$-methenyl) are sources of carbons 2 and 8 of **purine** bases such as **adenine**. These are critical to the biosynthesis of nucleoside bases of DNA and RNA.



A deficiency of folic acid results in **anaemia** as well as other metabolic abnormalities. The anaemia is due to a lack of one-carbon units required for DNA and RNA biosynthesis and hence

new erythrocyte formation. A deficiency of vitamin B_{12} also results in anaemia because it is critical to the use of *N*5-**methyltetrahydrofolate** as a methyl source in methylation of **homocysteine** to form methionine. The deficiency results in the available tetrahydrofolate being tied up as *N*5-methyltetrahydrofolate so that less is available for other reactions, in effect creating a folate deficiency. This accumulation of folate intermediates as *N*5-methyltetrahydrofolate is known as the 'folate trap'. (NJB)

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Folic acid:

see Folate

Food allergies

Adverse reactions to foods that invoke an immune response. Examples include allergies to specific proteins in **soybean** and **groundnut** products. In livestock, the main concerns are with soybean **antigen**s in calves and piglets given soya-based milk replacers. The soya proteins glycinin and conglycinin are resistant to **digestion** in unweaned animals and can be absorbed into the **intestinal mucosa**, eliciting an immune response. When soya products are used in milk replacers or creep diets for piglets and

calves, the lymphoid tissue (**Peyer's patch**) in the gut produces the immunoglobulins IgA and IgM. These antibodies are secreted into the gut and react with the soya antigens to prevent them from being absorbed. Antigens that escape antibody detection initiate an inflammatory response in the mucosa, causing the **villi** and microvilli to be damaged. The villi become shortened and broader, the microvilli are stunted and dysfunctional and the crypts of Lieberkuhn become deeper (crypt hyperplasia).

When calves or baby pigs are first exposed to soya products, and if absorption of the antigenic proteins occurs, the animals become sensitized to them. Subsequent exposures result in intestinal lesions, causing malabsorption, increased gut **motility**, growth of opportunistic pathogens and **diarrhoea**. Conventional heat processing of soya products does not inactivate the antigenic proteins but they can be removed by extraction with hot, aqueous **ethanol**. Alkali treatment with **sodium** hydroxide inactivates the proteins and can be used to prepare non-allergenic soya products for use in piglet and calf diets. Giving small amounts of soya products before **weaning** may sensitize young animals to later exposure to the antigens. A high intake of soya products before weaning has the opposite effect of inducing **immune tolerance**, which is achieved when the system no longer has the capacity to express a cell-mediated or humoral immune response.

Food allergy is a problem in dogs, causing atopy and pruritus (skin itching). A food elimination diet is used to isolate the offending food. Feeding sources of **unsaturated fatty acid**s is helpful (*see* Skin diseases). (PC)

Food and Agriculture Organization (FAO)
An agency of the United Nations, with responsibility for the development of agriculture and food supply in UN member states. FAO publishes statistics on many aspects of world food production, and specialized publications on the nutrition of animals and humans. (MFF)

Food chainA simple way of showing a food relationship between organisms. It encapsulates the living part of the ecosystem in which a living community depends on each member and its surrounding environment. In this usually linear sequence of organisms, nutrients and energy are transferred from one organism to the other at different trophic levels. The primary producers utilize the non-living matter such as minerals and gases from their environment to support life. In the broadest sense, the food chain's four major components are: first, the sun providing the energy for everything on the planet; secondly, the producers or all autotrophs such as **phytoplankton**, cyanobacteria, **algae**, green plants, which transfer all the nutrients to the third component, consumers – the largest part of the food web, such as herbivores, carnivores, parasites and scavengers (e.g. vultures, dung beetles); and then to the final part, the decomposers, such as fungi, bacteria etc., that convert organic waste materials into inorganic materials like nutrient-rich soil or land. However, within this broad scheme, individual food chains depict possible pathways that energy and nutrients can follow through the ecosystem.
Planktons and plants are therefore the second main component of the food chain. Many **aquatic organisms**, such as snails, mussels,

shrimp, jellyfish and sea star, consume these plants. Small fish feeding on plankton become food for larger fish, e.g. tuna and mackerel, which are in turn eaten by larger fish and animals, such as shark and dolphin. Other organisms such as fungi and bacteria that feed on dead plants and animals reduce their remains to minerals and gases. Each level of consumption in a food chain is called a trophic level.

Algae → water beetle → dragonfly nymph → fish → heron

Phytoplankton → small crustaceans → fish → dolphins → killer whale

Grass → grasshopper → field mouse → snake → owl

Two principal types of food chains, the detritus and grazing food chains, are also recognized. The detritus food chain begins with dead organic material and covers the work of diverse species of organisms and plants like algae, bacteria, fungi, protozoa, mites, insects, worms etc. These are the decomposers and detritivores which are eaten by smaller carnivorous organisms, such as maggots, which then become a meal for larger carnivores, such as frogs, snakes and so on. The grazing food chain starts with photosynthesis and green plants, which are eaten by herbivores, and then herbivores by carnivores.

Rising **temperatures** due to global warming pose a threat that could reduce the efficiency of food chains and threaten the survival of larger animals. A 4°C warming can reduce energy transfer in the plankton food webs by up to 56%. (SPL; DB)

References and further reading

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Food intolerance

An adverse reaction to foods that does not involve the immune system. For example, **lactose** intolerance occurs in individuals lacking adequate production of the lactose-digesting enzyme, **lactase**. Lactase deficiency results in fermentation of lactose in the gut, causing **dehydration**, **diarrhoea** and flatulence. Food intolerance also includes bacterial **food poisoning** and pharmacological reactions (**caffeine**, food preservatives, food colours, **monosodium glutamate**, aspartame). Food intolerance in livestock primarily involves adverse responses to lactose in milk products (e.g. **whey**) in weaned animals. (PC)

Food poisoning

The toxic effects of consumption of contaminated foods, for example with bacteria, viruses, parasites, other infectious agent or toxins in food. Symptoms usually include fever, nausea, vomiting, watery or bloody diarrhoea and stomach cramps. **Contamination** can occur at any stage in the production cycle – growing,

harvesting, processing, storing, shipping or preparing – but also often occurs due to cross-contamination from other foods by human transmission. High-risk individuals are the elderly, pregnant females, infants and immunocompromised people. Such people should avoid potentially contaminated soft cheeses, raw meat, eggs and sprouted vegetables (commonly known as sprouts), unpasteurized milk drinks and juices. Most causes of food poisoning do not cause major morbidity or mortality; however, listeria and *E. coli* O157 are potentially serious. Prevention relies on effective handwashing, separating uncooked and cooked foods, adequate cooking, prompt freezing and refrigeration of food, careful thawing of frozen food, and discarding food promptly after the sell-by date has passed. (CJCP)

Food wastes:
see Bakery products; Kitchen waste; *see also* individual crops and vegetables grown primarily for human consumption

Foot diseases
Diseases affecting the hooves include **ulcers**, white line disease and **laminitis**, in which excessive carbohydrate and protein may be causal factors. Those affecting the skin of the foot include foul-in-the-foot (interdigital necrobacillosis), digital dermatitis and foot rot, which are primarily caused by pathogenic organisms. **Ergot** poisoning causes gangrene of the feet. (WRW)
See also: Hooves; Lameness

Forage

The vegetable food of **grazing** or **browsing** animals. It includes both indigenous plants (e.g. grasses, forbs, shrubs, trees, lichens and mosses) and crops cultivated specifically as animal fodder (e.g. sown grasses, **legumes**, **cereal**s, **turnip**s, **kale** and **rape**), whether grazed or cut and fed. (AJFR)

Forage crop
A crop harvested in its entirety as a feed for animals. Forage crops are commonly preserved as **silage** or **hay**. (JMW)

Foraging
The act of harvesting forage by grazing or browsing. (AJFR)

Foraging behaviour
Foraging behaviour is an innate feeding strategy whereby animals acquire energy and nutrients to meet their nutritional and physiological needs. For example, when rats have free access to diets containing 5, 25, 50, 100, or 200% of their **lysine** requirement, they forage all the diets and select the diet that contains 100% of their lysine requirement. Both dogs and cats avoid **arginine**-deficient diets, while preferring flavour components in meat and peptides (e.g. protein hydrolysates) and free amino acids (e.g. **alanine**, **histidine**, **leucine**, **lysine**) and **proline**, as well as **monosodium glutamate** plus 5′-**nucleotides**. Honey bees forage pollens that are rich in protein and **lipids** for well-being, health and productivity. Foraging is mediated by complex interactions among nutrients (in both the **gastrointestinal tract** and plasma), gastrointestinal sensing and

fill, hormones, neuropeptides and **neurotransmitter**s. (GW)

References

Gietzen, D.W., Hao, S. and Anthony, T.G. (2007) Mechanisms of food intake repression in indispensable amino acid deficiency. *Annual Review of Nutrition* 27, 63–78.

Tsuruda, J.M., Chakrabarti, P. and Sagili, R.R. (2021) Honey bee nutrition. *Veterinary Clinics of North America: Food Animal Practitioner* 37, 505–519.

Forb

A feed that animals eat by **browsing**, including shrubs and small trees or herbs in grazed pasture. (JMW)

Force feeding

Artificial cramming of dry or wet food into the oesophagus or crop, via a funnel with a rigid tube (long enough to reach the crop) and ramrod, or a syringe and flexible tube (for wet food in paste form). It is often used for experimental measurements (e.g. of **digestibility** or **true metabolizable energy**) when precisely known amounts of food are to be given. It is also used commercially (for **foie gras** production, when it is known as gavage). It is potentially harmful and, to avoid injury and impaction, must be done carefully, with limited amounts of food. Also called tube feeding. (JSav)

Foregut

In common parlance, that part of the digestive tract lying anterior to the pyloric sphincter, i.e. stomach, oesophagus, pharynx and mouth. (RNBK)

Forestomach

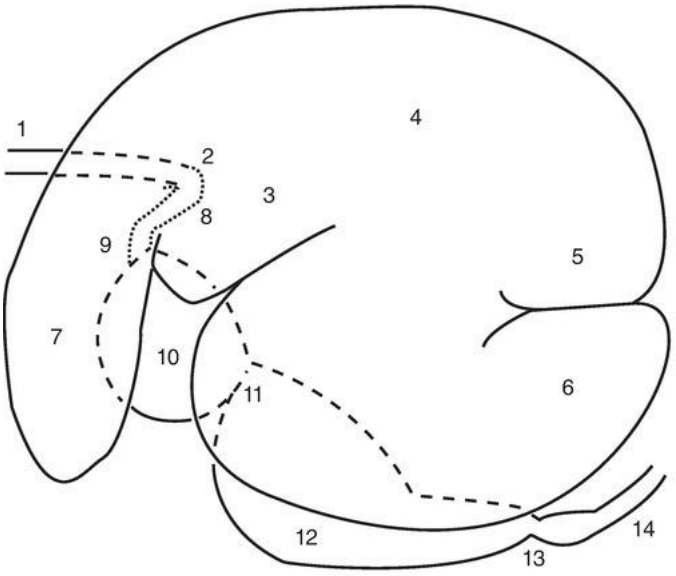
Places in the digestive tract of herbivores where microbial digestion occurs anterior to the glandular stomach. These include the **rumen**, **reticulum** and **omasum** of ruminants; the **foregut** of macropods; the C1 and C2 compartments of the camelid stomach; and the equivalent gastric compartment(s) in other herbivores practising fermentative digestion (see figure in 'Forestomach development'). (RNBK; GMcLD)

Further reading

Hofmann, R.R. (1973) *The Ruminant Stomach*. East African Literature Bureau, Nairobi, Kenya.

Forestomach development

At birth, the **abomasum** of the ruminant is well developed but the forestomach is small. Once solid food is taken, all the compartments of the forestomach (**rumen**, **reticulum** and **omasum**) start to enlarge. The whole stomach reaches its adult proportions (forestomach 0.8, abomasum 0.2, by weight) when **weaning** is complete at about 8 weeks of age. Bulky **roughages** encourage an increase in forestomach volume; digestible roughages and the **volatile fatty acid**s arising by microbial **fermentation** encourage papillary growth. Animals retained on a milk-only diet fail to show this development of the forestomach. (RNBK)



1 Oesophagus
2 Cardiac orifice of oesophagus
3 Cranial sac of rumen
4 Dorsal sac of rumen
5 Caudodorsal sac of rumen
6 Caudoventral sac of rumen
7 Reticulum
8 Ruminoreticular groove
9 Reticulo-omasal orifice
10 Omasum
11 Omasoabomasal opening
12 Abomasum
13 Pyloric orifice
14 Duodenum

The four-chambered stomach of the ruminant (based on the sheep), seen from the left.

Formaldehyde

A simple **aldehyde**, CH_2O. It is used to preserve **silage** by inhibiting the **fermentation** process. It has been shown to reduce **protein degradation** in silage and to provide a more palatable feed. Aerobic deterioration of silage during feed-out may be problematic, due to **oxidation** of residual **sugars**. A 40% solution of formaldehyde is commonly used as a sterilizing agent known as formalin. (RJ)

Formic acid

HCOOH, both produced and consumed in **metabolism**. It can be produced in the metabolism of the methyl group of **methionine** and can be metabolized as a **folate** one-carbon unit initially as N^{10}-formyltetrahydrofolate to provide carbon for methylation of

homocysteine and for **purine** biosynthesis. As an acid, formic acid has many uses in manufacturing and as both the acid and calcium salt it has been used as a feed preservative. It is volatile and an irritant. The salt may be less effective as a preservative. (NJB)

Formiminoglutamic acid (FIGLU)
An intermediate in the normal **catabolism** of L-**histidine**. Under the influence of the enzyme **glutamate**, formimino transferase, formiminoglutamate and **tetrahydrofolate** are converted to N^5-formiminotetrahydrofolate. Thus, formiminoglutamate is important from a nutritional perspective because its excretion in urine is a unique and specific indicator of a folic acid deficiency. (NJB)

Fowl feeding:
see Hen feeding

Fractionation, green-crop
A process in which green crops, most commonly **grass** in Western Europe, are separated into their component parts. There are two extraction concepts: (i) **protein extraction** for human consumption, with the fibre being fed to ruminants and the '**whey**' to pigs and poultry, used as a fertilizer or growth substrate for microorganisms; and (ii) separation into a thick, protein-rich green juice for non-ruminants and a fresh or ensiled fibre-rich fraction for ruminants.

To obtain maximum protein, three crop factors need

consideration: (i) rapid plant growth such that cells divide quickly and produce maximal protein; (ii) harvest before the plant is too mature, when protein content decreases and fibre content increases (the latter decreases the efficiency of extraction); and (iii) the crop must grow over a long season and re-grow quickly following defoliation.

The extraction process, commonly carried out by pulping, involves: (i) pulping the crop with metal beaters; (ii) compressing the pulp into layers 1 cm thick for a minimum of 7 s to allow the protein- and carbohydrate-rich fractions to flow from the fibre; (iii) filtration of the juice, followed by protein precipitation by heating (80–90°C) or acidification (pH 4.0–4.5); (iv) separation of the coagulated protein 'curd' (dry matter 10%) from the carbohydrate-rich 'whey' (dry matter 2–3%) by centrifugation; (v) washing and pressing the curd into a cake with the texture of cheese (dry matter 30–40%); and (vi) conservation and storage of the cake by acidification (pickling), salting, canning, high-temperature drying, **freeze-drying** or **freezing** at −10°C. The product must be maintained in a dark, oxygen-free environment and under these storage conditions it will keep for up to 1 year. (DD)

Free fatty acids (FFAs)

Also called non-esterified fatty acids (NEFAs), fatty acids that are not esterified to **glycerol** or another alcohol such as **choline** or **cholesterol**. In **blood plasma** or serum, FFAs are not really free but bound to plasma **albumin**. (NJB)

Free radical

Any compound that contains one or more unpaired electrons. Free radicals are usually short-lived highly reactive compounds that react with a wide range of cellular molecules and macromolecules. They have a strong tendency to react with other compounds in order to gain or lose an electron, thereby becoming less reactive. Free radicals are produced in three ways: either to fulfil some purpose in the cell, as **by-product**s of normal metabolic processes or in response to certain pathological insults. Some of the common free radicals in the body are those derived from **oxygen**, such as **superoxide** anion, singlet oxygen and hydroxyl radical, or **nitrogen**-derived species like **nitric oxide** and peroxynitrite (a very short-lived radical formed from nitric oxide and superoxide anion). Free radicals can be based on other atoms such as hydrogen, sulphur, carbon or minerals. Superoxide anion is generated by macrophages as a part of the immune response. In addition, macrophages and certain other cell types generate nitric oxide (NO·), which is a free radical. NO· can be a signalling molecule or it can be used to help to kill cells, as in the case when macrophages attack tumour cells or bacteria. They can also be generated as part of the reaction mechanism of certain enzymes and in these cases they remain bound to the enzyme. One example of this is the enzyme ribonucleotide reductase, which generates the **substrates** for DNA synthesis. Some enzymes produce free radicals as one product of their reaction mechanism. These include **xanthine oxidase**, **amino acid** oxidase and the ferroxidase centre of the H subunit of the **iron** storage protein, **ferritin**. Superoxide anion is also produced by mitochondria during the

process of ATP formation: it is estimated that between 1% and 5% of the oxygen consumed by this organelle is not completely reduced to water in the process of ATP formation. Free radicals are also produced in certain pathological situations such as those that occur in response to iron or **copper** overload. When present in excess, iron in the reduced state, Fe^{2+}, can react with **hydrogen peroxide** in the cell in a process referred to as the Fenton reaction. This leads to production of a highly toxic free radical, the hydroxyl radical. Free radical production increases during ischaemic events (e.g. strokes) when **blood** supply to an organ is reduced or cut off. Oxidants including free radicals are produced in response to certain drugs and to defoliants such as paraquat. Excessive production of free radicals is thought to result in increased incidence of some diseases. (RSE)

Free range

A method of housing and managing poultry and livestock that allows them unrestricted access to outdoor runs during daylight hours. This allows the animals to access a land area sufficient for them to perform mostly natural behaviours, including foraging. Some countries and regions such as the EU have quite detailed specifications and requirements for free range; for example, the outdoor runs must be mainly covered with vegetation and not used for other purposes other than orchards, woodland and livestock grazing. For laying hens the maximum stocking density of the runs must not be greater than 2500 hens per hectare or one hen per 4 m^2 (EU, 2008). Before the advent of intensive animal production

systems, most farm animals were kept in free range units. (RB)

Reference

EU (2008) Commission regulation (EC) No 543/2008 of 16 June 2008 laying down detailed rules for the application of Council Regulation (EC) No 1234/2007 as regards the marketing standards for poultry meat. *Official Journal of the European Union* L 157, 17 June 2008, pp. 46–87.

Freeze-drying

A process of drying, also known as lyophilization, in which food and other heat-sensitive products (e.g. **blood plasma**) are rapidly frozen and dehydrated under high vacuum. The ice sublimes off as water vapour without melting under the low pressure. Freeze-dried materials are undamaged or little changed and there is less loss of flavour and texture of food than with other drying methods. For accelerated freeze-drying, controlled heat may be applied to the process without melting the frozen material. Freeze-dried products are porous and often rehydrate rapidly. (SPL)

Freezing

The **water temperature** of aquatic habitats reaches close to freezing point in **fresh water** at 0°C and **sea water** at –1.86°C. The serum of a typical marine vertebrate freezes at –0.7°C and fish are at risk of freezing at this water temperature (DeVries, 1982). Several Antarctic and Arctic **fish** can tolerate freezing temperature, due to the presence of proteinaceous antifreeze unless they are exposed to ice below –2.2°C. Antifreeze proteins may be present in concentrations up to 10 mg ml^{-1}, which may account for as much as

3% of the total serum protein. **Cod** and **Atlantic salmon** are farmed in sea water but the latter does not produce antifreeze proteins. Most farmed fish are essentially isothermal with their **aquatic environment** and cope with the problem of variable body temperature (poikilothermy) by a diversity of biochemical mechanisms. Generally, food consumption ceases at freezing temperatures and handling of fish is minimized to improve survival. (SPL)

Key reference

DeVries, A.L. (1982) Biological antifreeze agents in coldwater fishes. *Comparative Biochemistry and Physiology* 73A, 627–632.

Fresh water

Water that is not salty, i.e. with < 1 g dissolved solids l^{-1}. Most naturally occurring fresh waters are within the range of 50–300 mg total dissolved solids l^{-1}, the average of all rivers being 100–150 mg l^{-1}. The dominant inorganic constituents of typical fresh water are carbonates and **bicarbonate**s of **calcium** and **magnesium**. In soft, acid waters, **sulphate** may be the dominant anion; while near sea coasts, **sodium** and **chloride** may be elevated by sea spray contribution. (RHP)

Freshwater fish

Freshwater fish inhabit a variety of aquatic ecosystems, including streams, rivers and lakes. In these various environments, fish display diverse feeding habits – herbivorous, omnivorous or carnivorous. These can provide insights into a fish's nutritional needs when subjected to artificial conditions in **aquaculture**.

Protein is an extremely important component of fish diets. Satisfying a fish's dietary requirement for protein with a balanced mixture of amino acids is critical to ensure proper growth and health of the fish. Providing excessive levels of dietary protein is both economically and environmentally unsound, because protein is the most expensive dietary component and levels above that needed to satisfy requirements will result in elevated nitrogenous waste excretion into receiving waters. Most herbivorous and omnivorous fish evaluated to date have been determined to require crude protein at 25–35% of diet; carnivorous species may require crude protein at 40–50% of diet. This difference appears to be related to the limited use of carbohydrate for energy by carnivorous species, which in turn are very proficient at using dietary protein for energy. The efficient use of protein for energy is largely attributable to the way in which **ammonia** from deaminated protein is excreted via the gills with limited **energy expenditure**. Although protein requirements are generally expressed as a percentage of the diet, **feed intake** must also be considered in determining the amount of protein needed to satisfy metabolic requirements. Energy density of the diet and the ratio of energy to protein in the diet may also influence dietary protein requirements.

Quantitative dietary requirements for ten indispensable amino acids – **arginine**, **histidine**, **isoleucine**, **leucine**, **lysine**, **methionine**, **phenylalanine**, threonine, **tryptophan** and **valine** – have been determined for several freshwater fish species. Of the ten other dispensable amino acids that commonly make up

protein, two are particularly important for their ability to replace partially or spare indispensable amino acids. **Tyrosine** can spare approximately 50% of phenylalanine in meeting the total aromatic amino acid requirement of fish species; **cystine** generally can replace a similar amount of methionine as part of the total **sulphur** amino acid requirement.

Carbohydrates are not specifically required in the diet of fish but may provide a rather inexpensive source of energy. The ability of fish to utilize dietary carbohydrate for energy varies considerably, with most carnivorous species having more limited ability than herbivorous or omnivorous species. The amount of soluble carbohydrate included in prepared diets for carnivorous species is generally less than 20% while diets for omnivorous species generally contain from 25% to 40% soluble carbohydrate. Carnivorous species tend to use **lipid** preferentially and use it more effectively than carbohydrate. **Non-starch polysaccharide**s such as **cellulose** and **hemicellulose** are essentially indigestible by fish and do not make a positive contribution to their nutrition. **Crude fibre** in fish diets is typically restricted to < 7% to limit the amount of undigested material entering the culture system.

Lipid, in the form of triglycerides, is an important dietary component because it provides a concentrated source of energy that is typically well utilized by aquatic species. Carnivorous and omnivorous species both utilize dietary lipid efficiently for energy. Dietary lipid also supplies **essential fatty acid**s that cannot be synthesized by the organism. Whereas marine species appear to

have very limited ability to elongate and desaturate **short-chain fatty acid**s, many freshwater fish have been shown to meet their essential fatty acid requirements with dietary **linoleic acid** or **linolenic acid**. Dietary lipids also serve as precursors of steroid **hormone**s and **prostaglandin**s in fish as well as providing a vehicle for absorption of **fat-soluble vitamins**. Lipid from the diet, deposited in the fish, may affect the flavour and storage quality of edible products derived from the fish.

Minerals are required by fish for tissue formation and other metabolic functions just as they are required by terrestrial animals; however, waterborne minerals also play a role in osmoregulation of fish and may contribute to meeting metabolic requirements. In terms of osmoregulation, freshwater species lose ions to the hypotonic environment and therefore suffer from hydration; thus, these organisms generally do not drink water but excrete large quantities of excess water as dilute urine. Dissolved minerals in the **aquatic environment** may contribute to satisfying the metabolic requirements of fish and interact with dietary requirements. In particular, **fresh water** of moderate hardness (~50 mg l^{-1} as $CaCO_3$) has been shown to provide fish with adequate **calcium** to sustain metabolic functions in the presence of very low levels of dietary calcium. In the presence of low levels of waterborne calcium, however, the essentiality of dietary calcium has been established for various freshwater species. **Chloride**, **potassium** and **sodium** are other minerals that may be present in fresh water at concentrations sufficient to assist in meeting metabolic requirements of fish.

Dietary deficiencies of most of the macrominerals generally have been difficult to produce with fish species because of the presence of these minerals in the water. **Supplementation** of **phosphorus** in fish diets is usually the most critical, because its presence in the water and utilization by fish are limited. A phosphorus deficiency can cause reduced growth along with other specific deficiency signs in a relatively short period of time. The availability of phosphorus from feedstuffs also may vary considerably; thus, supplementing diets on the basis of available phosphorus is important.

Of the microminerals, **selenium** and **zinc** have been demonstrated, in some fish species, to be most important as supplements in diets due to low levels in feedstuffs or to interactions with other dietary components that may reduce their bioavailability. Although supplementation of practical diets with other microminerals has not been shown to be necessary in most instances, an inexpensive trace mineral premix is typically added to most nutritionally complete diets to ensure adequacy.

Most vitamins that have been established as essential nutrients for terrestrial animals have also been demonstrated as being essential for various fish species. Dietary deficiencies of almost all of these vitamins have been shown to cause reduced growth and other specific deficiency signs in fish. Quantitative dietary requirements for as many as 15 vitamins have been determined for freshwater species such as the channel **catfish**, **common carp** and **rainbow trout**. These requirement values have been used to provide guidelines for vitamin supplementation of diets for these

and other fish species. (DMG)

Further reading

National Research Council (1993) *Nutrient Requirements of Fish*. National Academies Press, Washington, DC, 114 pp.

Frog meal

Rendered **by-product** from the frog leg industry. The meal is produced from the remaining parts of the frog (forelimb, head, body, entrails, etc.) after the hindlegs have been removed. On an average, these portions constitute about 65% by weight of the whole frog. Yield of the meal varies from 18% to 22% of the fresh frog waste. Meals prepared from frog waste conform to standards prescribed for fish meal and can therefore be used for **supplementation** of animal feeds. (JSA)

Chemical composition of frog meal

Proximate composition	**(%)**
Dry matter	93.00
Crude protein (CP)	64.55
Crude fibre	0.80
Ether extract	14.00
Ash	12.50
Amino acids (% of CP)	
Methionine	4.40
Lysine	8.95
Tryptophan	1.07

Proximate composition	(%)
Leucine	7.81
Isoleucine	6.50
Valine	6.90
Arginine	4.12
Histidine	5.50
Phenylalanine	6.70
Threonine	3.20
Minerals	
Ca (%)	9.20
P (%)	4.60
Mg (%)	0.55
Fe (%)	0.01
K (%)	1.30
Na (%)	1.10
S (%)	0.70
Mn (mg kg^{-1})	68.00
Zn (mg kg^{-1})	70.00

FructansPolysaccharides of β-D-fructofuranose residues, with a non-reducing terminal D-glucopyranose, synthesized from **sucrose**. Common fructans include **inulin** and levan (phlein). The predominant linkage in inulin is (2→1) fructosyl-**fructose**, and in levan it is (2→6) fructosyl-fructose. Fructans are widely present in

the grasses, but in high concentration only in the northern grasses (subfamily Pooideae). Fructans are the principal storage carbohydrate in several of the Alliaceae (**onion** bulb and garlic clove), Asterales (**chicory** root, **Jerusalem artichoke** tuber, edible burdock root, endive root) and bulbs of several ornamental plants (hyacinth and dahlia tubers), and they are produced by some bacteria. Inulin is a linear fructan. Inulin in roots of Jerusalem artichoke, chicory and garlic consists of about 70 **sugar** residues. Levan in higher plants is a relatively small, usually highly branched polymer. Bacteria synthesizing fructans include the Enterobacteraceae, Streptococcaceae and Bacillaceae. Bacterial fructans are of the levan type, except for inulin formed by certain strains of *Streptococcus mutans*, a major component of dental plaque. Inulin from chicory may have health benefits through an increase in the proportion of bifidobacteria in the **colon** of non-ruminants. (JAM)
See also: Carbohydrates; Fructose; Oligosaccharides; Storage polysaccharides

Fructosamine
An amino **sugar**, $C_6H_{13}NO_5$, molecular weight 179, in which the hydroxyl group on carbon 2 of **fructose** is replaced by an $-NH_2$ group. It may occur in the urine of individuals with **diabetes** mellitus. (JAM)

Fructose
A **hexose**, $C_6H_{12}O_6$, molecular weight 180, also called levulose, with an anomeric carbon atom at position 2 which can be in

furanose or **pyranose** (levulose) ring form. One of the two **monosaccharide**s in **sucrose**, it is found in fruit juices and honeys, and is the major constituent of **inulin**. (JAM)
See also: Carbohydrates; Fructans

Fruit
The edible product of a plant or tree consisting of its seed or envelope, especially the latter when juicy or pulpy as in the **apple**, **orange**, plum, **olive**, etc. Fruit may be available for animal feeding both as waste whole fruit or as the **by-product**s of processing. These materials are mostly bulky and wet and are therefore best suited to immediate use, but they may be a semi-dry pomace or dried into pulp. Fruit and fruit by-products require **supplementation** with protein, vitamins and specific minerals.

Citrus fruit (oranges, grapefruits, etc.) and apples are frequently grown for human consumption, but surplus fruit and by-products may be used as animal feeds. Cattle can consume < 40 kg fresh fruit per day with no apparent harmful effects. Fresh oranges can produce higher **milk** yields than clover pastures but they should be offered following milking, to avoid flavouring the milk. Fresh citrus fruit contain little protein, **calcium** or **phosphorus** and should be fed with protein and mineral supplements. Pigs prefer oranges and tangerines to grapefruit and limes. To avoid the danger of whole citrus fruits getting stuck in the gullet, they should be sliced. Fresh fruit can be included in the diet up to the following levels: calves and lambs 20%, dairy cattle 25%, ewes and beef cattle 30%, grower and finishing pigs and breeder and layer chickens 5%, **sows** 10% and broilers 2.5%. The dry matter (DM) content of whole citrus

fruit is 319 g kg^{-1} and the nutrient composition (g kg^{-1} DM) is **crude protein** 113, **crude fibre** 42.3, **ash** 66, **ether extract** 94 and NFE 304 (McCann and Stewart, 2000). (JKM)

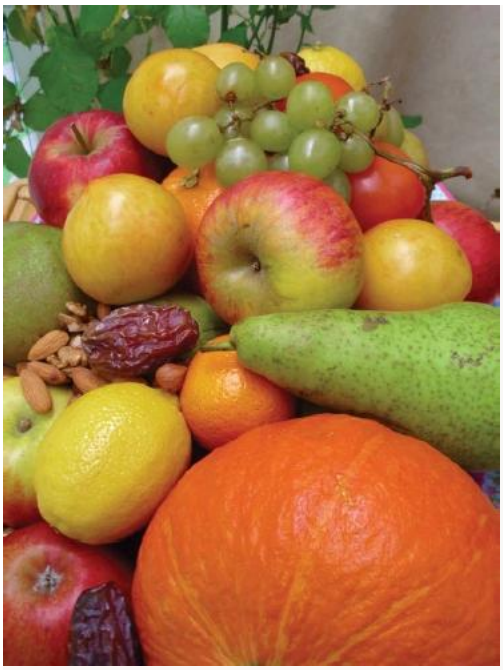
See also: Citrus products; Kiwifruit; Winemaking residues

Key reference

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Fruitarian

The fruitarian diet is a restricted **vegan** diet, concentrating on raw fruit, but with very limited or no vegetables, dried fruit, nuts and seeds. Claimed benefits include stimulation of bowel movements, improved immune system with high **vitamin C** fruit, increased intake of **antioxidant**s, **potassium** and fibre. However, there are risks of malnourishment, and **diabetes** due to the high concentrations of **sugar** in some fruit. (CJCP)



A fruitarian diet has claimed advantages but also some risks. Photo courtesy of Natubico. Licensed under CC BY-SA 3.0.

Fucose
A deoxy **sugar**, 6-deoxy-L-**galactose**, $C_6H_{12}O_5$, molecular weight 164, created by substitution of a hydrogen for the hydroxyl group of carbon 6 of galactose; found in **oligosaccharide** components of **glycolipid**s (e.g. gangliosides) and glycoproteins (e.g. mucins (mucoproteins) and immunoglobulins). (JAM)
See also: Carbohydrates; Deoxysugar; Galactolipids; Mucin

Fuel:
see Energy

Fumaric acid
A **dicarboxylic acid**, HOOC·CH=CH·COOH, one of the intermediates in the **tricarboxylic acid** (TCA) cycle in which it is derived from **succinate** and is in equilibrium with **malate**. Fumaric acid is used as a feed additive to reduce digestive

disturbances, especially in young pigs. (MFF)
See also: Acidification

FumonisinsMycotoxins produced by the fungus *Fusarium moniliforme*, also known as *F. verticillioides*. Fumonisins cause species-specific pathologies such as leukoencephalomalacia in horses, pulmonary oedema in pigs, liver lesions in ruminants, and possibly oesophageal cancer in humans. Poultry are resistant to the toxic effects. There are several fumonisins, including B1, B2, B3, B4, A1 and A2. They are structurally similar to sphingosine, a constituent of **sphingolipid**s. Fumonisins inhibit sphingosine biosynthesis. Pathology is related to defective sphingolipid biosynthesis in nerve tissue and cell membranes. Fumonisins are primarily a problem in **maize**. (PC)

Functional food
A food that benefits one or more functions in the body in addition to supplying nutrients. The benefit usually relates to an improved state of health and well-being or to a reduction in the risk of disease. (MFF)
See also: Nutraceutical; Pharmafood

Fungal diseases
Fungal diseases (mycoses) are caused by inhalation, ingestion or traumatic introductions of fungi into the animal body. Pathogenic fungi establish in apparently healthy hosts, causing diseases such as histoplasmosis, coccidiomycosis and blastomycosis. Opportunistic fungi establish in a host that is debilitated or immunosuppressed,

or following prolonged administration of antibiotics. Other examples of mycoses include **aspergillosis**, candidiasis, chromomycosis, cryptococcosis, entomophthomycosis and histoplasmosis. Treatment involves administration of specific antifungal agents. (PC)

Fungi
Eukaryotic microorganisms. Eukaryotes have a nucleus and other subcellular structures, in contrast to prokaryotes, which have no nuclear membrane. They exist in unicellular (**yeast**) and filamentous (mould) forms. Fungi can cause disease (mycotoxicoses) or can produce toxic **metabolite**s (**mycotoxin**s); they are also the source of antibiotics. Rumen fungi have a role in fibre digestion, and some yeasts (e.g. *Saccharomyces cerevisiae*) are used as **feed additives** to enhance rumen **fermentation**. Various fungi (moulds) may grow on moist feedstuffs, producing adverse odours and reducing **feed palatability**. Spores released by moulds growing on feeds or bedding may cause **respiratory disease**. (PC)

Furanose
The five-member ring structure of a **monosaccharide** created by the reaction of the alcoholic hydroxyl group on carbon atom 5 with the carbonyl group at carbon atom 2, or by the reaction of the oxygen of the hydroxyl group on carbon atom 4 with the carbonyl group on carbon atom 1. (JAM)
See also: Arabinose; Carbohydrates; Xylose

Futile cycles

Futile cycles or **substrate** cycles involve the repeated interconversion of a substrate and product with the loss of a discrete amount of energy in each precursor–product cycle. An example would be production of glucose-6-phosphate from **glucose** + ATP followed by its **hydrolysis** to glucose. Each cycle involves the loss of one ATP equivalent of energy. Futile cycles may be regarded as energy wastage (inefficiency) but may also be a means of producing heat. Organisms avoid futile cycles by differentially regulating the opposing pathways, such that one is more active than the other at any given time. (NJB; DB)

G

Gadoleic acid

cis-9-Eicosenoic acid, a 20-carbon monounsaturated fatty acid, 20:1 n-11 (Δ^9), $CH_3{\cdot}(CH_2)_9{\cdot}HC{=}CH{\cdot}(CH_2)_7{\cdot}COOH$, found in very low concentrations in brain **phospholipid**s and fish liver oils. (NJB)

Gain:feed ratio

A key measure of an animal's efficiency in converting feed inputs or nutrients into productive output such as increased body mass. It is also called feed conversion efficiency (FCE). In growing animals, it is the body weight gained per unit of feed consumed, i.e. the inverse of **feed:gain ratio**. It can also be applied to other production situations, such as laying hens (the weight of eggs produced per unit of feed consumed) or milk production (the weight of milk produced per unit of feed consumed). Due to the variability of water content, feed is measured as dried matter. (SPR; DB)
See also: Efficiency of feed conversion (FCE); Feed conversion ratio (FCR)

Gait disorders
Gait disorders can be caused by neurological disorders, associated with **leg weakness** or **ataxia**, or by a muscular abnormality or a systemic illness leading to **lameness**, leg weakness or **tetany**. Gait can be assessed by observing an animal moving on a firm non-slip level surface, and several systems for scoring locomotion have been devised (Ward, 1998; Whay and Main, 1999). Neurological gait disorders with nutritional causes include **enzootic ataxia** and swayback (**copper** deficiency) and **rye-grass** staggers (**mycotoxin** from *Neotyphodium lolii*, a fungus growing on rye-grass). Lameness of nutritional origin includes acute **laminitis** and sole **ulcer** (excess **starch** or protein).

Abnormal gait associated with muscular abnormality includes nutritional muscular dystrophy or white muscle disease (**selenium/vitamin E** deficiency). Gait disorders associated with

systemic illness include **milk fever** or **parturient paresis** (**hypocalcaemia**), **grass tetany** (**hypomagnesaemia**), azoturia in horses (excess **carbohydrate** relative to work load), porcine stress syndrome (selenium deficiency), splay-leg in pigs (selenium deficiency and genetic predisposition) and muscular dystrophy in cattle and sheep (selenium/vitaminE deficiency). (WRW)
See also: Calcium; Foot diseases; Magnesium; Muscular diseases

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Galactan

Homopolysaccharide of β-linked **galactose** residues, usually D-galactose, in either **pyranose** or **furanose** ring form. **Carrageenan** in red **algae** (**seaweeds**) and galactocarolose in the mould *Penicillium charlesii* are linear polymers. Molecular weight 1500–20,000. (JAM)
See also: Carbohydrates; Dietary fibre; Gums; Storage polysaccharides

Galactolipids

The three major classes of these derivatives of ceramide are cerebrosides, gangliosides and ceramide **oligosaccharide**s. Cerebrosides, abundant in **myelin** sheaths of nerves, consist of a sphingosine, a **fatty acid** and either **glucose** or **galactose**; hence

they are also called glucolipids or glucocerebrosides and galactolipids or galactocerebrosides, respectively. Gangliosides, also in nerves and spleen, are cerebrosides with additional molecules of **carbohydrate** as **amino sugars** and sialic acid. The ceramide oligosaccharides are ceramide derivatives containing one or more molecules of carbohydrate and termed ceramide mono- (or di-, tri- etc.) saccharides. A fourth class comprises galactosylacylglycerides, which are present in small amounts in plants. (JAM)

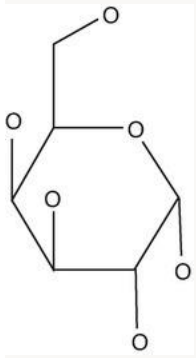
Galactomannans
Heteropolysaccharides consisting of linear chains of 1→4-β-D-mannopyranose with αβ-D-galactopyranose side chains, varying widely in molecular weight and in the proportion of **galactose**. Found in plant cell walls and **endosperm**. Most seed galactomannans are water soluble and viscous in aqueous solutions, making them important food texture modifiers, for example **gums** of **locust bean**, **carob bean** and **guar**. The form and linkage of **mannose** and galactose in fungal and lichen galactomannans differ from those in plant sources. (JAM)
See also: Carbohydrates; Dietary fibre; Storage polysaccharides

Galactopoiesis
Milk formation. (JAM)
See also: Lactation; Milk

Galactosamine
An amino **sugar**, $C_6H_{13}NO_5$, molecular weight 179, in which the

hydroxyl group on carbon two of **galactose** is replaced by an $-NH_2$ group. Almost always occurring as the *N*-acetylated compound, *N*-acetyl-D-galactosamine, it is a component of **cartilage**, chondroitin **sulphate**, several glyco- and galacto-**sphingolipid**s and in secreted and surface glycoconjugates of the intestinal epithelium. (JAM)
See also: Carbohydrates; Monosaccharides

Galactose
A **hexose**, $C_6H_{12}O_6$, molecular weight 180, usually found in **pyranose** form. An epimer of **glucose** in which the bond of carbon four, containing the hydroxyl group, is inverted. It is linked with glucose in **lactose** and is also a component of plant **hemicellulose**s and of cerebrosides. (JAM)



See also: Carbohydrates; Galactolipids; Monosaccharides

Galactosidase
Glycolytic enzyme (α-galactosidase; melibiase; α-D-galactoside galactohydrolase; EC 3.2.1.22), in the **brush border** of mucosal cells of the **small intestine**, which specifically hydrolyses bonds with α-D-**galactose** (as in **lactose**). It does not hydrolyse bonds with β-D-galactose, as in the **oligosaccharide**s, **raffinose**,

stachyose and **verbascose**: these can be hydrolysed by microbial β-galactosidase, primarily in the **large intestine**. (SB)

Galactouronans

Heteropolysaccharides of α-D-**galacturonic acid** residues in **pyranose** form with L-rhamnopyranose interspersed in the linear chains and with side chains of neutral **sugars**. The carboxyl groups are frequently present as the methyl **ester**, and the hydroxyl groups may be acetylated. Found in seeds, flowers, leaves, bark, roots, fruit and vegetables as structural or storage **carbohydrates**. (JAM)

See also: Dietary fibre; Pectic substances; Rhamnogalactouronans; Storage polysaccharides

Galacturonic acid

A major constituent of pectins, $HOOC{\cdot}(CHOH)_4{\cdot}CHO$. D-Galacturonic acids are also found in plant **gums** and bacterial cell walls. Galacturonic acid is widely distributed in the plant world, functioning as a **structural polysaccharide** frequently in close association with **cellulose**, and as a **storage polysaccharide**. In the rumen it is fermented to the short-chain **volatile fatty acids**. (NJB)

Key reference

Van Soest, P.J. (1994) *Nutritional Ecology of the Ruminant*. Comstock Publications, Ithaca, New York.

Game birds, specialty birds and small mammals

This group includes birds raised for specialty meat purposes and

for hunting and shooting, as well as **rabbits** for **meat production**.



Illustration of game birds, from Sporting Sketches (1817–1818) by Henry Alken (1784–1851). Photo courtesy of Free Public Domain Illustrations by rawpixel. Licensed under CC BY 2.0.

Guinea fowl

Guinea fowl belong to the family Numididae and originated in semi-arid areas of Africa, where they continue to be raised traditionally on small family farms for meat and eggs. Production has expanded to parts of Asia, Europe and the Americas, France being the largest consumer of guinea fowl meat internationally and the only country with commercial breeding programmes.



Pearl grey guinea fowl foraging. Photo courtesy of Guinea Fowl Flock. Licensed under CC BY 2.0.

The helmeted guinea fowl (*Numinidae meleagris*) is the most common farmed species. **Egg production** is typically around 80–90 annually, each egg weighing about 45 g. The **incubation** period is 26–28 days and the eggs can be incubated naturally or in an incubator set to **turkey** specifications. The hatched chicks, known as 'keels', resemble young quail. According to European marketing standards for **poultry meat**, guinea fowl can be slaughtered at a minimum age of 94 days when raised on a free-range system. The yield of eviscerated **carcass** from birds weighing 1.25 kg at slaughter is around 78%, containing about 23% breast meat and about 21% leg meat. Guinea fowl meat is leaner and drier than chicken meat and with a 'gamey' flavour. Guinea fowl meat is characterized by a high protein content, and a low **lipid** content with a high ratio of **saturated/unsaturated fatty acid**s. Being foraging birds, free-ranging guinea fowl find much of their own food from forage, insects, grass, seeds, slugs, worms and caterpillars. Providing forage is necessary for a proper intake of fibre to aid digestion, together with a supply of grit. The nutritional

requirements of guinea fowl are similar to those of turkeys, therefore turkey diets can be used as supplementary feed. The feed should be available on an *ad lib* basis and provided only in **mash** or crumble form. A supply of clean drinking water is also required. Placing the feeders close to their housing will encourage the birds to return there in the evenings.

Pigeons

Certain breeds of pigeon (*Columba livia domestica)* have been developed specially for the production of meat from their young (named squabs). These include White King, Red Carneau, French Mondain and Giant Homers, housed in enclosed buildings. Each hen lays two eggs and after an incubation period of 17–19 days the squabs are hatched and receive 'pigeon milk' as their sole food, which is regurgitated from the crop of both parents during brooding. Squabs are harvested just prior to leaving the nest, around 26–30 days of age. Each squab weighs about 500–600 g. Since the hen starts laying again before the squabs have left the nest, it is usual to provide a second nest for each breeding pair to prevent disturbance of the squabs and interruption of egg incubation. This allows the hen to incubate the two eggs in the second nest while the male feeds the two squabs in the first nest. This cycle can be repeated during the main breeding season, each pair producing about 10–14 squabs per year.

A mixture of whole grains and seeds containing about 180 g **crude protein** kg^{-1} and 12 MJ ME kg^{-1} has been recommended for the feeding of adult pigeons, based on production of squabs (Sales and Janssens, 2003). Requirements for amino acids,

minerals and vitamins have not been established, therefore chicken values were suggested as a guide. Suitable ingredients include **maize**, **wheat**, **sorghum**, **oats**, **barley**, **rye**, **rice**, **pea**s, **soybean**s and **groundnuts**. Apparent ME values corrected for **nitrogen retention** (AMEn) for maize (14.76 MJ kg^{-1}), barley (12.36 MJ kg^{-1}), sorghum (13.87 MJ kg^{-1}) and peas (14.01 MJ kg^{-1}) did not differ substantially from values derived for poultry. A mineral mixture containing grit (regular and calcareous) and supplying Ca, P, Na, Cl, K, Mg plus trace minerals should be provided, together with a supply of clean drinking water.

Quail, pheasants, partridges

Of the seven families in the order Galliformes, the largest is Phasianidae, with 155 species of pheasant, partridge and quail. All strains and breeds are gallinaceous birds, related to grouse, wild and domestic turkeys, pheasants, partridges and chickens. Several types of quail are raised commercially as specialty meat birds. Bobwhite quail (*Colinus virginianus*) are native to the USA and are primarily raised for slaughter and sale as quail meat or for release in hunting preserves. The breed varies in body size, those used for meat weighing about 250–300 g when mature, the smaller varieties tending to lay more eggs than the larger varieties. The Eastern bobwhite is the most common species raised commercially in the USA. The common quail (*Coturnix coturnix*) is the smallest European species of the Phasianidae family. It weighs about 125 g and is used for hunting and shooting. Hungarian partridges (also known as the grey or hun partridge) were first imported to the USA from Hungary in 1908. These birds are marketed at about 20

weeks of age, when they reach a target weight of 600 g and provide an eviscerated carcass weighing about 450 g. The protein requirements of pheasants, quail and partridges are similar to those of turkeys; therefore turkey diets can be used for these species at appropriate stages. Several types of grouse, such as the moorland grouse, are raised for hunting and shooting, the birds providing a gourmet meat source. Grouse inhabit temperate and subarctic regions of the Northern Hemisphere and have **digestive system**s adapted to a diet based mainly on vegetation. These birds are not raised in captivity but in their natural environment, their management being designed to enhance their habitat and reduce chick losses, enhance the native food supply and minimize losses from predators.

Rabbits

Rabbits are small mammals in the family Leporidae belonging to the order Lagomorpha. They are gnawing herbivorous animals characterized by possessing two pairs of incisors in the upper jaw, one behind the other. Rabbits are raised as a specialty food item in some countries and may have significant potential as a meat source in developing countries that lack alternative sources of meat, since they breed rapidly and consume a forage-based diet. With adequate feeding, mature animals (4–5 months old) weigh up to 6 kg and yield a dressed carcass (including liver, heart and kidneys) weighing about 55% of liveweight. A wide range of breeds and varieties exists. Commercial rabbitries typically use a diet containing about 160 g crude protein kg^{-1} and about 200 g **crude fibre** kg^{-1} based on a combination of about 15% purchased

pelleted feed and 85% chopped forage and in amounts related to the stage of growth or breeding status of the animals. Ingredients used for the concentrate portion of the diet include wheat, wheat by-products, maize, sorghum, dehydrated **lucerne** meal, lucerne hay and grass, crumbles, plant protein meals, and minerals and vitamins. Rabbits are unique in that they produce two types of faecal material: a hard, dry faecal pellet and soft or 'night' faeces known as caecotropes. The soft faeces are produced in the **caecum** and are ingested directly from the anus as they are excreted (a practice known as **coprophagy** or caecotrophy). Coprophagy is a natural process that provides the rabbit with a source of B vitamins and protein. The process is somewhat analogous to **rumination** in animals that chew and regurgitate the cud to assist with breakdown of fibrous foods. (RB)

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Gamma-amino butyric acid (GABA)

γ-Aminobutyrate ($H_2NCH_2{\cdot}CH_2{\cdot}CH_2{\cdot}COO^-$), formed by **decarboxylation** of L-**glutamate** by L-glutamate decarboxylase primarily in the grey matter of the central nervous system. γ-Aminobutyrate is an inhibitory **neurotransmitter**. It is catabolized by γ-aminobutyrate transaminase to **succinate** semi-**aldehyde** which is converted to succinate. (NJB)

Gamma-linoleic acid (GLA)

An 18-carbon n-6 **unsaturated fatty acid**, all-*cis*-6,9,12-octadecatrienoic 18:3 n-6 ($\Delta^{6,9,12}$). γ-**Linoleic acid** is parent **fatty acid** of the n-6 family. After a two-carbon addition and insertion of an additional double bond, γ-linoleic acid becomes **arachidonic acid**, 20:4 n-6 ($\Delta^{5,8,11,14}$). (NJB)

Gas production

Gas is produced within the digestive tract of herbivorous animals both by microbial **fermentation** and by release of **carbon dioxide** from secreted **bicarbonate**. The rate of production in ruminant animals is very rapid, for example about 30 l h^{-1} in the reticulorumen of cattle. This gas is eliminated mainly by belching (unless it is trapped as a froth, as it is in animals suffering from **bloat**) and also by absorption and exhalation from the lungs.

Rumen gas typically contains about 65% CO_2, 27% CH_4, 7% N_2, 0.6% O_2, 0.2% H_2 and 0.01% H_2S. Part of the CO_2 and the CH_4, H_2 and H_2S represent end-products of microbial **metabolism**. Some

CO_2 also arises from salivary bicarbonate in amounts dependent on secretion rate and on rumen pH and CO_2 tension. The N_2 and O_2 are either swallowed with food or diffuse in from the blood.

Gas arises similarly from the fermenting content of the **large intestine**, especially in hindgut fermenters (pig, horse, rabbit), and is eliminated as flatus or by absorption and exhalation.

Considerable volumes of gas may be swallowed as froth during bottle-feeding of young animals and some is propelled into the **small intestine**. (RNBK)

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Gas–liquid chromatography

Gas–liquid chromatography (GLC, or GC) uses the general principle of **chromatography** to separate a mixture of compounds (solutes) in a **sample**. The sample is vaporized and injected on to a chromatographic column which has an immobilized stationary phase. It is separated into individual components by the flow of an inert carrier gas such as helium, hydrogen, argon or nitrogen. GLC separation occurs when the analyte partitions between the gaseous mobile phase and the liquid phase immobilize on the column as the stationary phase. Unlike certain other types of chromatography, the gaseous mobile phase does not interact with molecules of the analytes. A detector monitors the carrier gas as it emerges from the column and

generates a signal in response to variation in its composition due to eluted components. Four of the most widely used detectors for gas chromatography are the thermal conductivity detector (TCD), electron-capture detector (ECD), flame ionization detector (FID) and nitrogen–phosphorus detector (NPD). Gas chromatography can also be coupled with other selective techniques, for example in GC–**mass spectrometry** (GC–MS) and GC–infrared spectroscopy (GC–IR). These methods provide powerful tools for identifying the components of complex mixtures.

GLC is widely used for the analysis of fatty acids, amino acids, carbohydrates, pesticides and herbicides in feedstuffs and animal tissues. Prior to GC analysis of **oil** samples, the triglycerides must be split up and the individual fatty acids converted to their methyl esters (FAMEs). **Phospholipid**s are treated similarly to oils and wax esters can be studied as such or the fatty acids can be analysed as FAMEs and the alcohols as **acetate** esters. For other materials to be analysed by GLC, there can be acid **hydrolysis** of proteins followed by **esterification** (N-propyl esters) and silylation of carbohydrates to produce volatile samples for fatty acid, amino acid and **sugar** analysis, respectively. (RGA)

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Gastric emptying

Gastric emptying is achieved by a concerted action between the antrum, pylorus and upper **duodenum** in which contraction of the antrum is followed by sequential contraction of the pyloric region and the duodenum. The gastric contents are squirted a little at a time into the **small intestine**. Only the liquid phase and small particles can be evacuated by the pylorus. Therefore, solid aggregates (several millimetres) present in the food must be crushed by strong muscular contractions that **mash** and homogenize the digesta. Meals rich in **dietary fibre** can delay gastric emptying.

Several mechanisms control gastric emptying in order to permit adequate time for digestion in the small intestine. These include neural signals from receptors that respond to hyper- and hypo-osmolarity and to high hydrogen ion concentration in the duodenum. They also include endocrine signals from receptors responding to peptides and lipids in the duodenum, which trigger the release of **cholecystokinin** (CCK), and from receptors that respond to lipids in the **jejunum**, which trigger the release of gastric inhibitory polypeptide. (SB)

Gastric juice:

see Acidity of the gastrointestinal tract; Stomach

Gastric ulcers

Open lesions in the wall of the **stomach**, usually in the pars

oesophagea, due to erosion of the epithelial tissue by **hydrochloric acid** and peptic enzymes in gastric secretions. They are most common in pigs, where a prevalence of about 1% can occur. About 4% of neonatal deaths can be attributed to gastric ulcers. Normally the stomach wall is protected by its thick mucous secretions but these can become lessened by certain conditions, including prolonged stress. Chronic lesions may occur in either the glandular or squamous-lined regions of the stomach. The disease is multifactorial but stressful housing conditions are the commonest cause. Fine grinding of **cereal** (especially **wheat**) diets can also increase the incidence of ulcers in the oesophageal region of the stomach of growing pigs. Associated causes in pigs include swine fever, fungal infections of the gut that are acquired from infected bedding, and some parasitic infections. (JMF)

Gastrin
A 34-, 17- or 14-amino acid polypeptide **hormone** secreted by cells in the fundic region of the stomach. The 17-amino acid **peptide** is the major form with regard to gastric acid secretion. Gastrin increases the secretion of **pepsin** (a proteolytic enzyme) by the stomach and increases the growth of the mucosa of the stomach and intestines. It also increases gastric **motility**. (NJB)

Gastroenteritis:
see Digestive disorders

Gastrointestinal disease:
see Digestive disorders

Gastrointestinal hormones

A number of **peptide** hormones that contribute to the regulation and optimization of the digestive processes in the **gastrointestinal tract** (GI). According to a close sequence homology they can be grouped into families, i.e. **secretin** family (secretin, **glucagon**, vasoactive intestinal polypeptide (VIP) and gastric inhibitory peptide (GIP)) and **gastrin** family (gastrin and **cholecystokinin** (CCK)). Other GI hormones are somatostatin, gastric releasing peptide (GRP) and substance P. GI hormones also regulate the further metabolism of absorbed nutrients by stimulation of the secretion of **insulin** from the **pancreas**. (SB)

Gastrointestinal microflora

The **gastrointestinal tract**s of farm animals are inhabited by large populations of **microorganism**s. The host animals and their gut microbes form an integrated and mutually beneficial ecological unit. The density of microbial colonization and their species diversity vary with region of the gut, tending to be greatest in the stomach (reticulorumen, crop) and in the **large intestine** (**caecum** and **colon**). The microorganisms of the alimentary tract can be split into two groups: those occurring in the gut lumen, either free living or intimately associated with digesta particles; and those associated with the gut's mucosal epithelium. Ruminants such as cattle, sheep, goats and camelids are principally **foregut** fermenters (although some fermentation does occur in the hindgut), whilst non-ruminants such as pigs, horses and rabbits are largely hindgut fermenters. Several factors, such as diet, age, season, time of day, geographical location, temperature, pH,

osmolarity, dissolved gases, digesta flow rates, metabolic inhibition and predation, are known to affect the numbers and diversity of gastrointestinal microbiota.

The digestive tract of the unborn mammalian fetus is sterile: microbial colonization of the gut commences during birth. The neonate acquires microorganisms successively from the mother's vagina and faeces, and then from food, other animals and the environment. Microbial colonization of the alimentary tract is a fast and complex process, and may reach completion within 48 h in non-ruminants. Although the neonate is exposed to many microorganisms of a very diverse species composition, it is the gut conditions such as the availability of **growth factor**s and pH that determine the particular strains that establish successfully and eventually form the commensal gut microflora, whilst others fail.

Commensal gastrointestinal bacteria are known to enhance immune competence by increasing the resistance of the gut to colonization by pathogens. However, the main role of alimentary tract microorganisms is **digestion**. Mammalian enzymes are unable to hydrolyse β-glycosidic linkages between **glucose** or **pentose** units of plant structural **carbohydrates**; **cellulase**s of gut microbes impart this capability. Bacteria of the rumen, caecum and colon are capable of synthesizing a variety of vitamins, especially vitamins B and K. Rumen bacteria confer additional advantages to their hosts. They synthesize **microbial protein** of high **biological value** from poor-quality nitrogen sources such as **urea**; they can degrade ingested **antinutritional factor**s and toxins; and they recycle endogenous nitrogen. Nevertheless, rumen

microbes also have adverse effects. The production of gases (**hydrogen** and **methane**) during microbial fermentation represents an energy loss. Some ingested proteins of high biological value, which do need to be fermented, are degraded and used to produce microbial protein, which may be of lower quality. Microbes may also produce toxins from non-toxic precursors.

The reticulorumen environment is highly variable, due to its sensitivity to the nature, type and amount of feed consumed and its requirement for a complex buffering mechanism for the maintenance of optimum pH in order to keep the fermentation working efficiently. On the other hand, the hindgut environment is more constant and less influenced by diet, since the source of nutrients for caecal and colonic bacteria is undigested dietary **polysaccharide**s, sloughed epithelial cells and endogenous secretions.

Ruminants

In cattle, sheep and goats the reticulorumen contains vast numbers of archaea, bacteria, ciliate protozoa, phycomycete fungi and bacteriophages (examples in Table 1). Its archaeal population is 10^8–10^9 ml^{-1} **rumen fluid**; bacterial population (Table 1) is about 10^{10}–10^{11} cells ml^{-1} rumen fluid; and its protozoal population some 10^5–10^6 cells ml^{-1} (Wang *et al*., 2017). There are more than 125 morphological types of bacteriophages in the rumen, which outnumber rumen bacteria by two- to tenfold. Rumen fungi (Table 2) can constitute up to 8% of the microbial biomass. The rumen environment is anaerobic, hence virtually all rumen microbes are strict anaerobes or facultative anaerobes.

Rumen protozoa fall into two main groups. The holotrichs, which are ovoid organisms and covered with cilia, include the genera *Isotricha* and *Dasytricha*. The entodiniomorphs include many species that vary in shape, size and appearance, and include the genera *Entodinium*, *Epidinium*, *Diplodium*, *Eudiplodium*, *Ophryoscolex* and *Polyplastron*. Holotrichs utilize **sugars** and other soluble feed components, whilst the entodiniomorphs depend on particulate food sources such as fibrous particles and bacterial cells.

Table 1. Major groups of rumen archaea and bacteria (sources: Hespell *et al.*, 1997; Wang *et al.*, 2017).

Group description	Species
Archaea	*Methanobrevibacter ruminantium*, *Methanobacterium formicum*, *Methanomicrobium mobile*
Gram-positive or Gram-variable, straight or curved rods or coccobacilli	*Lachnospira multiparus*, *Lactobacillus vitulinus*, *Lactobacillus ruminis*, *Eubacterium limosum*, *Eubacterium ruminantium*, *Eubacterium cellulosolvens*, *Eubacterium xylanophilum*, *Clostridium aminophilum*, *Clostridium pfennigii*

Group description	Species
Gram-negative coccus-shaped	*Megasphaera elsdenii, Veillonella parvula, Anaeroplasma abactoclastium, Syntrophococcus sucromutans, Magnoovum eadii, Quinella ovalis*

Table 2. The common genera and species of rumen fungi of sheep and cattle (source: Hespell *et al.*, 1997).

Genus	Species
Neocallimastix	*frontalis patriciarum hurleyensis*
Orpinomyces	*bovis joyonii*
Anaeromyces (*Ruminomyces*)	*Anaeromyces mucronatus Ruminomyces elegans*

In ruminants, substantial fermentation of nutrients also occurs in the hindgut (caecum and colon). However, the microflora of their hindgut is not as well understood as that of the rumen. Caecal fermentation in sheep may account for up to 13% and 17% of total methane and **volatile fatty acid** production, respectively. Under conditions of high **cellulose** intake, the numbers of cellulolytic bacteria in the caecum of sheep can exceed those of the rumen (Mann and Ørskov, 1973). In Mann and Ørskov's study, the caecal

bacterial flora tended to be dominated by Gram-negative rods belonging to the genera *Bacteroides*, *Butyrivibrio* and *Fusobacterium*, with a small proportion of *Streptococcus bovis*, *Streptococcus faecalis* and also bacteria from the genera *Peptostreptococcus*, *Micrococcus* and *Selenomonas*.

Domestic fowl

The alimentary tracts of domestic fowl also harbour an extensive microbiota (Table 3). In general the crop has a preponderance of **lactic acid**-producing bacteria with no strict anaerobes such as *Bacteroides* species. The **proventriculus** and **gizzard** are quite inhospitable environments to microorganisms, due to their low pH (ranging from 1 to 4), therefore microbial proliferation in this region is mainly influenced by their acid tolerance (Mead, 1997). Nevertheless, *Lactobacillus* spp. (up to 10^8 cells g^{-1}) and small numbers of ***Escherichia coli***, *Streptococci* and **yeasts** have been reported. The duodenal and ileal microflora are similar, comprising a mixture of anaerobic and obligate anaerobic bacteria. In the caecal and colonic lumen, mainly obligate anaerobes proliferate, whilst yeasts, moulds and protozoa are rarely found. Poultry have a short colon and it is therefore impossible to differentiate its microflora from those of the caecum. The main factors affecting numbers and species composition of the alimentary tract of chickens are age, diet and the use of microbial **feed additives**.

Table 3. Microbial species distribution in the regions of the poultry gut (sources: Mead, 1997; Ewing and Cole, 1994).

Alimentary tract region	Genus/species
Crop	*Lactobacillus* (*L. salivarius*), *Streptococcus* spp., *Staphylococcus, Escherichia coli,* yeasts
Duodenum and ileum	*Lactobacillus*, *Streptococcus, Staphylococcus*, *E. coli*, *Clostridium, Eubacterium*, *Propionibacterium, Fusobacterium*
Colon and caecum	*Eubacterium, Clostridium, Fusobacterium, Bacteroides* (*Prevotella*), *Methanogenium, Eubacterium, Bifidobacterium, Gemmiger, Peptostreptococcus*

Pigs

Some of the bacterial species that have been identified in the pig's gut are listed in Table 4. According to Stewart *et al*. (2001), lactobacilli predominate in the pig's stomach and small intestine, whilst *Bacteroides* species tend to be absent from these sections. By contrast, there are similar numbers of lactobacilli and *Bacteroides* in the pig's colon. However, the pig caecal microflora is dominated by *Prevotella ruminicola*, *Selenomonas ruminantium*, *Lactobacillus acidophilus* and *Butyrivibrio* (Stewart *et al*., 2001). Some cellulose-fermenting strict anaerobes such as *Fibrobacter*

succinogenes and *Ruminococcus flavefaciens*, normally found in large numbers in the rumen, have also been isolated from the pig's large intestine. According to Stewart *et al*. (2001), not all known species of gut anaerobic bacteria have been isolated from pigs. Streptococci are the main faecal bacteria of pigs, constituting over 25% of all isolates. (SC; GMcLD)

Table 4. Principal microorganisms isolated from the pig's gut and faeces (sources: Ewing and Cole, 1994; Stewart, 1997; Stewart *et al*., 2001).

Alimentary tract region	**Species**
Stomach	*E. coli, Lactobacillus, Streptococcus*
Small intestine	*E. coli, Lactobacillus, Streptococcus*
Caecum and colon	*Eubacterium, Bacteroides (Prevotella), Ruminococcus, Selenomonas, Lactobacillus, Butyrivibrio, Streptococcus, Peptococcus, Peptostreptococcus, Megasphaera elsdenii*

Alimentary tract region	Species
Faeces	*Streptococcus, Lactobacillus, Eubacterium, Fusobacterium, Bacteroides, Peptostreptococcus, Bifidobacterium, Selenomonas, Clostridium, Butyrivibrio, Escherichia, Ruminococcus, Succinivibrio, Veillonella, Propionibacterium*

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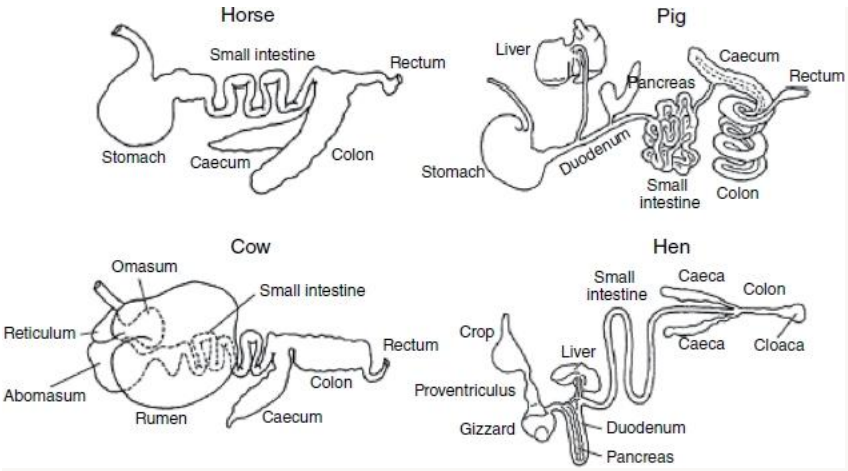
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Gastrointestinal tract

A long tube-like structure that extends from mouth to anus (see figure). The inside of the gastrointestinal tract (GIT) can be considered as outside the body proper. Before food substances can enter the body, they must be broken down into smaller entities by physical, chemical and enzymatic processes collectively called **digestion**. The digested end-products then cross the intestinal epithelium and enter the body: this is called **absorption**.



Gastrointestinal tract in various farm animals including the horse (non-ruminant herbivore), the cow (ruminant), the pig (non-ruminant omnivore) and the hen). Adapted from Moran (1982).

The GIT consists of several compartments and associated organs (**pancreas** and liver) and a large number of different glands. These include the salivary glands in the mouth, glands for producing HCl, pepsinogen, mucus and **gastrin** in the **stomach**, glands for producing HCO_3^-, digestive **enzymes** (or their precursors) and **hormone**s in the pancreas, glands for producing **bile** (solution of bile salts, bilirubin, **cholesterol**, **lecithin** and **electrolytes**) in the liver, and glands for producing HCO_3^- (**Brunner's gland**s) in the **duodenum** and mucus (**mucin**) throughout the intestines.

The principal parts of the GIT are the mouth (including **teeth**, tongue and pharynx), oesophagus, stomach, **small intestine** (sequentially duodenum, **jejunum** and **ileum**) and **large intestine** (sequentially **caecum**, **colon**, **rectum**) and anus. This organization describes the GIT of simple-stomached animals, e.g. the pig.

In ruminants, a **forestomach** (of three parts: **reticulum**,

rumen and **omasum**) serves as a large **fermentation** chamber before the food enters the true stomach, called the **abomasum**.

In avian species, a forestomach (the **crop**) serves as a storage organ. The true stomach is called the **proventriculus** and is followed by another compartment called the **gizzard**. The small intestine ends at the ileocaecocolic junction, from where the digesta can pass into the two caeca or (as can also happen in mammals) directly into the **colon**. Birds also differ from mammals in that **urine** is excreted in semi-solid form along with the **faeces** (with N incorporated in uric acid rather than in **urea**).

In **fish**, the morphology varies widely among species. Some species (e.g. Cyprinidae) have no stomach (agastric); however, most species have a stomach, often J-shaped and consisting of a descending cardiac or fundic region and an ascending pyloric region (e.g. Salmonidae). In the **eel** a gastric caecum extends caudally, whereas in other fish (e.g. Acipenseridae) the pyloric region is modified into a muscular gizzard-like region which has a special grinding function.

The organization and dimensions of the individual compartments have evolved in various ways according to the physical nature and **chemical composition** of the feed to which the particular animal has become specialized. The adult pig has a stomach of 6–8 l and a relatively long small intestine of 15–20 m. The stomach is only about 4% of body weight, whereas in sheep and cattle it is about 25%.

The degradation of nutrients in the GIT is always accompanied by fermentation from a resident **gastrointestinal microflora**,

and the development of the GIT has been strongly influenced by this action. Because the host animals can utilize the microbial degradation products from **dietary fibre** which cannot otherwise be utilized by the animal itself, the microflora has a symbiotic function. This is particularly important for **herbivore**s and omnivores and less important for **carnivore**s. Mammalian farm animals can be separated into the following groups according to their fermentation activity:

1. Pre-gastric fermenters
    a. Ruminants (cow, sheep, goat)
2. Hindgut fermenters
    a. Caecal fermenters (rabbit)
    b. Colon fermenters
        i. Sacculated colon (horse, pig)
        ii. Unsacculated colon (mink)

The relative capacity of the different compartments varies considerably between the different species (see table).

Approximate relative capacity (%) of the compartments of the gastrointestinal tract of different farm animals.

	Stomach	**Small intestine**	**Caecum**	**Colon**
Cattle, sheep, goat	70	20	2	8
Horse	10	30	15	45

	Stomach	Small intestine	Caecum	Colon
Pig	30	35	5	30
Dog, cat	65	20	–	15

The digestion of the food is initiated in the mouth, where it is disintegrated by **chewing** or **mastication**. Birds have no teeth but may use their **beak** (and **claws**) to reduce the size of food components. Furthermore, the action of strong muscles in the wall of the gizzard, often with the help of small stones that are swallowed, reduces **particle size** and thus compensates for birds' lack of mastication.

During the process of mastication, **saliva** is added, primarily from three pairs of glands: the submaxilliary, at the base of the tongue; the sublingual, underneath the tongue; and the parotids, below the ear. Some species also have other smaller salivary glands. In the saliva of many animals an α-**amylase** initiates the enzymatic degradation of **starch**, and in young (**sucking**) animals a **lipase** initiates the degradation of milk **lipids**. In ruminants the saliva provides a significant source of N (from urea and mucoproteins), P and K which, together with **bicarbonate**, are essential for the microorganisms in the rumen.

In ruminants, in contrast to most other animals, the ingested food is fermented by microorganisms before it is exposed to the typical processes of digestion, which occur in the true stomach and intestine. The **metabolite**s resulting from fermentation can be

absorbed in the rumen. The reticulum functions to move ingested food into the rumen or into the omasum and in regurgitation of ingesta during **rumination**. The omasum helps to control the passage of digesta into the abomasum.

Some herbivorous non-ruminant animals such as horses and rabbits have a sacculated stomach with quite intensive microbial activity. In the crop of poultry, microbial fermentation may occur together with a continued action of salivary amylase on starch degradation.

In the true stomach (in birds, the proventriculus), HCl and **pepsin** are secreted, proteins are denatured and partially degraded and microorganisms are killed. Mucus is produced for protecting the gastric wall against the action of HCl and pepsin. Pepsin is secreted in an inactive form and activated by pepsin and HCl. In young sucking mammals, rennin, rather than pepsin, is secreted. Rennin, which is also secreted in an inactive form and activated by HCl, coagulates **milk** by specific cleavages of milk proteins.

Shortly after passing through the pylorus into the **duodenum**, the **digesta** are mixed with **pancreatic juice**. This is alkaline and neutralizes the acid digesta from the stomach. It also contains a variety of digestive enzymes from the pancreas, including amylase, proteases, lipases and nucleases for digesting starch, proteins, lipids and **nucleic acid**s. At this point also the hepatic duct brings bile from the liver; bile salts are important for **lipid absorption**. In the sheep, the pancreatic duct is joined to the hepatic duct.

The surface for absorption in the small intestine is enlarged

enormously by folds and by **villi**, which are finger-like extensions of the gut wall covered with epithelial cells. These cells in turn have microscopic finger-like extensions called microvilli, which form the **brush border**. It is through these membranes of the epithelial cells that absorption occurs. In the brush border are specific enzymes for hydrolysing oligomers and saccharides into monomers, and other enzymes for hydrolysing oligomer peptides. Dipeptides and tripeptides are mostly absorbed as such and hydrolysed to **amino acid**s in the cytoplasm of the epithelial cells. In each villus is a blood capillary that drains into the portal system which goes directly to the liver.

The morphology of the small intestine is affected by the gut microflora. Small intestines are heavier in conventional than in **germ-free** chickens. The brush border is wider in germ-free birds and the area per unit of gut is greater.

The large intestine consists of caecum, colon and rectum. Dimensions vary greatly, depending on diet. Non-ruminant herbivores generally have a capacious large intestine. Horses and **ostrich**es have a large colon whereas **rabbits** have a relatively large caecum. Often animals with a big caecum, e.g. the rabbit, practise **coprophagy** (or more accurately caecotrophy), which is a re-digestion of soft faeces, which are excreted during the night and which have a high content of **microbial protein** and vitamins, with less fibre than the hard faeces excreted in the daytime. The caeca of birds are two blind sacs which have some fermentative capacity but this is often of little nutritional importance.

The main site of **cellulose** breakdown in horses is the colon, as

well as the stomach. Horses and ruminants differ from most other species of mammals in their capacity to absorb nutrients through the epithelium of the large intestine. (SB)

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Gavage:

see Force feeding

Geese:

see Goose

Gelatin

A protein prepared from bones, skin etc. It is devoid of **tryptophan**. (MFF)

Gender differences in human nutrition

The essentials of healthy diets are the same for both men and women. However, there are differences in sex **hormone**s between men and women, and women are more sensitive to adrenergic activation by **catecholamines** (for example, greater **lipolysis** in white **adipose tissue** exposed to **epinephrine**). Overall, the **respiratory quotient** (volume of CO_2 produced/volume of O_2 consumed) and basal **energy metabolism** per kg body weight both at rest and during endurance exercise are greater in men, compared with nonpregnant women. Expressed per kg body weight, the dietary requirements of men for **energy**, **amino acid**s and **fatty acid**s are greater than those of nonpregnant women. On

the contrary, compared with men, women are at greater risks for **iron**-deficiency **anaemia** during menstruation with **blood** loss, and for **folate** and iron deficiencies during pregnancy.

Women are more likely to have a positive attitude to their health and animal **welfare** compared with men. They are more likely to avoid **meat**, especially meat from beef, lamb and to some extent pork, than men. (GW)

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Genetically modified (GM) crops and food products

A very important technological development in food production was the introduction in 1996 of grain and fruit crops for human and animal feeding that had improved traits such as resistance to viruses, insects, fungi and herbicides by the use of genetic modification (GM), the work of the major scientists involved being recognized in the award of the 2013 World Food Prize.

The main reasons for the use of GM in crop improvement are: resistance to diseases; resistance to pests that attack crops; tolerance to herbicides used to kill weeds; delayed ripening process to allow products to be transported over long distances; increased survival in **drought** conditions; and improved nutrient content. Food organisms can be altered in genetic makeup by:

1. Traditional selection and cross-breeding techniques
2. Exposure to chemicals or irradiation (mutagenesis)
3. Genome editing (the process of changing the genetic makeup by altering, removing or adding **nucleotides** to the genes)
4. Introduction of a gene from one species into another species (genetic modification, genetic engineering (GE), transgenesis).

Generally it is method 4 that receives most attention with regard to potential effects on human or animal health, requiring toxicological and environmental assessment before the GM plant or animal can be approved by regulatory authorities for food or feed use. In 2018 the European Union ruled that products from crops modified by gene editing (method 3 above) would be subject to **EU regulation**s governing GM foods. Mutation breeding (method 2 above) is considered a conventional breeding technique, the products being excluded from the regulatory assessment required for those developed by method 4. Some countries allow organisms modified genetically by method 2 to be considered organic.

One component of genetic modification is termed genetic engineering (GE), in which recombinant **deoxyribonucleic acid** (rDNA) methods are used to allow a gene or genes from any species

to be inserted and subsequently expressed in a food crop or other food product.

Evidence from a large number of peer-reviewed scientific investigations and from reviews of the available evidence by many different competent authorities indicates that the nutritional composition and **nutritive value** of approved GM food and feed sources are equivalent to those of their related, non-GM cultivars, except when the GM cultivars have been developed with an enhanced nutritional profile (Blair and Regenstein, 2015). Some variation in composition between GM and related non-GM crops has been reported but the differences are generally small and within the range of variation found for conventional crops. Environmental and soil conditions have been shown to have a greater influence on composition than genetic type.

The global area devoted to GM crops increased from 1.7 million hectares in 1996 to over 175 million hectares in 2013. Thus, biotech crops are considered as the fastest adopted crop technology in the history of modern agriculture. In 2019, the 24th year of commercialization of biotech crops, 190.4 million hectares of biotech crops were planted by up to 17 million farmers in 29 countries (ISAAA, 2019). According to Brookes and Barfoot (2020) over 90% of farmers planting biotech crops (16.5 million) are small and resource-poor and have benefited financially by their adoption. Other benefits reported were an alleviation of global poverty, **malnutrition**, food insecurity, crop diseases and **climate** change. The trend of increasing adoption of the technology continues, the main crops being **soybean**s, **maize**, cotton and canola. One effect

of this expansion was a reduction in the amount of conventional feedstuffs such as soybean meal suitable for the organic feeding of poultry, pigs and cattle and a restriction in the growth of these industries, since farmers found it more profitable to grow GM crops. Other GM products include cantaloupe, eggplant, plums and papaya, **lucerne** (**alfalfa**), **pineapple**, **potato**es, **safflower**, squash, **sugarbeet**, sweetcorn (maize), **rice** (golden) and **tomato**es, one apple cultivar and one animal (salmon), together with a range of **microorganism**s, for example those used in beer and wine production. As a result, it became more practical to use **insulin** produced by GE microbes (GEMs) rather than from the **pancreas** of slaughtered pigs, the original source of insulin. Similarly, microbially produced **trypsin** and chymosin came into use as alternatives to harvested trypsin or rennet from animal sources such as pigs and cows; and cheese began to be made mainly with chymosin (the active **milk** protein-coagulating enzyme in rennet) produced with GEMs, instead of harvesting the enzyme from calf stomachs. Other examples of GEM products that came into use in the 21st century for food and feed use include vitamins, amino acids, food enzymes, functional proteins (e.g. texturants), nutritional proteins, **oligosaccharide**s, flavours and sweeteners. Plant-based burgers containing haem from fermented GM **yeast** to simulate the look and taste of bleeding meat became mainstream.

The introduction of GM foods and food products required special regulatory procedures to ensure their safety and effectiveness. In the USA – the country producing most of the GM foods and food products – three federal agencies within the US

government work together to regulate most GMOs (FDA, 2023). These are the Food and Drug Administration (FDA), the Environmental Protection Agency (EPA) and the US Department of Agriculture (USDA). These agencies also monitor the impact of GMOs on the environment. A Coordinated Framework for the Regulation of Biotechnology, established in 1986 and revised in 2017, outlines how the agencies work together to regulate GMOs.

The European legislation is based on a precautionary approach, imposing a pre-market authorization for any GMO to be placed on the market and a post-market environmental monitoring for any authorized GMO (Bruetschy, 2019). The European Food Safety Authority (EFSA), in collaboration with Member States' scientific bodies, is responsible for the risk assessment, which needs to demonstrate that, under its intended conditions of use, the product is safe for human and animal health and the environment. By 2021 only one GM crop (insect-protected maize) had been approved for cultivation, although over 70 GMOs had been authorized for food and feed use.

Based on the findings of regulatory agencies, independent scientists and respected scientific agencies in many countries (including the European Academies Science Advisory Council), a broad scientific consensus developed that all approved foods and feeds derived from GM crops and organisms are as safe to eat as similar foods derived from organisms modified by conventional improvement techniques (Blair and Regenstein, 2020), A declaration by more than 100 Nobel Laureates, together with other scientists, called upon biotech critics to cease and desist opposition

to GM crops, and for governments around the world to reject campaigns against biotech crops. In 2021 the Council for Agricultural Science and Technology (CAST) of the USA released a report that without GM crops as a part of the global cropping systems and food production, the second of the 17 Sustainable Development Goals of the United Nations to end **hunger**, achieve food security and improved nutrition and promote sustainable agriculture would be compromised. The report (CAST, 2021) outlined how, within the span of 25 years since their first widespread commercial adoption, GM crops had transformed cropping production systems, contributed to better pest and weed control, facilitated the adoption and maintenance of reduced and no-tillage agriculture which has helped to reduce levels of soil erosion, increased soil moisture conservation, improved soil health, reduced levels of greenhouse gas emissions and had reduced food costs.

A consistent conclusion from the evidence relating to human health is that much, or all, of the transgenic DNA from GMO food products is degraded in the **gastrointestinal tract** of the human or animal consumer and that none is absorbed actively into the tissues (Van Eenennaam and Young, 2017); Blair and Regenstein, 2020). Over the period 1996–2011, Van Eenennaam and Young (2014) assessed the scientific evidence on the health and productivity of animals consuming feed containing GM ingredients and the composition of products derived from them, since on a global basis food-producing animals consume 70–90% of the biomass of GM crops. These datasets, representing over 100 billion

animals, did not show any unfavourable trends of concern. Also, the researchers found that no study had shown any differences in the nutritional profile of animal products derived from GM-fed animals. Although some consumers expressed concerns about the safety of GM foods, this was attributed largely to the fact that they had not been made aware of the extensive database of favourable findings, a very unfortunate aspect of the introduction of GM foods and food products.

As the journal *Nature Biotechnology* (Anonymous, 2013) stated in an editorial:

> Three decades after transgenes were first introduced into plants, why do so many consumers remain so negative about genetically modified (GM) food? … It does not matter that no adverse health effects have been recorded from eating them. Nor does it matter that august agencies, such as the World Health Organization, the US National Academy of Sciences, the European Commission or the American Medical Association, have come out with ringing endorsements of their safety. The fact is, negative attitudes remain entrenched and widespread. And changing them will require a concerted and long-term effort to develop GM foods that clearly provide convincing benefits to consumers and something that seed companies have conspicuously failed to do over the past decade.

In its analysis, the editorial outlined various factors that have contributed to the situation. One is that reports claiming negative effects on health are seized upon by anti-GM activists 'no matter how flimsy the evidence or flawed the study design' and 'All too often, an uncritical and sensationalist media leaps upon negative findings, continuing the cycle of scares, urban myths, and downright mistruths about GM food, all of which serve to stoke consumer paranoia.' The editorial found also that the public mistrusts most mainstream sources of data on GM foods, including large corporations, regulators, governments and even scientists. In

addition, European regulators have deepened the existing prejudices 'by creating a regulatory system that singles out GM products as sufficiently threatening to merit special attention'.

Although the main focus in assessing the relationship between GM crops and human health is safety, it is important to point out that the introduction of GM crops has had demonstrable human health benefits (Blair and Regenstein, 2020; Smyth, 2020). These benefits can be attributed to reductions in chemical use, increased crop yields and improved farm profits, resulting, for instance, in an improvement in financial well-being and a reduction in suicides among Indian cotton farmers. Grain quality has also been improved and, importantly, dangerous mould **contamination** decreased as a result of prevention of insect damage to crops. As outlined by Smyth (2020), smallholder farmers in developing countries gain most of the human health benefits because they generally lack the mechanized systems of **pesticide** application and the necessary protective clothing used in developed countries. Pesticide applications, especially on crops such as cotton and brinjal (eggplant, *Solanum melongena*), require numerous applications throughout the course of the growing season to ensure that insect damage is minimized. This can result in skin absorption of chemical residues by the farmers and pesticide **poisoning**. The introduction of GM crops, particularly Bt cotton, has resulted in significant reductions in farmer pesticide poisoning cases in China, India, Pakistan and South Africa, due to fewer applications and reduced levels of insecticide exposure (Smyth, 2020). Plewis (2014) examined the data under the aegis of the UK Royal

Statistical Society and found that the pattern of changes in suicide rates in India over the previous 15 years was consistent with a beneficial effect of Bt cotton, though not in every cotton-growing state in India. It is also clear from these data that glyphosate is a safer herbicide than alternative pesticides and requires a lower application rate. Glyphosate is one of the least toxic pesticides to animals (Duke and Powles, 2008). According to these authors, glyphosate is less acutely toxic than common chemicals such as **sodium chloride** or aspirin, with an LD50 for rats of over 5 g kg^{-1} compared with the LD50 of sodium chloride of 3000 mg kg^{-1} (rat) or aspirin at 200 mg kg^{-1} (rat). It is not a **carcinogen** or a reproductive toxin, nor does it have any subacute chronic toxicity. No toxic effects were observed in a chronic feeding study with dogs fed up to 500 mg kg^{-1} body weight per day, the highest dose tested. The introduction of insect-resistant crop varieties has also begun to have a noticeable potential to improve human health through a reduction in cancer rates (Smyth, 2020). Prior to the commercialization of Bt crops (maize in particular), insect damage to the harvested crop increased the likelihood of the development of products harmful to health due to mould contamination. A study of 21 years of maize production found that Bt maize contained lower concentrations of **mycotoxin**s (29%), **fumonisin**s (31%) and tricotecenes (37%) (Pellegrino *et al*., 2018). Mycotoxins are both toxic and carcinogenic to humans and animals and are of most concern in developing countries (WHO, 2018) related to factors such as climate, lack of food choices and food regulations. Fumonisins have also been linked to higher rates of neural tube

defects in consumers of high maize-based diets (Missmer *et al*., 2006).

Part of the background to the distrust of some consumers and elected officials in GM foods can be traced to the alarm raised by reports of two scientists, both of which were proved to be erroneous. The first was by Arpad Pusztai of the Rowett Research Institute in Aberdeen, Scotland, who in 1998 made the startling claim that diets containing GM potatoes had a deleterious effect on the gut of rats (Blair and Regenstein, 2015). Initial reporting of his findings was made in a very unusual way. Usually scientists present their findings at conferences of their peers, receive criticisms and comments, and subsequently publish the findings in peer-reviewed scientific journals. Later publication in magazines aimed at the general public may follow. According to the account of Fedoroff (2011), Pusztai announced his findings when he appeared on the British TV show 'World in Action' on 10 August, 1998. In the course of that interview, he was reported to have stated that his experiments demonstrated that rats fed a diet of GM potatoes showed stunted growth and reduced immune function. In answer to a question, he was further quoted as saying that he would not eat GM food and that he found it 'very, very unfair to use our fellow citizens as guinea pigs'. The announcement made headlines around the world. The most important aspect of the pronouncement by Pusztai was that not only was the transgenic potato that he was testing unsafe to eat, but that transgenic food in general was unsafe. This was the first major criticism of GM foods to be made by a respected scientist.

The pronouncement had several repercussions. An audit committee appointed at the Rowett Research Institute later that year studied Pusztai's laboratory reports and data and in an internal report concluded that the findings did not support the conclusion that the transgenic potatoes had a deleterious effect on growth, organ development, or immune function in rats. The report and the response of Arpad Pusztai and Stanley Ewen to members of a UK technical committee related to the studies were published in the 1999 *Annual Report of the Committees on Toxicity Mutagenicity Carcinogenicity of Chemicals in Food, Consumer Products and the Environment* (UK Department of Health, 1999). On the other hand, more than 20 scientists who had studied Pusztai's findings issued a memorandum supporting him, since he was regarded as an authority in the field of **lectin** chemistry. The Royal Society (1999) reviewed all the relevant material and issued a summary statement in June of that year. The consensus of the experts appointed by the Royal Society and by the Department of Health was that the experiments were poorly designed, the statistical analysis inappropriate, and the results inconsistent. Their recommendation was that the experiments be repeated and the results published. Pusztai published some results in 1999 as a member of the Department of Pathology, University of Aberdeen (his employment contract at the Rowett Research Institute had been cancelled). The paper appeared in a medical journal *The Lancet* (Ewen and Pusztai, 1999) as a Research Letter and provided summarized data on the effects of diets containing parent-line potatoes (Desiree), GM parent-line potatoes containing the GNA

gene from the *Galanthus* plant (which allowed the GNA lectin protein to be synthesized), or parent-line potatoes supplemented with 25.4 μg purified GNA g^{-1}, on the gut histology of rats. GNA was selected for expression in potatoes with the aim of making the crop resistant to insects and nematodes, as had been done with other crops. Also, it had been shown that the initial effect of GNA on the rat small intestine was minimal. ELISA analysis confirmed that the expression level in raw transgenic potatoes was 25.4 μg g^{-1} dry matter (DM) and was 4.9 μg g^{-1} DM after boiling for 1 h. Six rats were randomly allocated to each group and were fed the diets for 10 days. All the diets were isocaloric and contained an average of 6% protein. It was reported that the presence of GNA in the diets, irrespective of whether originating from GNA-GM potatoes or from parent-potato diets supplemented with GNA, was associated with significantly greater mucosal thickness of the stomach when compared with parent-potato diets. This effect was observed with both raw and boiled potatoes. Crypt length in the **jejunum** of rats fed on raw GM potato diets was significantly greater than in those given parent-line or parent-line plus GNA potato diets. However, the increase in jejunal crypt length was not seen in rats fed the diets containing boiled GM potatoes. GNA had no significant effects on the **ileum**, but rats fed boiled potatoes had shorter ileal crypts than rats given respective raw potato diets. Rats fed the diets containing boiled GM potatoes had significantly thinner caecal mucosae than rats fed the diets with boiled parent-line potatoes, with or without GNA supplementation. Therefore the authors suggested that 'the promotion of jejunal growth was the

result of the transformation of the potato with the GNA gene, since the jejunum of rats was shown to be stimulated only by GM potatoes but not by dietary GNA'. That conclusion is debatable, since the stimulatory effect was seen only with the diets containing raw potatoes. **Peyer's patch**es were reported to appear normal in all rats and GNA binding in the jejunum and ileum was found to be about the same, irrespective of whether the potato diets contained a supplement of GNA or GM potatoes. No data supporting the earlier claim of stunted growth were presented. This was a relatively small trial and it seems clear that no definitive conclusions could be made from the data presented, either as to the safety to the human consumer of the specific transgenic potatoes in question or transgenic foods in general. A fact that appears to have been omitted from the discussions related to this whole matter is that consumers were never exposed to any possible dangers from consuming the GM potatoes in question. These potatoes were at the testing stage and had not been approved for marketing to the public by any regulatory authority. Any alarm at the possible exposure of consumers to the GM potatoes was, therefore, somewhat premature and erroneous. In addition, the consumption of raw potatoes is never advised, since they are relatively indigestible and may contain a toxin that is destroyed by high-temperature heating.

The second report was a paper in *Food and Chemical Toxicology* in 2012 by a French group of scientists led by Gilles-Eric Séralini claiming that genetically modified (GM) maize caused cancer in mammalian species (Séralini *et al*., 2012a). The media

publicized the findings worldwide (Blair and Regenstein, 2015). Understandably, consumers were alarmed at the possibility that eating GM maize could kill them. The maize in question was Roundup Ready maize that was introduced by Monsanto in 1998 to tolerate spraying with glyphosate to control weeds in the maize fields. The maize cultivar had been approved for food and feed use in a number of countries, following a detailed assessment of its safety and nutritional equivalence to regular maize, an assessment procedure similar to that used in the approval process for new pharmaceutical drugs. Within weeks of the publication several hundred letters critical of the quality of the research were sent to the journal, especially since the conclusions were of such potential importance. Regulatory agencies in several countries, including Canada, Germany, Australia and New Zealand, as well as the European Food Safety Authority, stated that the research was of insufficient scientific quality to be considered valid. It was obvious from the Séralini data that deaths and incidence of cancers did not increase consistently as the amount of GM maize in the rat diet was raised. His data suggest that the observed mortality was unrelated to the presence of GM maize in the diet and was related more to advancing age of the test animals. The strain of rat used in his test is known to develop cancer spontaneously as it ages. As Séralini conceded in a rebuttal to the critics: 'The variability in rates of mortality can indeed, if looked at in isolation, arise in principle by chance.' Neither he nor any other group replicated and confirmed his findings.

The criticisms forced the journal to retract the paper. David

Spiegelhalter, Winton Professor of the Public Understanding of Risk at the University of Cambridge, UK, is reported as commenting:

> It was clear from even a superficial reading that this paper was not fit for publication, and in this instance the peer review process did not work properly. ... At least this has now been remedied and the journal has recognised that no conclusions can be drawn from this study, so I suppose it is better late than never. ... Sadly the withdrawal of this paper will not generate the publicity garnered by its initial publication.

A logical interpretation of the Séralini *et al*. (2012a) findings is that much more detailed research is required before the claim that GM maize causes cancer can be substantiated. While the study conducted by these researchers reported cancer induction in rats fed GM maize, the incidence may have been spontaneous and unrelated to treatment. The study was too small to differentiate these separate effects. Additionally, the toxic effects claimed were not dose-related, which was unusual if the GM maize (and glyphosate) were indeed toxic. Another conclusion is that Séralini *et al*. (2012a) may have had a point in suggesting that the testing period for GM foods should be longer than 90 days, but that any study designed to investigate long-term effects would have to follow an approved protocol and involve a suitable species of test animal. After carefully reviewing the study, six French national academies (Agriculture, Medicine, Pharmacy, Science, Technology and Veterinarians) issued an extraordinary joint statement condemning it and the journal that published it. The paper was also reviewed and refuted by the most prominent independent international science organizations and every food standards agency of note, including French HCB and the National Agency for

Food Safety; the Vlaams Instituut voor Biotechnologie, Technical University of Denmark; Food Standards Australia New Zealand; Brazilian National Technical Commission on Biosafety; and the European Food Safety Authority (EFSA). Six EU Member States (Belgium, Denmark, France, Germany, Italy and the Netherlands) also identified many of the same weaknesses in the methodology and design of the paper as raised by EFSA: unclear study objectives, the low number of rats used in each treatment group, a lack of detail on the feed and treatment formulation, key information missing on the statistical methods employed and incomplete endpoint reporting.

EFSA (2012) issued an official response to the paper by Séralini *et al*. (2012a) stating that it did not meet acceptable scientific standards and there was no need to re-examine previous safety evaluations of genetically modified maize NK603. In the course of the review process, EFSA had requested that Séralini *et al*. (2012a) provide further information on their study documentation. No such material had reached the Authority before publication of the EFSA statement. However, on 9 November 2012, Séralini *et al*. (2012b) published a general reply to the reactions from across the globe to their paper. After carefully examining this reply, EFSA concluded that it provided only a limited amount of relevant information, which failed to address the majority of the outstanding questions raised in the Authority's first statement. In their 'Answer to critics' document, Séralini *et al*. (2012b) conceded that the sample size of their treatment groups was too small to allow them to draw conclusions with regard to long-term carcinogenicity and mortality.

EFSA noted this acknowledgement from the authors but pointed out that it was inconsistent with the overall conclusions regarding the tumours and mortality made in the original paper.

Similar reviews and rejection of the claims made by Séralini *et al*. (2012a) and a decision to make no change to the existing authorization for the use of Roundup Ready Maize NK603 and the herbicide glyphosate in food production were made by Health Canada and the Canadian Food Inspection Agency (CFIA); the German Federal Institute for Risk Assessment (BfR); Food Standards Australia New Zealand (FSANZ); and the French Agence nationale de sécurité sanitaire de l'alimentation, de l'environnement et du travail (ANSES). These agencies reviewed information submitted previously to the regulatory agencies as well as published scientific literature on Roundup Ready Maize NK603 and glyphosate in addition to the Séralini *et al*. (2012a) data.

It should be noted that Séralini and co-workers claimed in previous publications (Séralini *et al*., 2007; Spiroux de Vendômois *et al*., 2009) that GM crops caused liver and kidney pathologies. The studies involved three cultivars of GM maize (NK 603, MON 810 and MON 863). However, the claims have not been supported by regulatory agencies and other scientists (Doull *et al*., 2007; EFSA, 2007, 2010; FSANZ, 2009a,b; HCB, 2009). MacKenzie *et al*. (2007), He *et al*. (2008) and Appenzeller *et al*. (2009) found no evidence of toxicity when GM maize 1507 or a related hybrid (1507 × 59122) were fed to rats.

In its response to the Séralini *et al*. (2012a) claims, EFSA indicated that one of the datasets used in the initial approval

process for Roundup Ready Maize NK603 was described by Hammond *et al*. (2004). This study involved a 13-week feeding study in which Sprague–Dawley rats were fed diets containing Roundup Ready or a commercial line of isogenic (not GM) maize at a concentration of 11% or 33% (w/w). There were 400 rats in the study, divided into ten groups of 20 rats/sex/group. Overall health, body weight, food consumption, clinical pathology parameters (haematology, blood chemistry, urinalysis), organ weights and histopathology of tissues were monitored. No significant differences in the study parameters were recorded. No health problems were recorded and all 400 animals appeared normal throughout the study. One male fed the diet containing 33% GM maize died unexpectedly on day 82, from an undiscovered cause: the animal had previously appeared healthy. No apparent cause of death was determined at necropsy, following microscopic examination of tissues. One male from a reference control group was euthanized on day 86 following an accident. Neither of these deaths was considered to be related to treatment.

Subsequent findings do not confirm the claim made by Séralini *et al*. (2012a). Hardisty *et al*. (2013) conducted a 13-week study in which young adult male and female Sprague-Dawley rats were fed diets containing grain from GM maize (DP-004114-3) that was either untreated (4114) or treated in the field with glufosinate ammonium (4114GLU). Control rats were fed diets containing the same concentration of near-isogenic, non-GM maize grain (091) or one of three types of commercially available non-GM maize. At the end of the test period renal tubule tumours were reported in two

male rats consuming diets containing the 4114 maize. Histopathological examination of the kidney tumours found that these were characteristic of amphophilic-vacuolar (AV) tumours. AV atypical tubular hyperplasia is reported to occur sporadically in young Sprague-Dawley rats. No degenerative/regenerative or cytotoxic changes consistent with nephrotoxicity leading to tumour induction were observed in the rats, supporting the conclusion that the tumours were unrelated to the test maize.

Delaney *et al*. (2013) conducted a similar study with GM maize 4114 (a stacked-trait cultivar with tolerance to glufosinate herbicide and resistance to insects) that was included at a level of 320 g kg^{-1} in diets fed to Sprague-Dawley rats. A control diet contained an isogenic line (091 maize). The GM maize was from crops either untreated or treated with glufosinate ammonium. This study was conducted in accordance with OECD guidelines, for a total of 91 days. No significant ($P < 0.05$) treatment differences in body weight, food consumption, or clinical pathology parameters (haematology, blood chemistry, urinalysis, or organ weight) were observed.

Zhu *et al*. (2013) fed diets containing 12.5%, 25% and 50% GM (glyphosate-tolerant) or a non-GM isogenic control in a 90-day feeding study with Sprague-Dawley rats. An additional group of rats was fed a commercial diet as a control. Body weights, food consumption, serum biochemistry, haematology, and absolute and relative organ weights were compared, and gross and microscopic examination of tissues was conducted. No adverse effects related to GM maize were detected.

Thus, other than the Séralini work, all similar studies reported in peer-reviewed publications show no safety issues. No other investigators appear to have replicated the findings reported by Séralini *et al*. (2012a). Nevertheless, the issue of conducting a proper long-term study remains.

In an interesting development Séralini republished the rejected paper in an open-access environmental journal without peer-review (Séralini *et al*., 2014).

At least one section of the media understood the importance of the claims by Séralini and their rejection by the scientific community. 'This whole episode has taken us farther away from knowing the truth,' Ivan Oransky (a journalist with a medical degree who is also vice president and global editorial director of MedPage Today, and a founder and editor of retractionwatch.com), told CBS News (CBS News, 2014). 'The ratio of politics to science when it comes to discussions of GMOs [genetically modified organisms] is so high that I think it often ceases to be useful.'

Oransky noted that retracted papers do get republished on occasion, and that of the 1.4 million scientific papers published every year, most are inconclusive: 'It is the nature of science.' Even research of the highest quality needs to be confirmed or extended:

> This is a good example of what happens when people with hardened beliefs manipulate a system for the result they want. Science should be about following the evidence, appropriately changing your mind if the evidence warrants it. But in this case people seem to reject the evidence that doesn't suit their needs.

What emerges from a consideration of the facts surrounding GM foods is that support or opposition to GM technology is not based simply on established scientific facts. The situation is

complicated by biases, ethical and moral considerations and international trade considerations.

As a result of the controversy not all countries and regions adopted biotechnology to improve the quality and yield of food crops, in particular Europe. According to assessments by leading European scientists, this can be attributed to a policy that discriminates against the cultivation of GM crops (e.g. Masip *et al*., 2013), based on a stated uncertainty of the technology and the public attitude to GM foods. This EU policy was criticized as a trade barrier to the importation of cereal grains and grain products from countries using GM technology, resulting in the USA bringing a case to the World Trade Organization (WTO) against the EU's failure to implement a timely, science-based approval system for food and feed products enhanced through biotechnology. Several other countries, including Argentina, Australia, Canada, Chile, Colombia, El Salvador, Honduras, Mexico, New Zealand, Peru and Uruguay, joined the USA in the complaint because they also wished to ensure that science-based determinations are applied to regulatory decisions. In 2006 the WTO ruled that the EU had failed to meet its WTO obligations of implementing a timely, science-based system for the approval of biotech-enhanced agricultural products. As a result, the European Community in 2006 announced its intention to implement the ruling. In 2021 it issued the following statement:

> Following the mutually agreed solutions reached with Argentina (document WT/DS293/41) and Canada (WT/DS292/40), the European Union remains ready to continue its discussions with the United States with the goal of resolving this dispute and related issues.

British farmers also objected to the EU policy of restricting the cultivation of GM crops – one of the reasons why the UK left the EU in 2020.

As a result of the controversy regarding GM foods and food products, several countries introduced special **labelling** requirements, since no policy had been internationally agreed. In 2003 the EU introduced a requirement that in the case of pre-packaged GM food/feed products, the list of ingredients must indicate 'genetically modified' or 'produced from genetically modified [name of the organism]'. In the case of products without packaging, these words had to be clearly displayed in close proximity to the product (e.g. a note on the supermarket shelf). These labelling requirements did not apply to GM food/feed products 'in a proportion no higher than 0.9 percent of the food/feed ingredients considered individually and if the presence was adventitious or technically unavoidable'. In addition, GM food served in restaurants does not appear to be subject to mandatory labelling requirements in any country.

Whereas the regulatory system in the EU focused on the technology used in the development of GM crops, other countries such as the USA and Canada regulated GM foods and food products on the basis of the traits expressed and not on the basis of the method used to introduce the traits, whether achieved using conventional breeding, mutagenesis, or GM technology. This was in line with the policy of the American Association for the Advancement of Science (AAAS, 2012) which stated that:

> … it is the long-standing policy of the Food and Drug Administration (FDA) that special

> labelling of a food is required if the absence of the information provided poses a special health or environmental risk. The FDA does not require labelling of a food based on the specific genetic modification procedure used in the development of its input crops. Legally mandating such a label can only serve to mislead and falsely alarm consumers.

Nevertheless in 2018 the USA announced the National Bioengineered Food Disclosure Standard, with a mandatory compliance date of 1 January, 2022. The Standard defines bioengineered foods as those that contain detectable genetic material that has been modified through certain laboratory techniques and cannot be created through conventional breeding or found in nature. The Standard requires 'food manufacturers, importers, and certain retailers to ensure that bioengineered foods are appropriately disclosed'. Canada did not follow the lead of the US in requiring the special labelling of GM foods and food products. As outlined in the regulations in Canada (Government of Canada, undated):

> There are no specific laws in Canada about labelling GM foods differently. They are labelled like any other food because our safety assessments have found them to be as safe and nutritious as non-GM foods. It is not mandatory to identify the method of production, including genetic modification, used to develop a food product. All food products, whether organic or non-organic, must comply with the labelling rules of the Food and Drugs Act and the Safe Food for Canadians Act.

On the other hand, special labelling is required for all foods, including GM foods, where there are health and safety concerns such as: the potential to cause allergic reactions, changes to the composition of the food, or changes to the nutritional quality of the food. Singapore and several other countries also do not require special labelling of GM foods, although these foods must meet stringent safety and efficacy standards. Japan (one of the largest

importers of GM foods) and China adopted labelling regulations more in line with those of the EU. The regulations introduced in Australia and New Zealand require that all GM foods and ingredients (including food additives and processing aids) that contain novel DNA or novel protein must be labelled with the words 'genetically modified'. Their labelling is intended to allow consumers to make an informed choice about the food they buy, not about safety.

The effect of food labels on purchasing choices has been studied by several researchers. Sleenhoff and Osseweijer (2013) pointed out one of the limitations of survey responses, namely the discrepancy between stated buying intentions and actual buying behaviour. With a mandatory labelling scheme for GM food in Europe since 2004 it was possible to measure consumer choice in practice. These researchers studied the actual purchase behaviour of European consumers of GM food products and compared it with their stated intentions to buy GM foods. They found that despite a majority of consumers expressing a negative attitude toward GM food, over 50% of respondents did not actively avoid the purchase of GM foods and 6% actually purchased one of the few available GM labelled food products. This type of result, apart from suggesting the unreliability of some food choice surveys, might be expected, with GM foods and food products becoming an integral part of the food supply and consumers becoming better informed. A survey in the USA (IFIC, 2018) found that 36% of respondents knew very little or nothing at all about bioengineered or genetically modified foods, the same number as those who knew at least a fair

amount. Despite the low level of knowledge, 47% said they avoid GM foods at least part of the time. The vast majority (85%) of those who avoid GM foods did so out of human health concerns. Fernbach *et al*. (2019) obtained similar findings in a survey of consumers in the USA, France and Germany, extreme opponents knowing the least about GM foods but thinking they knew the most.

Addressing this issue by ensuring that consumers are better informed on the established facts relating to GM foods remains an obvious priority. However, a major challenge will be determining and applying the most effective method of doing so while warning notices still appear on the labels of GM foods, indicating that politicians also need to become better informed about GM foods. As noted by Blair and Regenstein (2020), it is likely that consumers, particularly young people, are now more receptive to news about GM foods than previously. More balanced reports on food quality are being published in the popular media, written by better-educated journalists. This may explain why a survey conducted by the *New Scientist* (Lawton, 2018) in the UK on public attitudes to science, technology, medicine and environment found that the UK public is well-informed and supportive of current developments in science and technology. The survey was conducted in August 2018 with a representative sample of 2026 UK adults, not all of whom were readers of the *New Scientist* magazine. Results showed that the issues of most importance were genetic engineering, artificial intelligence, cancer and climate change, since they were regarded as most likely to have an impact on society and human life. In addition, the survey showed that majority (69%)

were in favour of (GM) crops, stating that they could help feed the world. A large percentage (80%) also believed that genetic engineering could help cure or eradicate diseases. Social media were perceived by survey respondents negatively, largely because of fake news, trolls and peer pressure on young people. One surprising finding of the survey was that politicians were regarded as ignoring public hopes and fears, reinforcing the suggestion above that politicians need to become better informed on current issues in science and technology, particularly in relation to GM foods.

In a welcome initiative in Africa, the Uganda Biosciences Information Center initiated a series of teachers' training workshops in 2018 to create and increase a countrywide appreciation of integration of biosciences in the country's formal education system. Developing a better appreciation of the benefits of biotechnology in relation to food production in the general population of consumers is an objective that should be adopted universally. (RB)

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Genotype

The term genotype refers to a combination of genes that are found within a species, giving rise to consistent identifiable breed characteristics. The Global Databank contains information on almost 4000 breeds within 28 domesticated animal species. There is enormous genetic diversity within species, affecting a wide range of traits related to body size and conformation, physiology, biochemistry, disease resistance, etc. For example, over 350 breeds of pig have been identified, of which almost half originated in Asia. One of the most obvious characteristics is colour and at least 25 different colour-related alleles have been identified within the pig population. In poultry, sex-linked genes creating yellow and a variety of red, brown and black patterns in the down of day-old chicks allow colour-sexing in brown-feathered layers and some broilers. Coat colour and length (or, in the case of birds, feather colour and cover) can be important adaptations to particular environments. For example, in domestic poultry a major gene reduces body feather cover by 25–30% and is useful in enhancing broiler performance in hot climates.

Within species certain breeds have particular production traits, which have been exploited by genetic selection. Cattle are used mainly for production of meat, milk or both, although they were traditionally used as draught animals and still are in developing economies. Certain breeds, e.g. Charolais, are more suited to fast lean growth and reach high mature weights and are thus particularly suitable for beef production. Others, such as Holstein and Ayrshire, are less suitable for **meat production** but produce high milk yields and the small dairy breeds (Jersey and Guernsey)

are noted for high contents of **butterfat** in the milk. Within the cattle population there are two main subspecies: *Bos taurus*, the main source of domesticated breeds in Europe and North America; and *Bos indicus*, source of many breeds in Asia and Africa. *Bos indicus* has a very different body shape from *B. taurus*, with a shoulder hump, pendulous dewlap and a higher number of **sweat** glands, which help the animal to survive much better in hot conditions.

Commercial domestic fowl have been selected, especially over the past 40 years, for either egg or meat production. Most egg-laying strains produce eggs with white or brown shells. The world market is split almost equally between white and brown shells. Egg-laying breeds of low mature body weight have been intensively selected to increase egg numbers while keeping the maintenance **energy requirement**s low to improve production efficiency. On the other hand, the larger breeds have been selected for high food intake leading to fast efficient growth. The skin of the majority of chickens is white or yellow. Some markets prefer a meat chicken with a yellow skin and this can be enhanced by feeding a diet high in xanthophylls or other yellow pigments.

Mature size differences are a common feature in all species. For example, many of the hill sheep breeds are small, thus reducing energy requirements in times of food shortage; lowland breeds may be twice as large. Similarly, within the horse species, there is a range of pony breeds on the one hand in contrast to the large draught horses such as Shire, with stallions weighing up to 1000 kg.

One danger arising from intensive selection of a few breeds with particular production traits is the possibility of losing breeds and thus diminishing the genetic pool. This has been particularly noticeable with pigs and domestic chickens, where breeding programmes tend to be dominated worldwide by a handful of breeders. One good example of the economic benefit of maintaining genetic diversity is in the increasing use of the Chinese Meishan pig in cross-breeding programmes to introduce improved prolificacy and mothering qualities into the more efficient Landrace breeds that have dominated because of fast, efficient production of lean meat. (KJMcC; KDS)

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Genotype–nutrition interaction

The performance of a trait by individuals or groups of animals of one breed or strain – the phenotype – is determined by the

response of the **genotype** to the environment. Environment in the broadest context includes all aspects of husbandry and management from conception or incubation, and includes nutrition. The performance of an individual is an example of an interaction between a specific genotype and nutrient intake from a specific **feed formulation**. When a flock or herd of one breed or strain is considered there is variation in the genotype, because even siblings are not clones. Each individual has a unique assembly of genes. Given a situation in which all other aspects of environment are the same, groups of animals receiving the same nutrient intake may be expected to differ in performance; this is the result of an interaction between the genotype and the nutrients consumed. Given that there will be variation in the nutrients in different samples of feed (i.e. the samples that individuals consume each day), the interaction between the genotype and feed can be considered as the normal variability of performance. The practice of nutrition – formulation, feed compounding and feed distribution – attempts to minimize the variability of nutrient intake between individuals and the contribution it makes to phenotypic variance. These types of interaction are often referred to as micro-environmental. The subject is the individual, whose experience of the nutritional conditions is independent of conditions encountered by other members of the flock or herd.

Important genotype–nutrition (G × N) interactions occur when large genotype differences are combined with large differences in nutrient supply. The changes in nutrient supply do not directly change the response of each genotype in the same manner. The

change in performance is not predictable from the average genotype and nutritional effects; in other words, the effects are non-additive and an interaction has occurred. The interaction demonstrates how gene expression may be changed by differences in nutrient supply. The following discussion will focus on poultry to provide examples of the types of interaction that occur; however, similar interactions occur in mammalian species and indeed the phenotypic variations are at least as large, due to the fact that mammalian females give birth to only one or up to 12 offspring at a time.

Horst (1985) examined 181 experiment reports, over the period 1938–1981, for various genotype × environment (G × E) interactions in laying hens. Of these experiments, 81 involved genotype and feeding and 37 (about 50%) reported the presence of an interaction. The traits showing interactions were body weight, age at sexual maturity, egg production, egg weight, albumen quality, shell quality, fertility and hatchability and mortality. These traits cover a wide range of heritability levels but the magnitude of the interactions was generally greater in traits with lower heritability. Thus there is a negative association between a high G × E interaction and a lower heritability. However, since heritability is a ratio between additive variance and phenotypic variance, a large G × E interaction would indicate a high non-heritable variation rather than a lack of heritable variation (Cahaner, 1990). Equally important is the fact that important economic traits – body weight, egg production, egg weight, age at first egg, and albumen quality – demonstrate a change in performance that may not be predicted by

known input–output relationships.

There are numerous complex relationships involved and three are highlighted below.

Carcass quality

Integrated broiler production and processing companies have the opportunity to use breed packages (parent stock from the same breeding company) or to choose male and female parents from different breeding companies, in order to maximize profits from the products they supply to the various markets. Extensive breed and breed-cross evaluation trials are conducted by some integrators. Breed choice decisions are based on live performance of parents and broilers and the end-product yields and quality. G × N interactions have been demonstrated in studies on carcass **meat yield**s involving breeds and breed crosses. After producing a short list of breeds or crosses, following extensive screening of breed candidates, further evaluation of feed nutrient levels is required to tailor the feeding programmes. The least-cost feed formulations can then be targeted to achieve optimum performance in the final product, be it whole **carcass**, pieces or a **meat product**. Increasingly, decisions on feed formulations to optimize feeding of commercial broilers are based on computer modelling. Awareness of G × N interactions is therefore crucial to the reliability of decisions based on the model technique.

Immunoresponsiveness

In general, selection for faster growth has reduced immunoresponsiveness to pathogens. Responses by different genotypes indicate that resource allocation to general fitness has

decreased as that to growth has increased. Various G × N interactions, such as those between feeding methods and broiler genotypes (post-inoculation lesion scores to ***Escherichia coli*** challenge; Boa-Amponsem *et al.*, 1991) and feed nutrient content and broiler versus layer genotypes (antibody titres to sheep red blood cells, and heterophil:lymphocyte ratios; Praharaj *et al.*, 1995), indicate that feeding regimes need to be tailored to optimize disease resistance (the phenotype) for specific genotypes. Deviations from the optimum nutrition would predispose susceptible genotypes to adverse thermal and gaseous environmental and infectious agent challenges.

Feed intake

There are differences among breeds of laying hens in the response of **feed intake**, and therefore **energy intake**, to changes in dietary energy content. In general, lighter breeds are able to adjust feed intake to maintain a constant energy intake whereas heavier breeds have a lesser ability for adjustment and show an increasing energy intake as dietary energy content increases. At a basic level of least-cost formulation of feeds it is important to establish the feed intake characteristics of a commercial layer. This relationship is then included in the formulation constraints and the outcome is least-cost feeding rather than least-cost per weight of feed. This is possible in cage operations where feed delivery is mechanized, often quantitatively accurately, for the expected performance of a layer. Extensive production systems, where layers are expected to scavenge for a portion of their daily requirements, may not be suitable for layers bred for cage systems. Those with a small

appetite may not be able to consume adequate nutrients for production and maintenance of an efficient immune system. Laying hens bred for cages have under-performed in scavenging situations and have been out-performed by scavenging breeds (e.g. Sørensen, 1999). (WKS)

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Gentiobiose

Disaccharide (molecular weight 342) of two β-linked (1→6) **glucose** units, in **pyranose** ring form. Gentobiose is an enzymatic or chemical degradation product of 1→6 β-linked D-glucose side chains of β-linked-D-**glucans**. Gentiobiose is found in brown marine algae, cereals, moulds, yeasts, lichens and bacteria. It is not metabolized by endogenous enzymes of non-ruminants. (JAM)
See also: Carbohydrates; Oligosaccharides

Geophagia

A form of pica. The intentional consumption of earth or soil, most usually by herbivorous animals. Benefits include improving the mineral status of animals, particularly, Na, Cu, P, Cu and Fe, and self-medication, since clay can bind a number of toxic compounds and microorganisms in the gastrointestinal tract. A fixated **appetite** for soil is common in some farm animal species,

particularly cattle, but with high individuality. **Kaolin** is used for gastrointestinal disturbances in humans and in parts of Africa soil consumption is a traditional practice. Although the intake of elements from ingested soil can be significant, their availability is often low due to the elements being **chelate**d in the soil matrix. Indeed, addition of certain soils to the diet, and in particular **zeolite**s, can reduce the absorption of some toxic elements. Health risks exist when soils with potentially pathogenic microorganisms or toxic metals are consumed. Many pathogenic bacteria survive in soil for considerable periods of time, sometimes in a dormant state, until consumed by a suitable host. Soil around metal workings or smelters is likely to contain potentially lethal concentrations of **heavy metals**, in particular lead. (CJCP)

Germ-free animals

Animals raised entirely free of **microorganism**s. Animals are normally sterile whilst in the uterus or the egg but acquire their first microorganisms during birth or hatching. To maintain a germ-free status, mammals are delivered by caesarean section or delivered naturally with special sterile precautions. Birds can more easily be reared germ-free by disinfecting the outsides of the eggs and hatching them in a sterile incubator. After birth or hatching, germ-free animals are kept continuously in a sterile enclosure, with filtered air and water and sterilized food, passed in through an air-lock. The main uses of germ-free animals are in disease research but they are also used in nutrition studies when the influence of the **gastrointestinal microflora** is to be studied. As a result of their lack of commensal gut flora, the **gastrointestinal tract**s of germ-

free animals tend to be enlarged and anatomically different from those of conventional animals. (MFF)

Germination

Seed germination requires moisture, oxygen and a suitable **temperature** (optimum 30°C). Seeds absorb water, raising the moisture content from 10% to 40%. **Protein** and **nucleic acid** synthesis increases. Proteases and **amylase**s catalyse the breakdown of the **endosperm** for translocation of nutrients, with **starch** in the endosperm being converted to dextrins, **maltose** and other **sugars**. Germination increases the **lysine** and sugar contents but decreases the starch and fibre contents of the seeds, with no other major change in composition. In **malting**, seeds are germinated for the purpose of brewing. The **by-product**s, which include malt culms, brewers' grains, brewers' yeast and draff, are used for animal feed. (JKM)



Germination of bean seeds. Photo courtesy of Ritesh M. Tamrakar. Licensed under CC BY SA 2.0.

Gestation:

see Cow pregnancy; Ewe pregnancy

Gestation period

The time (usually expressed in days) from conception to giving birth in viviparous animals. The gestation periods (in days) for farm animal species are as follows. (PJHB)

Species	Gestation period (days)
Cattle (*Bos taurus*)	279–290
Cattle (*Bos indicus*)	282–292
Sheep	144–152
Goats	144–151
Pigs	112–117
Horses	310–365
Red deer	225–245
Buffalo	310–330
Bactrian camel	370–440
Dromedary	355–390
Llama	330–340
Rabbit	30–32



Heavily pregnant goat. Final stages are marked by swelling of the udder. Photo courtesy of Jordan Fischer. Licensed under CC BY 2.0.

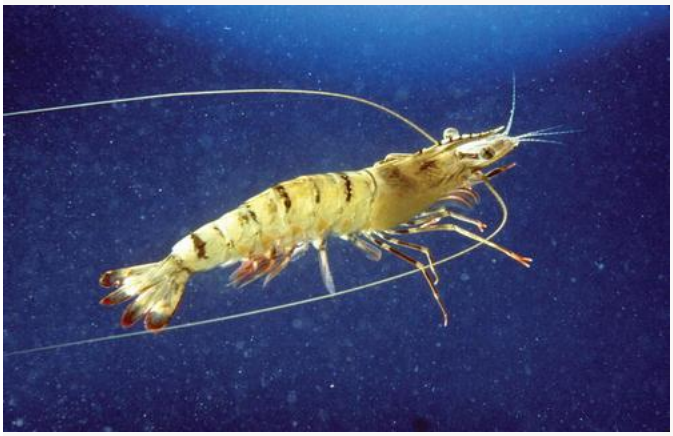
Ghrelin

A 28 amino acid **peptide** that in many vertebrate species is produced by the X/A-like endocrine cells in the stomach, and to a lesser extent the pituitary gland and other tissues. Discovered in 1999, it functions primarily as a **growth hormone** secretagogue and signal for **hunger** to the **hypothalamus** of the brain. Ghrelin levels increase dramatically before food consumption and then gradually subside. It has multiple other roles, including regulating the long-term **energy balance** and nutritional status, in which it increases body weight and adiposity. Exercise suppresses ghrelin production. It also contributes to anti-inflammatory responses. Stress triggers a more prolonged and greater increase in ghrelin in obese than lean individuals, which may explain links between stress susceptibility and **obesity**(CJCP)
See also: Leptin

Giant tiger prawn (*Penaeus monodon*)

Otherwise known as the black or Asian tiger **shrimp** (*Penaeus monodon*). The giant tiger prawn is currently the fourth most farmed crustacean species globally, with a total amount of 750,600 t (8.0% of cultural crustaceans) in the world in 2018. This species can tolerate a wide range of environmental salinity levels, ranging from 5‰ to 35‰ (Deris *et al.*, 2020; Rahi *et al.*, 2021). Because of the strong demand in international markets, black tiger shrimp farming has become prominent throughout the coastal regions of

Asia, Australia and many Pacific island countries (Ali *et al.*, 2008; Aziz *et al.*, 2011). *P. monodon* also acts as a major source of livelihood and export earnings for many tropical and sub-tropical countries. (QS)



Giant tiger prawn. Photo courtesy of CSIRO. Licensed under CC BY 3.0.

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Gills
Organs whose primary purpose is to obtain dissolved **oxygen** from water. They may also transfer inorganic ions or excrete wastes. They are filamentous processes of the pharynx of **fish**, but aquatic invertebrates possess a variety of functionally analogous structures (such as ctenidia in the molluscan mantle cavity). In teleosts, gill filaments radiating laterally from the pharyngeal arches bear 10–30 interdigitating lamellae where respiratory exchange occurs. The gill area may range from 150 to 2000 mm^2 g^{-1} body weight. (RHP)

Gilt
A young female pig. In the growing phase, gilts have a protein deposition rate and **feed intake** which is intermediate between those of castrates and entire males. The term gilt is also commonly used for young breeding sows during their first pregnancy and **lactation**. During this time, an additional allowance of nutrients must be made for their continuing **growth**. (SAE)

Gilthead sea bream (*Sparus aurata*)
A species that ranges from the Mediterranean and Black Sea to the eastern Atlantic Ocean from the southern part of the British Isles to Senegal. Sea bream is farmed in several Mediterranean countries; Greece, Turkey and Spain are the major producers. Juvenile fish (1–5 g) are stocked in either sea cages or land-based tanks and

earthen ponds. They reach a market size of 400–500 g over a period of 12–14 months. Gilthead sea bream are hermaphrodites and develop as males during the first year. After the **spawning** season, the males begin to develop ovaries until early autumn. At this stage, fish either develop as females or absorb the ovarian tissues and redevelop male gonads. (SPL)



Gilthead sea bream. Photo courtesy of Tony Hisgett. Licensed under CC BY 2.0.

See also: Marine fish

Ginkgo (*Ginkgo biloba*)
A tree native to China, with short branches of small, compact, kidney-shaped leaves and long branches of broad, two-lobed leaves, similar to the leaves of the *Adiantum capillus-veneris* plant. The petioles are long and the colour of the leaves turns yellow in autumn (Zargari, 1997).



Ginkgo tree. Photo courtesy of Pietro Zanarani. Licensed under CC BY 2.0.

Organic acid compounds, **terpenes** and certain **sterols** are present in the leaves. They also contain flavones, **flavonoids**, ginkgetol, isoginkgetol, and bilobetol. Gencolides A, B and C are extracted from the leaves and it is claimed that they have the pharmacological action of dilating blood vessels and increasing **blood** circulation. The extracts are claimed to be effective in treating blood circulation disorders, dizziness and headaches, and strengthening memory (Zargari, 1997; Boateng and Yang, 2022). The roasted seed of the plant has nutritional uses, after processing to reduce the content of toxic ginkgotoxin, ginkgotoxin-5-**glucoside** and gincolic acid, but the tree bark is a potentially toxic stimulant (Boateng and Yang, 2022). From the pure leaf extract, compounds called tanakan and ginkor are obtained, which are widely used in the formulation of medicinal compounds. The

global trade of the ginkgo plant in the field of food and medicine is estimated at more than US$1.26 billion per annum (Zargari, 1997; Shareena and Kumar, 2022). It is claimed that leaf extract can improve nutrient **digestion**, act as an antioxidant, reduce stress and improve growth in chickens and fish (Hajirezaee *et al*., 2021; Niu *et al*., 2019). (AS; BH-G; CJCP)

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Ginseng

Panax ginseng (Korean ginseng) and *Panax qinquefolium* (American ginseng), a plant used in Chinese medicine that naturally grows in mountainous areas of eastern USA and Canada.

Nowadays, due to its use in the pharmaceutical industry, it is also cultivated in favourable areas of China.



Ginseng (*Panax quinquefolium*). Figure courtesy of UWDigitalcollections. Licensed under CC BY 2.0.

The plant possesses a swollen root, and the compound leaves have five (or more) pointed toothed leaflets and umbrella-shaped flowers. The root of this plant contains the active compound paraquilon, which is a yellow water- and alcohol-soluble substance. It has a bitter **taste**, similar to glycerine. This compound is widely used as a **glycoside**. In addition, the root of this plant contains **starch**, resin, essential **oil**, **sterol**, group B vitamins and saponozoids (also called ginsenosides), with numerous pharmacological effects. It is claimed to be effective in relieving physical and mental fatigue, and strengthening the nervous system

(Zargari, 1997; De Oliveira Zanuso *et al*., 2022). It is mostly used in the formulation of medicine, claimed to inhibit inflammatory signalling pathways, provide antioxidant and anti-inflammatory benefits and protect the central nervous system. The use of ginseng extract to positively regulate **high-density lipoprotein**, reduce the level of low-density lipoprotein and triglycerides, and improve vascular endothelial function has also shown promising results (Zargari, 1997; De Oliveira Zanuso *et al*., 2022). Feeding ginseng to animals increases sex **hormone**s, and the administration of **saponin**s extracted from ginseng stems and leaves in drinking water to chickens improved their immune responses to vaccination against Newcastle disease, avian influenza and infectious bursal disease (Chaudhary *et al*., 2018). (AS; BH-G; CJCP)

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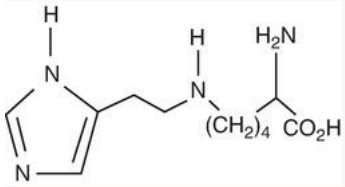
Gizzard

Sometimes known as the muscular **stomach** or ventriculus, present in birds but also found in some fish and invertebrates, the

gizzard is a large, bulbous, muscular organ located adjacent and distal to the **proventriculus**, lying partially between the lobes of the **liver** in the upper left-hand side of the abdominal cavity in birds. When the gizzard is empty, food and grit pass directly through the crop to the proventriculus. In adult domestic fowl, the gizzard measures about 5 cm in diameter and 2.5 cm in thickness and has a smooth, non-striated musculature rich in myoglobin. The inner aspect of the gizzard is of a hardened keratinoid membrane with a cuticle occasionally referred to as the 'koilin layer'. The asymmetrical arrangement of the muscles in the gizzard rotates as well as crushes and grinds the food, like millstones. Aided by the gastric secretions from the proventriculus, this ground food passes through the pyloric valve into the first section of the **small intestine**, the **duodenum**. The characteristic green or yellow colour of the gizzard is caused by regurgitation of **bile** from the duodenum via the pylorus. Some studies suggest that the gizzard may be under **circadian rhythm** control, with activity being reduced during darkness. (MMax)

Gizzerosine

$C_{11}H_{20}N_4O_2$, molecular weight 240. A **dipeptide**-like compound of **histamine** and **lysine**, formed by Maillard **browning** reactions during the heating of proteins, notably fish meal.



Gizzerosine causes **gizzard** erosion in poultry, characterized by

necrosis of the lining tissue with ulceration of the muscle wall. Gizzard erosion may also be caused by consumption of grains contaminated with **mycotoxin**s. (DRG)

Globe artichoke (*Cynara scolymus*)

A member of the Compositae family. Globe artichokes are grown for the immature flower buds, which are used as human food. The fleshy bases of the flower bracts and the receptacle to which the bracts are attached are known as the 'heart'. Commercially produced fresh globe artichokes are commonly found on the market all year round. They may be available for animal feed due to oversupply or inferior quality. They can be fed to dairy and beef cattle at 30% and to ewes at 20% of the total diet. The dry matter (DM) content of globe artichokes is 150 g kg^{-1} and the nutrient composition (g kg^{-1} DM) is: **crude protein**, 32.7; **crude fibre**, 54; **ether extract**, 1.5; **ash**, 11.3; and **starch** and **sugar**, 105; with GE of 197 MJ kg^{-1}.



Globe artichoke. Photo courtesy of 305 Seahill. Licensed under CC BY-ND 2.0.

The inclusion of *Cynara scolymus* powder and extract in

poultry nutrition may improve the **antioxidant** status of poultry blood. These effects are especially noticeable under stress conditions, leading to strengthening of the immune system and antibody production, and increasing the activities of hepatic antioxidative enzymes (Zaker-Esteghamati *et al*., 2021). The artichoke may offer a replacement for in-feed antibiotics. (JKM; AS; BH-G; CJCP)

Reference

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Globulins

One of the three major classes of plasma proteins (**albumin**, globulin and **fibrinogen**). The globulins are further subdivided into four identifiable forms: α_1, α_2, β and γ. The γ-globulin proteins comprise the well-known antibody fraction of plasma proteins. (NJB)

Glucagon

A polypeptide **hormone** of 29 **amino acid**s synthesized by α cells in the islets of Langerhans of the endocrine **pancreas**. Glucagon is the major metabolic hormone that is released in response to low concentrations of blood **glucose**. It acts through a cyclic-adenosine monophosphate (cAMP)-mediated intracellular pathway to stimulate the breakdown of **glycogen** in **liver**, thereby elevating blood glucose levels. (GG)

Glucanase
A class of enzymes that hydrolyse **glucans** involving either one or several types of linkages. Typical glucanases include 1,3-β-D-glucanase, 1,4-β-D-glucanase, 1,6-β-D-glucanase, 1,3-α-D-glucanase, 1,6-α-D-glucanase (dextranase), **cellulase** and lichenase. Different enzymes vary markedly in their **substrate** specificity, some being highly specific for a particular bond, others actively hydrolysing several different bonds. They are produced by bacteria, **yeast** and **fungi**. (NJB)

Glucans
Homopolysaccharides of linear or branched **glucose** residues, α- or β-linked, with molecular weight 20,000–1,000,000. The β-linked D-glucopyranose polymers are found as constituents of fungi, algae and higher plants, such as **cellulose**, callose, curdlan, laminaran, lichenan and β-glucans in cereals; α-linked D-glucopyranose polymers are found as constituents of moulds, yeasts, lichens, bacteria, higher plants and animal tissues and include **amylose**, **amylopectin**, **glycogen**, pullulan and dextran. Animals have endogenous α-**amylase**s but not β-amylases, but β-**glucans** are degraded by intestinal bacteria. (JAM)
See also: Carbohydrates; Dietary fibre; Starch

Glucoamylase
A glycolytic enzyme (exo-1,4-α-**glucosidase**; 1,4-α-D-glucan glucohydrolase; EC 3.2.1.3) that cleaves **glucose** from **maltose**, **maltotriose** and other polymers of glucose in α(1–4)-linkage. A number of industrial enzymes with this activity, purified from

microorganisms, are called **amyloglucosidase**. (SB)

Glucocorticoids
Steroid **hormone**s that are made from **cholesterol** in the **adrenal** cortex. In the rat, corticosterone is the glucocorticoid that promotes **gluconeogenesis**. In humans, cortisol is the glucocorticoid that promotes gluconeogenesis. Glucocorticoids increase gluconeogenesis most likely because they increase protein breakdown and amino acid **catabolism**, making the amino acid carbon available to the liver for **glucose** production. (NJB)

Glucofructans
Includes fructo-**oligosaccharide**s, both naturally occurring and those produced from **fructans** such as **inulin**. All naturally occurring fructans are really glucofructans, because the reducing end of the **fructose** chain is glycosylated to the reducing end of a glucose molecule. (JAM)
See also: Carbohydrates; Dietary fibre; Raffinose

Glucokinase
One of two enzymes involved in converting **glucose** to glucose-6-phosphate in the cytoplasm. Glucokinase is housed in the liver while hexokinase, the other enzyme, is in muscle. Both of these enzymes are involved in sequestering glucose into the cell by converting glucose to glucose-6-phosphate, which lowers the potential loss of glucose from the cell by **diffusion** because it is no longer glucose. The k_m of glucokinase for glucose is such that variations in the activity of the enzyme change with glucose

concentration in the physiological range. Thus, short-term regulation of the activity of the enzyme is built into the system by the k_m and changes in the amount (activity) of enzyme are not dependent on changes in its synthesis or degradation. (NJB)

Gluconeogenesis

The process whereby **glucose** is biosynthesized from products derived from glucose (**lactate**), from **sugars** that are not glucose (e.g. ribose), from the **glycerol** portion of **triacylglycerol**s, from some amino acids or from breakdown products that provide four (**propionate**, aspartate) or five (**glutamate**) carbon intermediates to the **citric acid** cycle. Gluconeogenesis occurs in the liver and kidneys. It is normally a cyclic process that occurs after consumption of a meal when **substrates** enter the body faster than they are catabolized. Thus, some of the extra energy can be stored in glucose that can then be incorporated into **glycogen** (a glucose polymer) in liver and muscle. Amino acids can provide carbon for gluconeogenesis in starving animals because visceral and muscle protein is being used as a fuel and some of the amino acids provide carbon for glucose production. Amino acids that can provide **pyruvate** carbon (**serine**, **glycine**, **alanine**, **cysteine**, threonine, **tryptophan**) can be net producers of glucose because pyruvate can be converted to a four-carbon intermediate (**oxaloacetate**), which is a net producer of glucose carbon. **Methionine**, **valine**, **isoleucine**, **phenylalanine** and **tyrosine** are gluconeogenic because they provide other four-carbon intermediates (fumarate and **succinate**). Glutamate, **histidine**, **proline** and **arginine** are gluconeogenic because they can provide

carbon for a five-carbon intermediate (α-ketoglutarate). The process of gluconeogenesis provides a means whereby in **starvation** a steady supply of glucose can be provided for tissues that require it by conversion of amino acids derived from protein breakdown into newly formed glucose. (NJB)

Glucose

$C_6H_{12}O_6$. D-Glucose is a central **metabolite** in animal metabolism. It is a primary metabolic fuel and can be stored as **glycogen** in the liver (1–5% of the wet weight) and muscle (~1% of the wet weight). It is the major energy **substrate** used by the brain and, in cases where glucose becomes limiting, can lead to serious physiological consequences. In cases where glucose **catabolism** is slowed, and **fat** catabolism increased, animals such as the lactating cow are often found to have **ketosis**, a metabolic problem that can be fatal.

Glucose can provide carbon for all the organic molecules in the body with the exception of **essential fatty acid**s, essential amino acids and vitamins. The glucose in **starch** makes up more than one-half of the **gross energy** of **grain**s. The other glucose polymer in plants, **cellulose**, is a structural element in the cell walls of **grasses** and grains. Starch can be digested and used by ruminant and non-ruminant animals. Cellulose can be hydrolysed to glucose by some **rumen** bacteria and then used as a source of **energy** by many bacteria. Cellulose can be partially digested and used by non-ruminants via **fermentation** in the **caecum** and **large intestine**. Horses and **rabbits** may digest 40% or more of some forms of cellulose in the lower intestine. The end-products of

fermentation (**acetate**, **propionate** and **butyrate**) are taken up by the **liver** and activated to their CoA forms. In this form they are able to contribute to the energy budget of the animal. Absorbed glucose is a major source of food energy in non-ruminant animals. A unique metabolic capability in animals (anaerobic glycolysis) allows glucose, unlike other metabolites, to provide a limited amount of energy (8 mol ATP mol^{-1} glucose) when **oxygen** becomes limiting. The **lactate** produced is returned to the liver, where it is reconverted to glucose (*see* Cori cycle). When oxygen is available in sufficient amounts, glucose can be totally oxidized to **carbon dioxide** and water ($C_6H_{12}O_6 \rightarrow 6\ CO_2 + 6\ H_2O$) yielding a total of 30 or 32 mol ATP mol^{-1} glucose catabolized, depending on how NADH is the cytoplasm is transported into the mitochondria. Glucose **metabolism** via the **pentose phosphate pathway** meets a number of other essential needs in animal metabolism. First, it is a source of D-ribose or 2-deoxy-D-ribose, the **sugar**(s) required for the nucleosides incorporated into both RNA and DNA, as well as the D-ribose required for **vitamin** co-factors such as NAD, NADP, FAD, CoA and B_{12}. Secondly, ribose is part of ATP, a critical co-substrate in cellular **energy metabolism**. Glucose carbon, via **serine**, **glycine** and **betaine**, can be a source of the one-carbon units in the **folate** system. Glucose carbon can provide the glycine required for the biosynthesis of **purine** bases needed for *de novo* synthesis of RNA and DNA. The other important product from the pentose phosphate pathway is NADPH, which is used to reduce the double bonds produced in the *de novo* biosynthesis of **fatty acid**s. The carbon in **glycerol** in

triacylglycerols is derived totally from glucose. Thus, the reducing equivalents (NADPH) and carbon used in *de novo* synthesis of fat are totally derived from glucose. In animals, glucose can provide the carbon skeleton for the dispensable amino acids, serine, glycine (via serine), **alanine**, **cysteine** (via serine), **aspartic acid**, glutamic acid, **proline** and **ornithine** (via glutamic acid only in some animals), **arginine** (via ornithine) and the methyl carbon of **methionine**. Glucose can provide all of the carbon for the steroid hormones, some of the carbon for **peptide** hormones but none of the carbon for hormones derived from the essential amino acids, **histidine**, **tyrosine** (via **phenylalanine**), **tryptophan** or the **essential fatty acid**s. Glucose is a carbon source for **creatine** and for part of **carnitine**. (NJB; GW)

Glucose tolerance
The response of plasma glucose concentration to an oral bolus of glucose. In 70 kg non-ruminant animals, doses of 50–75 g of glucose are used. In a non-diabetic animal plasma glucose concentration reaches a peak about 30 min after the bolus and then returns to the original concentration by 2 h. Diabetics have basal **blood** glucose levels that may be 1.5 times normal: in response to a bolus, glucose concentration may double by 1.5–2.0 h and then only slowly return to the original elevated level. (NJB)

Glucosidase
A general class of hydrolytic enzymes that cleave **glucose** units from **oligosaccharide**s, **polysaccharide**s and a vast array of non-carbohydrate **substrates**. The term does not distinguish

between those enzymes that hydrolyse glucose connected via α- or β-linkages to the hydroxyl group on the other molecule. Enzymes in this broad group are produced by essentially all living animal and plant matter and include digestive enzymes and lysosomal enzymes. (NJB)

Glucosides
Derivatives of **glucose** produced by the condensation of the anomeric hydroxyl group of glucose with the hydroxyl group of another **carbohydrate** molecule or non-carbohydrate moiety, thereby linking the two by an ether bond. (NJB)

Glucosinolates
Thioglycosides that yield isothiocyanate, nitrile or thiocyanate upon **hydrolysis** of the aglycone. Glucosinolates occur in many cultivated plants and in particular the genus *Brassica* (**cabbage**, broccoli, **kale**, rapeseed, **mustard** and **turnip**s); these may be referred to as glucobrassicans. Other examples of glucosinolate-containing plants are *Amoracia* (horseradish), ***Crambe***, *Limnanthes* (meadowfoam), *Nasturtium* (watercress), *Raphanus* (radish) and *Thlaspi* (stinkweed). The most important source of glucosinolates in animal nutrition is rapeseed (*Brassica napus*).

Glucosinolates are hydrolysed by enzymes known as glucosinolases, thioglucosidases or **myrosinase**s. These enzymes are found in the plant and released upon **mastication**, or produced by **rumen microorganism**s. Hydrolysis of the glucosinolates yields **glucose**, **hydrogen sulphate** and some form of isothiocyanate, thiocyanate or nitrile, depending on the

attached aglycone.

The major effect of glucosinolates in animal nutrition is that the metabolic products inhibit the function of the thyroid gland. Enlarged thyroids and **growth** depression are observed in poultry and pigs. Other effects include leg protrusion, reduced **egg production** and quality and **liver** damage in poultry. Pigs may have enlarged livers. (DRG)

Glucuronic acid

A derivative of **glucose**, $C_6H_{10}O_7$, molecular weight 194, in which carbon 6 of glucose is oxidized to a carboxylic acid. In animal tissues, it is produced by dehydrogenation of uridine diphosphate (UDP) glucose. The acid group is ionized at pH 7 and so it usually exists *in vivo* as glucuronate. Glucuronic acid is a constituent of glycosaminoglycans such as hyaluronic acid and chondroitin **sulphate**, which form the extracellular matrix of **connective tissue**s in many animal tissues. Dermatan sulphate, an important connective tissue proteoglycan, contains β-D-glucuronic acid and its carbon-five epimer α-L-iduronic acid. Glycosaminoglycans are covalently linked to extracellular proteins to form proteoglycans. Heparin has repeating units of D-glucuronic acid, usually sulphated at carbon two, and a sulphated glucosamine. Glucuronidation, conjugation of glucuronate, using UDP-glucuronate as the glucuronosyl donor, with foreign compounds, e.g. toxins or drugs, is a major detoxifying mechanism in animals; a more polar compound is produced that can be cleared more effectively by the kidney. Reduction of D-glucuronate by NADPH to L-glucuronic acid is the first step in **ascorbic acid** synthesis in plants and

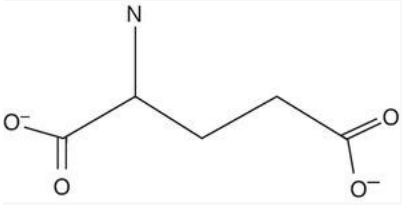
animals other than primates and guinea pigs. D-Glucuronic acid is produced by action of an oxygenase on **inositol**, the first step in the **metabolism** of inositol in animal tissues. Glucuronic acid is also a constituent of some bacterial and plant **polysaccharide**s, though **galacturonic acid** is the predominant **uronic acid** in plants. (JAM)

See also: Carbohydrates; Dietary fibre; Pectic substances; Uronans

Glutamate

The ionized form of L-glutamic acid, $^{-}OOC{\cdot}(CH_2)_2{\cdot}CHNH_3^{+}{\cdot}COO^{-}$. Glutamate is an abundant free amino acid in the milk of mammals (such as humans, cows and pigs) and the intracellular fluid of animal tissues, as well as an abundant amino acid in both animal (e.g. milk and muscle) and plant (e.g. **soybean** and **corn**) proteins. Dietary glutamate is a major metabolic fuel for the **small intestine** of swine and other mammals, as well as poultry, fish and shrimps. Two glutamate derivatives (*N*-acetylglutamate and phosphoglutamate) are present in animals. Free glutamate participates in many intracellular reactions, including **transamination**, dehydrogenation, **decarboxylation** and condensation, and stimulates specific receptors in **taste** buds to induce a 'savoury' or 'meaty' flavour. Glutamate has traditionally not been considered as a nutrient needed in diets for humans and other animals (including swine), due to the unsubstantiated assumption that animals can synthesize sufficient amounts to meet their needs. The lack of knowledge about glutamate nutrition has contributed to suboptimal efficiency of global livestock production.

Over the past 30 years, there has been growing interest in glutamate metabolism in pigs and other farm animals. There is evidence that dietary **supplementation** with 2% glutamate maintains gut health and prevents intestinal dysfunction in weanling piglets, while enhancing their growth performance and survival. Also, the inclusion of 2% glutamate is required for dietary **arginine** to maximize the **growth** performance and feed efficiency in growing pigs, and dietary supplementation with 2% glutamate reduces the loss of **skeletal muscle** mass in **endotoxin**-challenged pigs. Furthermore, supplementing a corn- and soybean-meal-based diet with 2% glutamate promotes milk production by lactating sows. Thus, an adequate amount of dietary glutamate as a quantitatively important major nutrient is necessary to support maximum growth, development and production performance of pigs and other farm animals. (GW)



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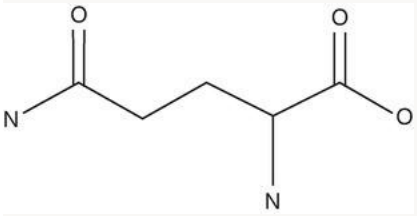
Glutamate dehydrogenase
A **liver** enzyme involved in utilizing or producing ammonium N which can be utilized by incorporating it into α-ketoglutarate to form L-glutamate ($NH_4^+ + {}^-OOC{\cdot}(CH_2)_2{\cdot}CO{\cdot}COO^- \rightarrow {}^-OOC{\cdot}(CH_2)_2{\cdot}CHNH_4^+{\cdot}COO^-$). This N can then be transaminated to **keto acid** precursors of the various L-amino acids. Production of ammonium-N from L-glutamate is the reverse reaction. Glutamate dehydrogenase enzyme is found in many tissues. (NJB)

Glutamic acid:
see **Glutamate**

Glutamine
Glutamine is a neutral amino acid ($(H_2N{\cdot}CO{\cdot}(CH_2)_2{\cdot}NH_2{-}COOH$, molecular weight 146.2), abundant in the milk of mammals (such as humans, cows and pigs) and the intracellular fluid of animal tissues (particularly **skeletal muscle**), as well as an abundant amino acid in both animal (e.g. milk and muscle) and plant (e.g. soybean, corn and wheat) proteins. Dietary and arterial glutamine is a major metabolic fuel for the **small intestine** and immunocytes of pigs and other mammals, as well as fish and shrimps. Glutamine participates in multiple metabolic pathways,

including renal **ammonia** production for the regulation of acid–base balance, the synthesis of **purine** and **pyrimidine nucleotides** that are essential for the proliferation of cells, the endogenous synthesis of **citrulline** and **arginine** in most mammals (e.g. pigs, humans, rats, cattle and sheep) via the intestinal–renal axis, and the formation of *N*-acetylglucosamine-6-phosphate (a common substrate for the synthesis of glycoproteins that are particularly abundant in mucosal cells and plasma membranes). In addition, glutamine regulates gene expression, antioxidative responses, **nitric oxide** synthesis and cell signalling pathways, via the mammalian target of the rapamycin pathway, AMP-activated protein kinase, extracellular signal-related kinase, Jun kinase, mitogen-activated protein kinase and nitric oxide. Exquisite integration of glutamine-dependent regulatory networks has profound effects on cell proliferation, differentiation, migration, metabolism, **homeostasis**, survival and function. Glutamine had traditionally not been considered as a nutrient needed in diets for pigs and other livestock species or even mentioned in classic animal nutrition textbooks, due to previous technical difficulties in glutamine analysis and the unsubstantiated assumption that animals can synthesize sufficient amounts of glutamine to meet their needs. However, the contents of glutamine and glutamate in plant and **animal protein**s are now available. The current version of NRC (2012) considers glutamine to be a conditionally essential amino acid for pigs. There is evidence that dietary **supplementation** with 1% glutamine maintains gut health and prevents intestinal dysfunction in low-birth-weight or

early-weaned piglets, while increasing their growth performance and survival. Also, supplementing 1% glutamine to a corn- and soybean-meal-based diet between days 90 and 114 of gestation ameliorates fetal growth retardation in gilts and reduces preweaning mortality of piglets. Furthermore, dietary supplementation with 1% glutamine enhances milk production by lactating sows. Thus, adequate amounts of dietary glutamine are necessary to support maximum growth, development and production performance of pigs and other mammals. (GW)
See also: Glutamate



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Glutamyltransferase

γ-Glutamyltransferase is an enzyme involved in transporting some amino acids across membranes in the kidney and liver. The amino

acid is converted to the γ-glutamyl amino acid by reaction with **glutathione** (γ-glutamylcysteinylglycine). The reaction is AA + GSH → γ-glutamyl-AA + cysteinylglycine. The amino acid is released and the GSH resynthesized. (NJB)

Glutathione

A tripeptide, γ-glutamylcysteinylglycine, found throughout the body. It is found as reduced glutathione (GSH) and oxidized glutathione (GSSG). It is the substrate for several enzymes. The enzyme glutathione reductase is involved in converting GSSG to GSH, i.e. GSSG + NADPH + H^+ → 2GSH + $NADP^+$. Under oxidizing conditions, **cysteine** in a polypeptide chain may be oxidized to form a **cystine** bridge. This may be required for the activity of the protein or render it inoperative. Reduced glutathione can react with one of the cysteines to make a GSH–cysteine mixed disulphide. Another GSH can react with this mixed disulphide to form oxidized glutathione (GSSG) and the cysteine in the polypeptide chain, thus restoring cysteine to its original form. Reduced glutathione also plays a role in protection against oxidative damage via its role as a substrate for the enzyme **glutathione peroxidase**. This same system is involved in reducing lipoperoxides produced by oxygen-dependent reactions catalysed by **iron** and **copper**. When involved in protection against oxygen damage, α-**tocopherol** becomes an α-tocopherol radical. GSH can react with the radical and regenerate α-tocopherol. Glutathione as a substrate for the glutathione *S*-transferase plays a role in detoxifying various xenobiotics. In these systems glutathione reacts with the xenobiotic (R) to form a

product that can be excreted, i.e. R + GSH → R-SG. (NJB)

Glutathione peroxidase (GPX)
A **selenium**-containing enzyme found in erythrocytes and many other tissues. It has **selenocysteine** at its active centre. The enzyme protects the cellular environment by destroying **peroxides** produced as a result of oxidative metabolism. The reaction for the destruction of hydrogen peroxide is 2GSH + HOOH → CSSG + $2H_2O$. In order for this system to function, the oxidized **glutathione** (GSSG) produced must be reconverted to reduced glutathione (GSH) by the following reaction: GSSG + NADPH + H^+ → 2GSH + $NADP^+$. The NADPH required for this reaction is produced by **glucose** metabolism in the **pentose** cycle. (NJB)

Gluten
A collective term describing the mixture of proteins mainly in the **endosperm** of wheat and other cereal grains. The most important proteins in gluten are prolamin (gliadin) and glutelin (**glutenin**), which are regarded as storage proteins in some food grains (Batey and Huang, 2016). Wheat gluten contains high concentrations of Glx (**glutamate** + **glutamine**) and **proline** (39% and 14.6% of total amino acids, respectively). The protein matrix is closely associated with the **starch** granules of the endosperm and is important in determining grain hardness. It has elastic properties that are important in bread making, but this property has beneficial and negative effects in the diets of animals and humans. A beneficial effect is that the inclusion of wheat in animal diets allows

the feed mixture to be pelleted without the addition of a pellet binder. However, the presence of wheat in poultry (and to some extent pig) diets can be negative, because of high **viscosity** found in the digestive tract reducing **nutrient digestibility** and destabilizing the resident microbiota. Supplementation of commercial feeds with **a** β-**glucanase** enzyme mitigates this effect. In humans, gluten can trigger adverse inflammatory, immunological and autoimmune reactions (coeliac disease) in some people, which has led to the widespread introduction of gluten-free foods. Enzyme therapy is being used with some success in affected humans (Wei *et al*., 2020). A major challenge is to secure rapid and complete enzymatic digestion of the immunogenic gluten peptides that are embedded in a complex food matrix. This must occur within the stomach and proximal small intestine before these peptides reach the mucosal immune system of the small intestine. (ED, RB)

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Glutenin

Also known as glutelin, one of the main proteins in the **endosperm** of **cereal grain**s. **Gluten** includes the four main proteins: glutenin, gliadins (prolamin), albumins and globulins, none of which are well balanced in amino acids for human or animal feeding. The glutenins and gliadins generally account for 75–80% of total gluten proteins in cereal grains. Glutenin makes up about 47% of the total protein content of **wheat** flour. It possesses much higher proportions of **lysine**, **glycine** and **tryptophan** and somewhat higher proportions of **arginine**, **tyrosine**, threonine, (**aspartic acid** + **asparagine**), **serine** and **alanine**, compared with gliadin. Gliadin is richer in **proline** (glutamic acid + **glutamine**), **cystine**, **phenylalanine**, **amide nitrogen** and **isoleucine**. Contents of **methionine**, **valine**, **leucine** and **histidine** are more similar in both types of protein.

Inter- and intramolecular disulphide linkages result in linear molecules of glutenins of either high or low molecular weight. Those of high molecular weight have been directly related to the quality of wheat **flour** for bread making. **Maize** glutelin, occurring in the endosperm and germ, is the second main type of protein found in maize kernels. Although its concentration is lower than

zein protein (main type), it does contain higher levels of the two essential amino acids, **lysine** and **tryptophan**. (RB; ED)

Further reading

Lásztity, R. (2017) *The Chemistry of Cereal Proteins*, 2nd edn. Routledge, Boca Raton, Florida, 328 pp. doi: 10.1201/9780203737057.

Glycerol

The **carbohydrate** backbone ($CH_2OH{\cdot}CHOH{\cdot}CH_2OH$) of neutral fats (**triacylglycerol**s) and of **phospholipid**s (i.e. **phosphatidylcholine**, **phosphatidylethanolamine**, etc.). Glycerol is derived from **glucose catabolism** via intermediate production of dihydroxyacetone phosphate in the cytoplasm of the **liver** and other tissues. Dihydroxyacetone phosphate can be reduced to glycerol-3-phosphate which can be used directly in triacylglycerol (neutral fat) and related syntheses. In neutral fat synthesis, two activated **fatty acid**s (acyl-CoAs) react with *sn*-glycerol-3-phosphate to form a 1,2-diacylglycerol phosphate. After dephosphorylation, the diacylglycerol reacts with one acyl-CoA to form one triacylglycerol. In another important metabolic role, glycerol-3-phosphate is the starting material for synthesis of surfactant (*sn* 1,2 dipalmitoyl **lecithin**) in which the two fatty acids of phosphatidylcholine (also called lecithin) are the 16-carbon **saturated fatty acid**, **palmitic acid**. Glycerol, as glycerol-3-phosphate, is the starting material for the synthesis of a number of phospholipids, phosphatidylcholine, phosphatidylethanolamine, **phosphatidylserine** and **phosphatidylinositol**. These products are critical components of membranes and phosphatidylinositol is a precursor of the second messenger, **inositol** triphosphate.

Although the structure of glycerol shown above appears symmetrical, enzymes that react with it treat the 1 and 3 carbon atoms differently. This requires a specific nomenclature, such that the positions 1, 2, 3 are noted by stereochemical notation, *sn* 1, *sn* 2 and *sn* 3, respectively. The *sn* 3 position is the position which is phosphorylated, and in milk fat it is the position in which a **medium-chain fatty acid** is found. Lingual **lipase** and pre-gastric esterases release fatty acids from the *sn* 3 position of glycerol.

Free glycerol can be activated by glycerol kinase to form glycerol-3-phosphate in one or more tissues. Glycerol-3-phosphate can be a source of glucose carbon as well as the glycerol portion of neutral fat. Glycerol from neutral fat is the only portion of fat that is a net contributor of carbon to **gluconeogenesis**. (NJB)

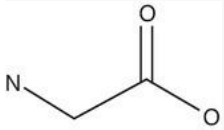
See also: Lipid metabolism

Key reference

Mayes, P.A. (2021) Oxidation of fatty acids: ketogenesis and gluconeogenesis and control of blood glucose. In: Kennelly, P.J., Botham, K.M., McGuinness, O., Rodwell, V.R. and Weil, P.A. (eds) *Harper's Biochemistry,* 32nd edn. Appleton and Lange, Stamford, Connecticut.

GlycerolipidsLipids in which **glycerol** is connected to **fatty acid**s by an **ester** bond. They differ from **sphingolipid**s (which involve an ester bond between the hydroxyl of **serine** and palmitate) and **cholesterol** esters (with long-chain saturated or **unsaturated fatty acid**s), both of which are classified as lipids but do not have glycerol as a component. (NJB)

Glycine
An amino acid found in protein ($H_2N{\cdot}CH_2{\cdot}COOH$, molecular weight 75.1). It is synthesized in the body, 4-**hydroxyproline**, **choline**, and threonine primarily from **serine**. In addition to its use in **protein synthesis**, glycine is used for synthesis of **purines** (including uric acid, the main nitrogenous excretory product in birds), **creatine**, haem, **glutathione** and various glycine conjugates. In **collagen**, the most abundant protein in the body, glycine makes up about one-third of the amino acids. Serine, which is synthesized from **glucose** and an amino group donor (**glutamate**), can be converted to glycine by exchange of the hydroxy methyl group and glycine back to serine. This serine hydroxymethyltransferase-catalysed reaction (serine → glycine) is thought to be an important source of *de novo* methyl group synthesis in the body. Oxidation of 4-hydroxyproline is a major source of glycine in young pigs. (DHB; GW)



Glycocholic acid
One of the **bile** acids which is a conjugate of **cholic acid** and **glycine**. It is formed from 7α-hydroxycholesterol via conversion to cholyl-CoA, which reacts with glycine to form glycocholic acid. (NJB)

Glycogen
A **glucose** polymer with no fixed molecular weight $(C_6H_{10}O_5)_n$. It

is a storage form of **carbohydrate**, found in measurable quantities in liver and muscle. Glycogen is a branched structure which has 10–15 α-D-glucopyranose units linked in α(1→4) glycosidic bonds after a 1→6 branch point where another series of 10–15 units are connected followed by another α(1→6) branch point. Because of the way glucose units are added to the glycogen structure, the last glucose molecule deposited is the first one to be released. Hence, glycogen does not act as a simple mixed pool.

Liver glycogen varies from as much as 4–6% of the wet weight of the liver soon after a meal (~2 h) to a trace 8–10 h after a meal. In muscle the variation in glycogen concentration is much less, being ~1% after a meal to traces by 8–10 h after a meal. The composition and size of the meal would be expected to have an effect on tissue glycogen concentration. If one takes the example of a 100 kg pig with a **metabolic rate** of 16,670 kJ per day (3980 kcal per day), the amount of glycogen in storage after a meal (¼ in liver, ¾ in muscle), if totally used, could meet the animal's energy needs for about 13.4 h (~ 500 g at 17.4 kJ g^{-1} at 4.15 kcal g^{-1}).

Glycogen is synthesized in liver and muscle from glucose as glucose-6-phosphate. In the liver, glucose-6-phosphate can come from glucose taken up by the cell or from the metabolic production of glucose-6-phosphate in the process of **gluconeogenesis**. In muscle, glucose-6-phosphate is produced from glucose taken up by the cell. Glucose-6-phosphate, when converted to glucose-1-phosphate, is added to the glycogen molecule, making the glycogen molecule longer by one glucose molecule. Release of glucose from glycogen (glycogenolysis) involves the enzyme phosphorylase,

which utilizes inorganic phosphate and releases glycogen-glucose as glucose-1-phosphate from the linear chain of α(1→4) linkages. Because glycogen is branched, **hydrolysis** of the α(1→6) branch must be broken by the debranching enzyme for the phosphorylase to complete the total hydrolysis of glycogen to glucose-1-phosphate. To be used for ATP production, glucose-1-phosphate must be converted to glucose-6-phosphate, so glucose residue from glycogen yields the 29–31 ATP equivalents while free glucose provides 30–32 ATP. (NJB; GW)

See also: Glycogenolysis

Key reference

Mores, P.A. (2021) Metabolism of glycogen. In: Kennelly, P.J., Botham, K.M., McGuinness, O., Rodwell, V.R. and Weil, P.A. (eds) *Harper's Biochemistry,* 32nd edn. Appleton and Lange, Stamford, Connecticut.

Glycogenesis

The process whereby **glucose** units can be stored in liver or muscle cells as the polymer **glycogen**. The glucose used in the process can come from the diet or can be derived by the process of **gluconeogenesis** in which non-glucose carbon can be converted into glucose in the liver and kidneys. (NJB)

Glycogenolysis

The breakdown of **glycogen** in the liver, kidney or muscle to **glucose**-1-phosphate. Glucose-1-phosphate is converted to glucose-6-phosphate, which is a source of metabolic energy in the form of ATP. Glycogen in liver and kidney can be a source of energy for other organs after glucose-6-phosphatase hydrolyses

glucose-6-phosphate to inorganic phosphate and free glucose. Muscle cannot release glucose from glycogen as free glucose for distribution to other tissues, because it lacks the enzyme glucose-6-phosphatase. (NJB)

Glycolipids
Modified sphingosines in which **long-chain fatty acid**s are added to form ceramide. Ceramide can be altered by addition of one or more sugars (**glucose** or **galactose**). These glycosphingolipids are found in all tissues in the body but higher concentrations are found in nervous tissue. They are found in the outer leaflet of the cell membrane and contribute to the **carbohydrates** on the cell surface. (NJB)

Glycolysis
The process whereby **glucose** in the form of glucose-6-phosphate is catabolized to **pyruvate** in the cytoplasm of cells. Glucose-6-phosphate is derived from glucose taken up by cells and converted to glucose-6-phosphate by **glucokinase** or by breakdown of **glycogen** with the conversion of the glucose-1-phosphate to glucose-6-phosphate. Under aerobic conditions, the pyruvate produced by glycolysis can be converted to acetyl-CoA and be further oxidized to CO_2 and H_2O in the mitochondrion. Under anaerobic conditions, the **catabolism** of glucose-6-phosphate in the cytoplasm produces NADH, which is later converted to NAD when pyruvate is reduced to **lactate**. Regeneration of NAD is essential for the continued catabolism of glucose-6-phosphate. Anaerobic glycolysis results in the accumulation of glucose carbon

in lactate. In this way ATP can still be produced from glucose when **oxygen** is not available. This process can only continue as long as glucose-6-phosphate is available and the cellular pH does not decrease (due to lactate accumulation) to a level that alters **enzyme activity**. Under normal aerobic conditions, glucose yields 30–32 ATPs in its conversion to CO_2 and H_2O. Under anaerobic glycolytic conditions where glucose-6-phosphate is converted to lactate, only eight ATPs can be produced. This ability to provide ATP under conditions of limited oxygen is a unique property of glucose catabolism. (NJB)

Glycosidases

Enzymes involved in hydrolysing **monosaccharide**s (or modifications of them) from glycoproteins. The enzymes cleave either terminal units (exoglycosidases) or specific linkages along the chains (endoglycosidases). For example, **galactosidase** is an exoglycosidase that removes the terminal **galactose** from an **oligosaccharide** chain. Endoglycosidases cleave at specific *N*-acetyl-glucosamine or *N*-acetyl-**galactosamine** sites in the **oligosaccharide**. They can also cleave **sugars** from non-carbohydrate substrates such as **purines**, **pyrimidine**s, anthocyanins and flavolols. (NJB)

Glycosides

Compounds formed by condensation of the hydroxyl group of the anomeric carbon of a **monosaccharide** with another compound that may or may not be another monosaccharide. If the unit attaching to the hydroxyl group is not a monosaccharide it is

identified as an aglycone. These may be alcohols, **glycerol**, **sterols**, phenols or others such as the **purine** bases. (NJB)

Glycosylation

The process by which **sugar** residues are attached to a **protein** to form a glycoprotein. Glycoproteins have many critical functions in the body. Proteins that end up in the plasma membrane or are secreted from the cell pass through the secretory pathway, which is composed of the endoplasmic **reticulum** and the Golgi apparatus, before reaching their final destination. Many such proteins become glycosylated during their movement through the secretory pathway. Glycosylation occurs only on certain residues in a protein, such as O-linked threonine and N-linked **asparagine**s, and only some of these residues are glycosylated. Sugar residues are specifically added in highly complex structures containing many **glucose**, **mannose** or other sugar residues. All cell types display, on their cell surface, proteins that are imbedded in, or associated with, the cell's plasma membrane. Many of these proteins are glycoproteins which have crucial roles in cell–cell and cell–ligand (e.g. **hormone**) interactions. **Blood** type differences are due to the variation in cell surface glycoproteins on the red cell plasma membrane. The mucus secreted by epithelial cells in the mouth or intestine is largely composed of glycoproteins. The glycoproteins in mucus are essential for its properties as a lubricant. Some of the soluble proteins in the blood, such as **antibodies** (immunoglobulins) or some hormones, are glycosylated. Additional extracellular proteins that are glycosylated include **collagen** and other proteins that make up the scaffolding (extracellular matrix)

that allows cells to form tissues. Glycoproteins can contain from as little as 4% of their weight as **carbohydrate** to as much as 60% or more. In **diabetes**, high levels of glucose can lead to glycation of **haemoglobin** but this does not occur through the normal process of glycosylation. (RSE)

Glyricidium
A medium-sized tree in the Fabaceae family that is a native of Mexico. It can be cut at regular intervals, normally every 2–4 months, for feeding to ruminant livestock. It has high dry matter yields and a high **crude protein** content. As the plant is a **legume** and fixes nitrogen, it has low requirements for nitrogen fertilizer. It is difficult to conserve and is mainly fed fresh, but it has a **palatability** problem that restricts intake, believed to be due to the smell of the leaves. **Wilting** the leaves before feeding aids acceptance. Its bark and seeds are toxic to many animals. Mature stems are deciduous, losing leaves in the dry season, which can be a valuable source of fodder to livestock. However, regular cutting encourages the plant to retain its leaves. It is not normally grazed *in situ*. It has few pests or diseases and is easily propagated. (CJCP)

GM crops:
see Genetically modified crops

Gnotobiotic animals
Animals raised entirely free of **microorganism**s and subsequently infected with known organisms. The main uses of gnotobiotic

animals are in disease research but they are also used in nutrition research when the influence of the **gastrointestinal microflora** is to be studied. (MFF)
See also: Germ-free animals

GnRHGonadotrophin-releasing hormone, a decapeptide produced in the **hypothalamus**. GnRH acts upon the anterior pituitary to bring about the release of the gonadotrophins, follicle-stimulating hormone (FSH) and **luteinizing hormone** (LH). (JRS)

Goat
Hollow-horned ruminant mammals of the family Bovidae. Evidence of the domestication of goats has been found in Neolithic sites at Jericho dating from 7000 BC; other sources claim that domestication of goats dates from 9000 BC. The domestic goat, *Capra hircus*, is now found throughout the world and is absent from only the extreme polar regions. It is thought to derive from the so-called Persian wild goat or bezoar, *Capra aegagrus*, found in Turkey, Iran and western Afghanistan. In the 1990s the world population of goats was estimated at around 490 million (Russel and Mowlem, 1999); it has since risen to about 1 billion (FAOSTAT, 2018).

Some breeds of goats and sheep look similar. Generally, but not infallibly, the two species can be differentiated by the fact the goats tend to carry their tails erect, whereas sheep's tails hang down. Male goats have a very distinctive odour, quite different from that of rams; and rams, but not goats, have a secretory gland on their

hind feet. The definitive difference, though not visible, is that goats have 60 chromosomes and sheep have 54. Male goats are known as bucks or billies; female goats are generally termed either does or nannies. The young are kids, and juvenile females (generally between 1 and 2 years old) are referred to as goatlings. The term yearling is also applied to juveniles of either sex.

Goats are truly dual-purpose animals. Most of the world's goat population is kept for the production of **meat** and **milk**. Some breeds, such as the Saanen, the Anglo-Nubian and the alpine breeds, have been selected for high levels of milk production, and yields of more than 1000 kg per annum are not uncommon. A world record milk yield of 3506 kg in one **lactation** was set in the late 1980s by a British Saanen (Mowlem, 1988).

Other breeds are kept principally for fibre production, the best known being the Angora, which produces mohair (not to be confused with the fibre 'angora' that comes from a breed of **rabbit**). Mohair is a long, lustrous and generally white fibre that is harvested by shearing the goats every 6 months. Annual levels of production (from two shearings) are generally between 4 kg and 6 kg. The diameter of the fibre increases with age, from < 25 microns (μm) at the first shearing to 35 μm or greater at about 4 years of age. **Angora** goats are single-coated, i.e. they produce only one type of fibre, though many fleeces contain a small proportion of coarse chalky fibres, or kemps, which is regarded as a fault.

Cashmere goats are also farmed for their fibre. Unlike the Angora, which is a single breed, there are many distinct breeds of cashmere goats, the characteristics of which have been reviewed by Millar

(1986). Cashmere goats are all double-coated, having an outer coat of coarse medullated guard **hair** and an undercoat, referred to variously as cashmere, down, pashm or pashmina, of fine unmedullated fibres. The mean diameter of cashmere fibres is typically around 15 μm, ranging from about 13 μm to 18 μm. Cashmere is harvested once a year, in the spring, either by combing the goats after they begin to moult, or by shearing. The combed fibre still contains a proportion of guard hair, although clearly much less than the fibre harvested by shearing. After harvesting, the two fibre types are separated by a specialized process known as dehairing. The weight of dehaired cashmere produced per goat ranges from about 150 g to 400 g, those with the higher levels of production generally producing coarser fibre.

Whereas sheep prefer to graze plant material close to the ground, goats readily browse on leaves and small branches of trees and shrubs. Given a choice of plant species, goats tend to concentrate on those plants that are commonly regarded as undesirable (e.g. thistles (*Carduus* spp.), gorse (*Ulex* spp.), blackberry (*Rubus* spp.) and willowherb (*Epilobium* spp.)) in preference to sown pasture species. There is thus considerable scope for the complementary **grazing** of goats and sheep on certain vegetation types, and particularly on the indigenous plant communities found on unimproved hill land. Concentrates are frequently fed to high-yielding dairy goats but it is recommended that their diet should contain a minimum of 40% **roughage**. In many of the larger dairy units the goats are housed all year round to minimize the risk of infection with internal parasites, as milk cannot be sold for human

consumption for some time after the animals have been treated with anthelmintics. In these units the goats are generally fed forage *ad libitum,* supplemented in most cases with concentrates. Fibre-producing goats, particularly cashmere goats, are generally kept outdoors and receive supplementary feeding during late pregnancy and early lactation.



Goats in rangelands in Tunisia. Kept on land without fences, these goats are shepherded by a human attendant who leads them to the best feeding areas. Photo courtesy of Dennis Jarvis. Licensed under CC BY-SA 2.0.

Goats are seasonally polyoestrous, with females coming into heat at regular intervals during the breeding season which, in the northern hemisphere, extends from about August to February. Female kids become sexually mature at about 6 months of age but are often not mated until they are approximately 18 months old, or

until they have attained 75% of their mature weight. Male kids can attain sexual maturity between 3 and 6 months of age and are therefore frequently weaned when they are about 12 weeks old. The **oestrous cycle** is about 21 days and oestrus generally lasts for 1–2 days. Gestation length varies from about 146 to 156 days and averages some 150 days. Dairy goats have an extended **lactation**, milking continuously for more than 18 months, and in some cases are mated only once every 2 years. Fibre-producing goats, which **suckle** their kids, have shorter lactations of 12–16 weeks and are mated each year.

Goats are susceptible to similar ranges of bacterial and viral diseases, **metabolic disorder**s and parasitic infections as in sheep. Where clostridial diseases are endemic these are generally controlled by vaccination. Goats tend to be more susceptible than sheep to helminth infections. These can be controlled by the same spectrum of anthelmintics as is commonly used in sheep. (AJFR)

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Goat feeding

As goats are ruminants, they feed on plant material. They graze grass and other low-growing plants, as do cattle and sheep, but, given the opportunity, they will also readily browse the leaves and branches of accessible trees and shrubs not normally eaten by those species. They are generally more selective in their food preferences than other domesticated ruminants and will not eat, for example, mouldy hay or feed that has been contaminated with faeces. They are fastidious in their selection of plants and parts of plants, but also adapt readily to the available food sources. Given a wide choice of plant species, goats will tend to concentrate on those plants commonly regarded as weeds, such as willowherb (*Epilobium* spp.), rushes (*Juncus* spp.), thistles (*Carduus* spp.), blackberry (*Rubus* spp.) and gorse (*Ulex* spp.), in preference to sown grass and clover, though clover flowers are avidly consumed.

On sown pastures, which are frequently mixtures of ryegrass (*Lolium* spp.) and clover (*Trifolium* spp.), goats require a higher sward surface height (i.e. taller pasture) than do sheep if they are to achieve the levels of herbage intake required for good performance. While sheep will perform well on pastures with a sward surface height of 4–6 cm, goats require a sward height of around 8–9 cm. Sward management for goats is thus more akin to that needed for cattle than sheep. On unimproved indigenous pastures with a wide variety of plant species, goats select a diet markedly different from that grazed by sheep, and there is thus considerable scope for the complementary grazing of the two species; indeed, goats have been used in such situations to improve the quality of grazing for the benefit of sheep. Goats utilize

medium- to high-quality foods (**organic matter** digestibilities of 0.6 or higher) with an efficiency similar to that of sheep, but with lower-quality foods they are able to maintain higher digestibilities than sheep, possibly because of higher concentrations of rumen **ammonia**, slower rates of passage of digesta through the alimentary tract and greater **rumen volume**s. They are thus better adapted than most other ruminants to survive, and indeed thrive, in adverse nutritional environments.

The feeding of goats must take account not only of size (i.e. body weight) and physiological state (e.g. pregnancy or **lactation**), but also of the products for which the animals are farmed. Goats kept for commercial **milk** production require substantially higher levels of nutrition than Angora or **cashmere goats** farmed primarily for fibre production. The goat's diet must also be balanced in terms of energy, protein, vitamins and minerals.

Many of the larger dairy-goat farms house their animals all the year round to obviate the need to use anthelmintics to control stomach worms picked up from infected pasture. (Milk from animals treated with anthelmintics, antibiotics, etc., is not allowed to be sold for human consumption for some time following treatment.) On these farms the goats are generally fed **forage** *ad libitum* in the form of hay, freshly cut grass or, more commonly nowadays, grass or maize **silage**, supplemented with cereal-based concentrates. **Maize** silage is preferable to silage made from grass, as the feeding of the latter entails the risk of listeriosis, a disease carried by a soil-borne organism. The concentrate part of the diet is usually fed in the milking parlour to enable the quantity offered to

be rationed in relation to the individual's level of milk production. In the case of high-yielding goats (producing more than, say, 1000 kg of milk per lactation) substantial quantities of concentrates may need to be fed to meet the animal's nutritional requirements, but it is important to ensure that the total diet contains at least 40% **roughage**. Examples of suitable diets for dairy goats are: for a 70 kg doe producing 5 kg milk per day, 1.5 kg good quality hay, 2.0 kg **kale**, 0.5 kg dried **sugarbeet** pulp and 1.25 kg high-energy concentrate; and for a 60 kg doe producing 3 kg milk per day, 1.2 kg good quality hay, 0.4 kg dried sugarbeet pulp and 1.4 kg medium-energy concentrate (Mowlem, 1988).

Fibre goats kept primarily for fibre production have lower **nutrient requirement**s than dairy goats. They generally acquire most of their nutrients from grazing and **browsing**, as there is no necessity to avoid the use of anthelmintics to control internal parasites. Some supplementary feeding is generally supplied during late pregnancy and early lactation.

Angora goats, which produce mohair and are shorn twice a year, may need to be housed for at least part of the year, depending on climatic conditions. In such situations the needs of non-pregnant, non-lactating animals can be met wholly from conserved forage, but in late pregnancy and during lactation some supplementary concentrates (about 0.5 kg per day, depending on the quality of the forage offered) will be required. The nutrient requirement for the growth of, say, 4–5 kg mohair per annum is comparatively small and similar to that required for **wool growth** in sheep. Mohair production is affected by nutrition, and particularly by the level of

dietary protein; high levels of feeding increase the weight of mohair produced but also increase the diameter of the fibre, i.e. there is an inverse relationship between fibre quantity and quality. The value of mohair produced per animal can therefore be regulated, at least to some extent, by feeding. The valuable fibre from cashmere goats is harvested only once a year, in the spring, by either combing or shearing. Where climatic conditions allow, cashmere goats are kept outdoors for at least the greater part of the year and obtain their nutrients from grazing, with some supplementary feeding being provided in late pregnancy and early lactation. The nutrient requirements for fibre production in cashmere goats are negligible and can be ignored in calculating dietary regimes. In contrast to mohair, the weight and diameter of the fine undercoat of cashmere goats is not influenced by dietary factors, though nutrition does affect the weight of the coarse outer coat or guard hair. There is thus no reason to restrict feeding in the expectation of improving fibre quality.

Angora and cashmere goat kids are reared naturally, **suckling** their dams until **weaning** at 3–4 months old. In dairy-goat herds, however, most kids, whether intended for herd replacements or for meat, are taken away from their dams at 1–2 days old, after receiving colostrum, and are artificially reared on a proprietary milk replacer. This may be offered *ad libitum* for the first 4–6 weeks or restricted to about 1 kg per **kid** per day, supplied twice daily. Thereafter the amount of milk replacer may be gradually reduced until the kids are weaned at 6–10 weeks old. A high-protein concentrate (16–18% **crude protein**) and good-quality

hay should be offered *ad libitum* from 2–3 weeks of age. By weaning, kids should be consuming 0.4–0.5 kg concentrate per day, at which level the concentrate input can be restricted but the hay or other suitable conserved forage should continue to be fed *ad libitum*. Comprehensive information on the energy, protein, vitamin and mineral requirements of goats for maintenance, growth, pregnancy and the production of milk and fibre is contained in the AFRC TCORN Report No. 10 (1997). (AJFR)

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Goat meat, effects of nutrition

Scientists have found that goat meat (cabrito and chevon) has less intramuscular fat content, a darker colour and a tougher texture than beef and lamb. In terms of **fatty acids** (FAs), goat meat has more of the desirable FAs (C18:0, C18:1, C18:2, C18:3, C20:5 and C22:5) and a greater proportion of **unsaturated fatty acid**s than lamb and beef. **Cholesterol** content of goat meat is also considerably less than other red meat sources. Limited **feed intake** and **undernutrition** can significantly affect lean tissue accretion and minimize fat deposition.



Goat carcass being sold at a cultural festival in Domboshaba, Botswana. Undernutrition of goats in rural Africa often reduces fat deposition. Photo courtesy of Mompati Dikunwane. Licensed under CC BY-SA 4.0.

For goats, as with other species, increasing dietary **energy** levels will result in higher subcutaneous and IMF levels, and lower lean:fat ratios. Generally, in intensive production systems, goats have heavier **carcass** weights, greater fat thickness and higher **dressing percentage**s compared with goats raised in semi-intensive production systems. Feeding concentrate-based diets increases carcass weight, dressing percentages and ribeye muscle area in goats. For example, in one study, supplementing East African goats with a concentrate diet (27% **sunflower** seed cake + 70% **maize** bran) increased carcass fat content (Safari *et al.*, 2009). However, the response of goats to the high concentrate diets (> 50% of ration) seems different to that in cattle and sheep. For example, increasing the concentrate level from 50 (41% dried-roll **corn** + 50% **alfalfa** hay) to 90% (77% dried-roll corn + 10%

alfalfa hay) has been shown not to affect growth and carcass fat content of goats. This discrepancy might be related to **feeding behaviour** and morpho-physiological characteristics of goats. Unlike cattle and sheep, which are grazers, goats are browser animals with specific **digestion** abilities. Goats have greater **saliva** secretion and **urea** recycling capabilities than cattle and sheep. Moreover, goats have salivary **tannin**-binding proteins or/and tannin-resistant bacteria (*Streptococcus caprinus*) in the **rumen**. Hence, goats are less sensitive to plant secondary **metabolite**s (e.g. tannins and **alkaloid**s) and inclusion of theses plant metabolites that are known as natural **antioxidant**s might improve **lipid** stability in goat meat. Recently it has been reported that feeding goats with *Acacia mearnsii* and peanut skins, which have high tannin contents, improved lipid stability and **meat quality** in goats (Kafle *et al*., 2021; Pimentel *et al*., 2021).

Physicochemical properties

The pH of goat muscle at 24 h post-mortem (pH_{24}) ranges between 5.7 and 6.4, which is higher than the values reported for beef and lamb. Feeding goats with concentrate-based diets as well as increasing the energy density of the diet leads to lower pH_{24} values. Pasture-finished goats have higher pH_{24} than concentrate-finished ones, due to less muscle **glycogen**. Goats finished on pasture produce darker (lower L^* values) meat in comparison with goats finished on concentrate diets, most likely due to a lower intramuscular fat content and/or muscle glycogen concentration. Adding natural antioxidants (**vitamin E**, **vitamin C**, etc.) and **polyphenol**s increases the colour stability of goat meat.

Increasing the **starch** content of a diet leads to lower pH_{24} values and consequently improves the tenderness of goat meat. Feeding goats with high-energy-level diets has been shown to increase μ-calpain activity and decrease calpastatin (inhibitor of calpains) activity, leading to an improvement in the tenderness of goat meat (Wang *et al*., 2015).

Chemical composition and fatty acid profile

The fatty acids in meat from goats grazed under **rangeland** conditions has a higher unsaturated:**saturated fatty acid** ratio, and a lower omega-6:omega-3 fatty acid ratio, than those raised intensively on concentrated **feedlot** diets or cereal **grain** rations (e.g. **total mixed ration**). Feeding concentrate-based diets to goats increases marbling score and total fat content of the meat. However, goats fed concentrate feeds have more **oleic acid** (C18:1) and omega-6 fatty acids, and less omega-3 fatty acids, compared with goats fed no concentrate. Feeding goats with a concentrate diet containing three times as much oleic acid (C18:1) compared with alfalfa hay diet increased C18:1 in both intramuscular (marbling) and subcutaneous fat (Lee *et al*., 2008). Thus, when goats were supplemented with a concentrate diet (27% sunflower seed cake + 70% maize **bran**), the proportions of C18:1, unsaturated fatty acids, vaccenic acid (C18:1*trans*-11) and C18:2n-6 in the omental fat increased, compared with non-supplemented goats (Mushi *et al*., 2010). The increase in C18:1 in muscle or **adipose tissue**s in response to increased concentrate in the diet may be due to the increase in the Δ^9 desaturase enzyme activities necessary for the *de novo* conversion of C18:0 to C18:1.

The effects of dietary **oils** on the fatty acid composition of goat meat (chevon) to a large extent depend on the fatty acid composition of the **oils**. Supplementing goat diets with oils rich in C18:1 (e.g. canola oil) and C18:2n-6 (e.g. sunflower or **soybean** oils) has increased C18:1 and conjugated **linoleic acid** in the meat, respectively (Najafi *et al*., 2012; Karami *et al*., 2013). When goats are fed with oils rich in linoleic acid, more of the linoleic acid is isomerized to *cis*-9, *trans*-11 conjugated linoleic acid and hydrogenated to C18:1 *trans*-11 in the **rumen**, increasing deposition in the muscle tissues. Related to this, supplementation of diets with oils rich in α-**linolenic acid** has increased the omega-3 fatty acid level in chevon. The incorporation of 3% canola oil, a good source of α-linolenic acid with the ratio of 2:1 of omega-6 to omega-3 fatty acids, into the goat's diet has enhanced α-linolenic acid in *longissimus lumborum* muscle, **liver**, and kidney fats (Karami *et al*., 2013).

Supplementation of diets with oils can affect expression levels of genes associated with meat quality in goats. A blend of **linseed** and palm oils (2:1) reduced both rumen biohydrogenation of α-linolenic acid and muscle **oxidation** of α-linolenic acid in cashmere goats (Wang *et al*., 2020). Diets supplemented with the blended oil, as compared with linseed alone, reduced the relative abundance of *Pseudobutyrivibrio*, a bacterial species that hydrogenates dietary C18:3n-3 in the rumen, increasing omega-3 fatty acid, leading to a decrease in the omega-3:omega-6 fatty acid ratio in goat meat. Furthermore, there was a decrease in the mRNA expression of CPT1β (a gene associated with fatty acid oxidation)

and an increase in the mRNA expression of FADS1 and FADS2 (genes associated with omega-3 **fatty acid synthesis**) with the inclusion of blended oil in the diet (Wang *et al*., 2020). Thus, dietary supplementation of oils rich in α-linolenic acid could be a beneficial strategy for improving the omega-3 fatty acid content of chevon. Diets containing phenolic components may act as positive agents in modifying healthy fatty acid composition and reducing lipid oxidation in goat meat.

Sensory characteristics

Meat flavour is an important quality and sensory parameter and is important for the acceptability of meat by the consumers. Goat meat flavour is not desirable for some consumers, due to strong odour components. However, it should be noted that the acceptance level of flavours (tastes) varies with populations from different demographic regions, country of origin, ethnic groups and religious backgrounds. Some flavours are desirable and acceptable by some consumers but categorized as off-flavours or **taints** by others. In general, fat, protein and vitamins are the most important precursor components responsible for the meat flavour; and off-flavours are unexpected volatile compounds commonly described as unpleasant odours and tastes (e.g. stale, cardboard-like, rancid, bitter and sour). Among various factors that affect meat flavour, animal nutritional background has a large influence via changes in IMF, fatty acid composition and/or vitamins (Najafi *et al*., 2012; Arshad *et al*., 2018).

Feeding concentrate-based diets to goats effectively produces chops with less off-flavours and malodours. When the volatile

components of meat extracts from Saanen goats fed differing concentrate-to-roughage ratios were analysed qualitatively and quantitatively, animals fed the low-concentrate feed had better aromatic qualities (Cimmino *et al*., 2018). The majority of flavour effects of diet are due to changes in fatty acid composition and most likely due to an increase in the PUFA content of meat. Even though PUFA are healthy for consumers, they may negatively influence meat flavours via increasing off-flavours (e.g. fishy taste) during long storage or cooking. In ruminants, use of fat-supplemented diets results in a significant increase of PUFA (e.g. omega-3 fatty acids) in meat. For example, supplementing the diet of goats with a high content of omega-3 fatty acid increased lipid oxidation and reduced sensory attributes of chevon and resulted in unusual odours and unpleasant flavours in meat (Moreno-Indias *et al*., 2012), which is not appreciated, because of the positive association between lipid oxidation and the content of omega-3 fatty acid in chevon (Abuelfatah *et al*. 2016). Concern about lipid oxidation of high-oil diets could be overcome by dietary supplementation with **antioxidant**s and **polyphenol** components – a conclusion that is relevant to all ruminant species.

Supplementation of diets containing polyphenols positively improves fatty acid profile and reduces malondialdehyde concentration (a lipid oxidation substance) in chevon. A dietary **green tea** by-product (included at 20 g kg^{-1} feed dry matter) increased the proportions of monounsaturated, polyunsaturated, polyunsaturated:saturated, omega-6 and omega-3 fatty acids of chevon (Ahmed *et al*., 2015). Dietary green tea by-product (Ahmed

et al., 2015) and extract from **olive** mill water waste (Cimmino *et al*., 2018) shows promise in reducing the thiobarbituric acid reactive substances (TBARS) levels in chevon. The inclusion of condensed tannins from an *Acacia mearnsii* extract improved the flavour, aroma, softness and overall acceptance of crossbreed Boer goat meat (Pimentel *et al*., 2021). The effect of feeds with high content of **phenolic compound**s on meat quality might be due to changes in ruminal biohydrogenation of fatty acids via limiting the activity of ruminal microbes and/or due to their antioxidant activities in muscle tissues (meat) via inhibiting lipid peroxidation and lipoxygenases by scavenging hydroxyl, **superoxide**, and peroxyl radicals. (AK; ENP)

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Goblet cells

Specialized cells in the epithelial layer of **villi**. These cells produce mucus consisting of mucopolysaccharides (**mucin**), which protect the epithelium against degradation by the luminal digestive enzymes. In birds, numerous goblet cells substitute for **Brunner's glands**, which are lacking in their **duodenum**. (SB)

Goitre

A condition characterized by enlargement of the thyroid gland as the body attempts to increase production of thyroid hormone. Generally this condition occurs because of **iodine** deficiency, or the presence of **goitrogen**s in the diet, which interfere with iodine utilization. (JPG)

See also: Hypothyroidism

Goitrogen
A compound that interferes with the synthesis or secretion of thyroid hormones and causes **hypothyroidism**. Goitrogens fall into two main categories. (i) Cyanogenic goitrogens impair iodide uptake by the thyroid gland. Cyanogenic **glucosides** can be found in many feeds, including **cassava**, **linseed**, raw **soybean**s, beet pulp, **maize**, **sweet potato**, white clover and **millet**. Once ingested, they are metabolized to thiocyanate and isothiocyanate. These compounds alter iodide transport across the thyroid follicular cell membrane, reducing iodide uptake and retention by the thyroid gland. This effect is easily overcome by increasing dietary **iodine**. (ii) Progoitrins and goitrins (thiuracils) found in cruciferous plants (**rape**, **kale**, **cabbage**, **turnip**s, **mustard**) and aliphatic disulphides (**onions**) inhibit thyroperoxidase, preventing formation of mono- and diiodotyrosine and the condensation reactions necessary to synthesize thyroid hormone. With goitrins, especially those of the thiouracil type, hormone synthesis may not be readily restored to normal by dietary iodine **supplementation** and the offending feedstuff needs to be reduced or removed from the diet. (JPG; CJCP)
See also: Goitre

Gonadotrophins
A group of glycoprotein hormones involved in the control of **reproduction**. Follicle-stimulating hormone (FSH) and **luteinizing hormone** (LH) are produced by the anterior pituitary. Chorionic gonadotrophins are produced by the chorion, the outer membrane surrounding the developing embryo. (JRS)

Goose

Geese were domesticated over 5000 years ago, probably by the Egyptians. Farmed breeds belong to the genus *Anser* and are descended from the wild swan goose, *Anser cygnoides*, and/or the western (*Anser anser anser*) or eastern (*Anser anser rubriostris*) greylag goose. They grow rapidly and some breeds reach a mature body weight of over 15 kg, with the gander (male) much heavier than the goose (female). They are farmed mainly for their **meat**, also down and feathers, and fatty **liver** (**foie gras**, a food delicacy). In addition they make excellent watchdogs and are effective in controlling weeds in a variety of crops and in waterways, dams and drainage canals. Geese are hardy, have a long lifespan and are resistant to many avian diseases. The most important country for goose production is China, with 95% of world production (2018), followed by Poland, Egypt and Hungary. The number of geese in Europe has dropped steadily since the introduction of modern chicken and turkey production systems during the 20th century. Factors that limit large-scale goose production internationally are: their relatively low **reproduction** rate (being seasonal breeders they do not come into lay until around 40–50 weeks of age); slow **growth** rate compared with chickens and turkeys; and the fact that development and marketing of improved breeds by corporations has not taken place in the way chicken and turkey production systems have been developed. Consequently on many farms goose production is an ancillary, rather than a main enterprise.



Embden geese are popular for farming for meat, originating in Germany in the 1800s. Photo courtesy of Daveness 98. Licensed under CC BY 2.0.

Goose meat is similar nutritionally to chicken or turkey meat but with a higher content of **fat** and **iron**. In general it is closer in flavour and appearance to **beef** than other **poultry meat**. The eviscerated **carcass** yield is around 71% and the breast yield around 7.5–8.5%. The practice of force-feeding to produce the fatty-liver condition (steatosis; liver **lipid** content being increased from a normal 5% to over 50%) is now banned in several countries for ethical reasons. Traditionally, goslings are force-fed several times a day for 14–35 days when 9–12 weeks of age. This delicacy has unique organoleptic properties. Goose liver is said to be of superior quality for making pâté de foie gras compared with that of ducks. The livers of force-fed geese can weigh over 1 kg. France is the largest consumer of liver fat at 15,000 t per annum: most of this is from ducks but about 800,000 geese are killed for their fatty

livers each year. Hungary and Israel are large producers, the latter using around 700,000 geese annually. China is likely to become a large producer of liver fat in a joint venture arrangement with France.

The most common goose breeds are the White Embden, Large Grey, Toulouse, African, Chinese, Pilgrim, Egyptian and Diepholz. The Large Grey goose is popular in Europe, because it grows rapidly and can be made to produce large fatty livers. Some strains of Toulouse geese produce 150 eggs per annum, while most breeds lay only 40–60 eggs. Egg weight (120–170 g) varies according to breed but gradually increases during the laying season. **Egg production** in geese is seasonal and is influenced by daylight length.

For breeding, the ratio of ganders to geese is 1:4 to 1:6. They should be run together for about 6 weeks before they will breed. **Fertility** (< 70%) is low compared with other poultry species, while hatchability in incubators is normally about 80%. Consequently only about 60 goslings hatch from 100 eggs. A goose can incubate 9–12 eggs, taking 31 days to hatch. Geese make excellent mothers. If eggs are artificially incubated, the goslings need artificial heat for the first 2 weeks.

Geese are excellent survivors and can be farmed out-of-doors with a minimum of shelter and care. There are many small flocks free-ranged on smallholdings throughout the world, and often with ponds that also provide a refuge from foxes. Geese also utilize **grass** seeds and scavenge for insects, snails, larvae, etc. In Europe, particularly in Hungary and Poland, geese are produced in

intensive systems on deep **litter** (straw). Shelter may be fully enclosed or have an outside fenced yard.

Nutrition

Geese are active foragers and require less attention than other domestic poultry. Semi-intensive systems, in which good-quality pasture is supplemented with **grain** or concentrates, allow excellent growth of goslings. Their **digestive system** is adapted to a high level of **forage** intake, with a large and muscular **proventriculus** and a well-muscled **gizzard** that together assist in the release of the soluble nutrients from the ingesta and allow the indigestible components to pass through the gut faster than in other avian species. Also, effective microbial breakdown of fibre takes place in the caeca and **large intestine** (Zhang *et al*., 2013). As a result geese are better able to utilize feeds containing high fibre levels than other avian species, though their main source of nutrients obtained by **grazing** is the soluble constituents in forage and weeds. They prefer to forage on young fresh growth; therefore the sward needs to be managed correctly and to be of high quality. Mowing is recommended if the sward height is more than 10–12 cm, since long grass can cause crop-binding. On good forage geese can survive with a minimum of supplementary feeding, or sometimes none, though productivity is likely to be lower. Geese prefer clover, bluegrass, orchard grass, timothy and bromegrass to **lucerne** and narrow-leaved tough grasses.

The **nutrient requirement**s of geese were estimated by NRC (1994) but are not as well defined as the nutrient requirements derived for other commercial poultry. Therefore it is common

practice to use diets similar to those formulated for **ducks** or **broiler chicken**s. Growth rate and protein deposition of goslings are very rapid, especially during the first 4 weeks when it is usual to provide diets similar to those used with starting broiler ducks, or, in some cases, broiler chickens. At that time the goslings can be allowed on range and should be provided with access to non-calcareous grit to assist with fibre **digestion**. A duck or broiler-type grower diet can be introduced at this stage, followed by a duck or broiler finisher diet for 3–4 weeks before processing, if the birds have been fed mainly on pasture. Geese are marketed at about 4–10 kg liveweight, depending on breed and age at slaughter. Many small-scale producers use a single starter–grower diet and a single layer–breeder diet successfully.

Ingredients used to make goose diets are similar to those used in other poultry diets, except that care should be taken to avoid feedstuffs contaminated with **aflatoxin** (*see* Mycotoxin). Geese (and ducks) are highly sensitive to this mycotoxin, particularly when diets are low in protein. The diets can be offered in **mash** or pelleted form; pellets are generally recommended to reduce wastage and build-up of caked feed on the bills of the geese and in drinkers. If fully fed on formulated diets, geese will reduce their forage intake; therefore, a common feeding programme is to allow goslings for the first 3 weeks to consume feed *ad libitum* for 15 min, 3–4 times per day. From then until market the feeding periods are reduced to twice per day. These recommendations assume that the pasture available is of good quality.

Some researchers now consider that **dietary fibre** is an

essential nutrient for geese. Li *et al*. (2017) fed diets containing different levels of **crude fibre** (CF) to starting/growing ducks for 70 days. Geese received diets with 2.5% and 6.1% dietary fibre for 70 days or a diet with 4.3% dietary fibre for the first 28 days and 6.1% dietary fibre for the next 42 days. The low-fibre (2.5% CF) diet had negative effects on growth performance, slaughter performance, serum biochemical parameters and nutrient utilization. Therefore, as herbivorous poultry, geese depend on dietary fibre for normal performance and this nutrient can be considered essential in their diet.

The utilization of fibre was reported by Zhang *et al*. (2013), who found that in a range of **by-product** feedstuffs the **digestibility** of neutral detergent fibre ranged from 6% to 45%, acid detergent fibre 5% to 33% and **hemicellulose** 19% to 62%. There was a significant negative correlation between energy digestibility and crude fibre content, a derived **true metabolizable energy** (TME) prediction equation being TME = 12.2 – 0.232 CF, where CF is crude fibre. These results suggested that geese are able to digest high-fibre diets effectively.

It can be concluded from the above findings and the results obtained by Song *et al*. (2017) that productivity of geese is optimized when they are allowed to forage on pasture and are provided with supplementary feed. The study reported by Song *et al*. (2017) involved 360 Yangzhou goslings assigned to one of four treatments from 29 to 70 days of age: (A) grazing only; (B) grazing, fed grain supplement mixture (64–70 days of age); (C) grazing, fed grain supplement mixture (29–70 days of age); and

(D) housed, no grazing, fed grain supplement mixture (29–70 days of age). The pasture was under-sown with **rye** and vetch forage. The grain supplement mixture was based on **maize** and **soybean** meal and for the 1–28-day period contained ME 11.46 MJ, CP 180.5, CF 40.7 g, Ca 7.2 g, P 5.6 g, **lysine** 8.3 g, **methionine** 3.9 g /kg; and for the 29–70-day period supplied ME 10.92 MJ, CP 160.2, CF 56.0 g, Ca 7.2 g, P 5.4 g, lysine 8.0 g and methionine 3.3 g kg^{-1}.

The results are summarized in the table and indicate that allowing access to grazing plus a grain supplement mixture for 29–70 days of age optimized overall productivity. Grazing alone resulted in a reduction in growth rate, in eviscerated carcass yield (attributed to a larger gut size) and in breast **meat yield**. A higher level of protein (including **collagen**) and a lower level of fat were found in the muscle in grazing geese, possibly due to the lower energy content of the feed and higher activity levels associated with grazing activity. Birds fed on grass and supplementary feed had a higher Mg and Cu content in breast muscle. No significant differences in content of Zn or Fe in breast muscle were recorded. (RB)

Effect of rearing system from 29 to 70 days of age on the productivity of Yangzhou goslings (Song *et al.*, 2017).

System	A **Grazing only**	B **Grazing + supplement** 64–70 days	C **Grazing + supplement** 29–70 days	D **No grazing + supplement** 29–70 days
Body weight at 28 days (g)	1225^{a}	1225^{a}	1226^{a}	1225^{a}
Body weight at 63 days (g)	3090^{Bb}	3033^{Bb}	3420^{Aa}	3484^{Aa}
Body weight at 70 days (g)	3157^{Bb}	3306^{Bb}	3647^{Aa}	3565^{Aa}
Feed consumption rate	0.51	0.60	2.42	3.37
Forage intake (kg)	98.09	77.26	54.74	0
Eviscerated carcass yield (g)	2021^{Cc}	2127^{Cc}	2381^{Bb}	2503^{Aa}
Breast muscle yield (g)	192.4^{Bc}	201.9^{Bc}	233.6^{Ab}	247.9^{Aa}

System	A **Grazing only**	B **Grazing + supplement** 64–70 days	C **Grazing + supplement** 29–70 days	D **No grazing + supplement** 29–70 days
Thigh muscle yield (g)	405.8^{Bb}	407.4^{Bb}	491.6^{Aa}	405^{Bb}
Protein in breast muscle (%)	22.23^{Bb}	22.09^{Bb}	22.53^{Aa}	22.06^{Bb}
Fat in breast muscle (%)	1.60^{BbCc}	1.96^{Bb}	2.24^{Bc}	2.63^{Aa}
Collagen in breast muscle (%)	1.49^{Aa}	1.51^{Aa}	1.50^{Aa}	1.11^{Bb}
Mg in breast muscle (µg/g)	258.60^{bc}	301.44^{a}	284.44^{ab}	264.06^{c}
Cu in breast muscle (µg/g)	4.95^{b}	7.24^{ab}	7.57^{a}	6.59^{ab}

System	A **Grazing only**	B **Grazing + supplement** 64–70 days	C **Grazing + supplement** 29–70 days	D **No grazing + supplement** 29–70 days
Zn in breast muscle (μg/g)	36.82[a]	32.17[a]	47.80[a]	29.14[a]
Fe in breast muscle (μg/g)	145.20[a]	105.91[a]	85.17[a]	76.14[a]

Note: Means with no common lowercase superscript differ significantly ($P < 0.05$); means with no common uppercase superscript differ significantly ($P < 0.01$).

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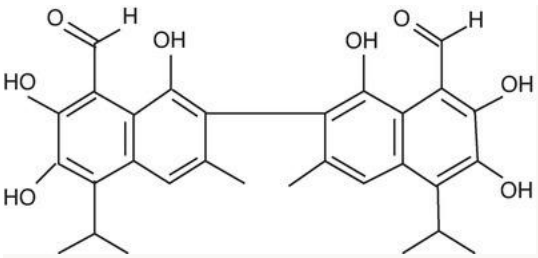
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Gossypol

$C_{30}H_{30}O_8$, molecular weight 518. A yellow **polyphenolic compound** found naturally in the pigment glands of cotton (*Gossypium* spp.). Gossypol is the predominant polyphenolic pigment but at least 15 other compounds of similar structure are present, which may be yellow, purple, blue or green. Gossypol can be found in **cottonseed** meal used as a **protein supplement** after **oil** extraction.

Gossypol may bind to proteins, reducing their nutritional **availability**. General effects of gossypol toxicity include depressed appetite and loss of body weight, cardiac irregularity and laboured breathing. **Reproduction** in both males and females may be impaired. In poultry, gossypol toxicity causes olive-green yolks in **eggs** and decreased egg hatchability. Toxicity of gossypol may be either acute or chronic, as the biological effects of gossypol are cumulative. Gossypol also binds minerals, especially **iron**. Iron salts can be added to help to bind gossypol and limit the depletion of minerals. Use of whole cottonseed or cottonseed meal should be restricted, to limit the possibility of gossypol toxicity. (DRG)



Gossypose:
see Raffinose

Grain
Also called a caryopsis, a grain is the edible seed of a grass, especially a **cereal** plant. Cereal grains comprise the embryo ('germ') and **endosperm**, surrounded by three protective layers (**aleurone**, **testa** and **pericarp**), together known as **bran**. **Starch**, as **amylose** and **amylopectin**, is the main **carbohydrate** present in cereal grains and occurs in the form of granules. The endosperm also contains proteins, which increase in concentration from the centre outwards. (ED)
See also: Barley; Maize; Oats; Rye; Triticale; Wheat

Grain legumes
Plants that utilize atmospheric **nitrogen** through root nodules in symbiosis with bacteria (*Rhizobium* spp.). They yield seeds in pods. Examples include **soybean**s, **pea**s, field **bean**s, **lupin**s, **groundnut**s, **leucaena**, acacia and others. The seeds tend to have higher protein contents than **cereal** grains but the proteins are often relatively low in **sulphur** amino acids. (TA)

Grain sprouting:
see Germination; Malting

Gramineae

The **grasses**, including pasture grasses and **cereal**s. (JMW)

Grape (*Vitis vinifera* L.)

The majority of grapes are grown for wine. After juice has been pressed from the berries, the residue (pomace) accounts for about 10% of the initial weight. If stalks have been removed before pressing, the pomace consists of 40% seeds and 60% skin and pulp. Seeds can be removed from dried pomace to leave skin and pulp (marc). Dried marc has value as a ruminant feed (Table 1). The seeds can be pressed for **oil** (8–22%), leaving oilseed cake, which has little feeding value due to its high fibre and **tannin** levels (Table 2).

Table 1. Grape nutrient composition (% dry matter).

	DM (%)	**CP**	**CF**	**Ash**	**EE**	**NFE**	**Ca**	**P**
Pomace – stalk, skin, pulp and seed	40.6	11.1–13.5	27.0–40.0		4.5–7.4	35.5–48.7		

	DM (%)	CP	CF	Ash	EE	NFE	Ca	P
Pomace – skin, pulp and seed	46.5	13.7	23.6	12.8	7.0	42.9	0.82	0.20
Marc	88.9	18.3	32.0	8.0	6.4	35.3	1.63	0.33

CF, crude fibre; CP, crude protein; DM, dry matter; EE, ether extract; NFE, nitrogen-free extract.

Table 2. Grape digestibility (%) and ME content.

	CP	CF	EE	NFE	ME (MJ kg^{-1})
Ruminant					
Pomace – stalk, skin, pulp and seed	18.4	8.5	77.8	40.9	6.04

	CP	CF	EE	NFE	ME (MJ kg^{-1})
Pomace – skin, pulp and seed	9.2	34.5	45.3	41.9	5.15
Pomace – stalk, skin and pulp	14.0	27.0	55.0	36.0	4.65
Marc	5.5	5.0	58.9	42.2	5.03



Grapes are valuable food for humans and feed for animals. The biggest producer is China, then Italy and the USA. Photo courtesy of RVWithTito. Licensed under CC BY 2.0.

Pomace from stalked grapes can be fed to **dairy cattle** up to 6.5 kg per day, supplemented with concentrates and **legume hay**. Inflammation of the digestive **mucosa** has been reported at higher levels of inclusion. Well-balanced broiler diets with up to 20% pomace allow excellent **growth**. Up to 10% of the ration for horses

can comprise grape marc, which has a lower fibre content than pomace. The **digestibility** of marc is improved by soaking in hot water. (LR)

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Grass

Grasses belong to the family Poaceae (**Gramineae**), which also includes **cereal**s. They have long narrow leaves, jointed stems and spikes of small wind-pollinated flowers. Temperate (C3) and tropical (C4) grasses follow different photosynthetic pathways. C4 grasses have evolved a photosynthetic mechanism that allows efficient use of CO_2 when the stomata of the leaves have been closed to reduce water loss. This mechanism involves a leaf anatomy (the Krantz anatomy) which means that the leaf is more fibrous, and hence less digestible, than that of C3 species. C4 grasses are generally larger, but are less digestible and have less **protein**, than C3 grasses.

Grass is the major feed resource for **herbivore**s and, therefore, for most ruminant livestock production systems. It occurs naturally, as in most of the world's natural grasslands (including **rangeland**s) and permanent pasture (both of which may be improved by the introduction of beneficial species, often members of the **legume** family), or is planted, using selected species, to meet a defined production objective. Whereas many sown pastures are on land that could be used for either grass or arable crop production, permanent pasture and natural grasslands often

occupy land unsuitable for arable use.

Grasses are annual, biennial or perennial. Propagation is either by seeds or by vegetative reproduction, or both. To obtain a dense sward, tillering above ground (stolons) and below ground (rhizomes) is of major importance.

Natural grassland usually contains several species of grasses, legumes and herbs, often interspersed with larger species such as bushes and trees, making it a suitable habitat for both grazers and browsers. Natural grasslands in temperate areas often consist of unfenced uplands or common lands. Extensive management is practised, with grazing- and fire-resistant species such as purple moor grass and heather often being dominant (Frame, 1992). In tropical semi-arid regions, natural rangeland consists of a mixture of annual and perennial grasses, of which perennials are often more highly valued nutritionally. However, after **drought**, if the soil seed bank is adequate, annuals recover first.

Permanent pasture is unlikely to be ploughed for arable cropping. It may evolve from natural pasture or be sown and is usually based on perennials, often with some soil-nitrogen enriching legumes (e.g. clover), thus reducing the need for nitrogenous fertilizers. Management should concentrate on maintaining a dense sward of nutritious species, not open to invasion by poor-quality and low-yielding grasses such as Yorkshire fog (*Holcus lanatus*), meadow grasses (*Poa* spp.) and bent (*Agrostis* spp.) in temperate pastures, or by barbedwire grass (*Cymbopogon refractus*), wiregrasses (*Aristida* spp.) or lovegrass (*Eragrostis curvula*) in tropical grasslands.



Grass is the major feed resource for sheep. This has a major impact on land use patterns in hill and upland regions. Photo courtesy of Bernt Rostad. Licensed under CC BY 2.0

Leys are normally sown on arable land and have a lifespan of 2–5 years. They need to contain easily established and rapidly growing species, such as the ryegrasses (*Lolium pratense* or *L. multiflorum*), with or without a legume.

When establishing grass, the choice of species is governed by ease of establishment, persistence, yield and **nutritive value**. The quality of grass pasture is influenced by the amount of herbage available for grazing, its nutritive value – particularly its **organic matter digestibility**, and protein and mineral contents, the acceptability of the grass species present to grazing animals, and the way that pasture structure affects the access to preferred species and plant parts. Soil type, rainfall and **temperature** preference are also important. In the growing stage grasses have

variable protein contents, ranging from > 300 g kg^{-1} dry matter (DM) in young, heavily fertilized grass down to 30 g kg^{-1} DM or even less in mature tropical grasses, and relatively low in indigestible fibre. Fibre content tends to be inversely related to protein content, ranging from 200 g kg^{-1} DM in young grasses to > 400 g kg^{-1} DM in mature grasses. The DM content of young growing grass is lower (150–250 g kg^{-1}) than in the mature crop (350 g kg^{-1}) but the DM of standing tropical grasses in the **dry season** can be even higher. Green grass usually contains many of the B-group vitamins and **vitamin E**. It is also rich in carotene, a precursor of **vitamin A**. At any stage of growth the DM is influenced by the **climate**. At and after flowering the stem increases in fibre (**cellulose**, **hemicellulose**s and **lignin**); **carbohydrates** and protein move into the seeds. Leafiness is a major determinant of nutritive value, and management (particularly of sown pastures) is aimed at encouraging leaf growth and use of the plant (grazing or conservation) at a young stage (see table).

Between the vegetative and milk stages, the digestibility of **crude protein** and **crude fibre** of *Hyparrenia rufa* in sheep fell from 604 and 619 g kg^{-1} DM to 165 and 473 g kg^{-1} DM, respectively (Speedy and Waltham, 1998).

Dry matter (g kg^{-1}) and composition (g kg^{-1} DM) of *Hyparrenia rufa* at four stages during growth in Brazil (from Speedy and Waltham, 1998).

		Composition		
Stage of growth	**Dry matter**	**Crude protein**	**Crude fibre**	**Ash**
Vegetative	297	92	289	149
Full bloom	343	35	314	136
Milk stage	352	28	337	115

Utilization of grass is by grazing, cutting for feeding green or conservation as **hay**, dried grass or **silage** for winter feeding. In tropical rangelands the grass is often left as 'standing hay', the nutritive value of which will deteriorate rapidly as the dry season progresses. It is usually taken as a bulk crop after the grass has reached the full-flower stage. Grass may also be cut at a younger stage and, if necessary, dried artificially in a high-temperature drier. Silage is made at an earlier growth stage than hay, ensiling being carried out at, or shortly after, cutting. Many grassland systems are based on a mixture of grazing and conservation, rather than a single use. (TS; GMcLD)

See also: Grazing

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Grass carp (*Ctenopharyngodon idella*)
One of the major Chinese carp of the family Cyprinidae. Although mainly monocultured in China, using pelleted diets, it has been introduced into the **fresh water**s of many regions in the world such as Southeast and Central Asia, Japan, America, Europe and the Arabian Peninsula, for both **aquaculture** and aquatic weed control. As the name implies, grass carp are herbivorous and feed on **aquatic plant**s. A very popular fish in culture, often in polyculture with other **freshwater fish**. The grass carp, like other Cyprinids, has a toothless mouth but has specialized pharyngeal **teeth** for rasping aquatic vegetation. The total production of grass carp in the world was 5.79 million tons – 11.8% of the total finfish production in 2020. This makes it the most popular fish species farmed for aquaculture in the world. (RMG; QS)



Adult grass carp. Photo courtesy of Asian Carp Regional Coordinating Committee. Licensed under CC BY 2.0.

Grass tetany
Hypomagnesaemic **tetany**, usually associated with the

consumption by ruminants of lush, high-quality pasture that is low in **magnesium** or contains high concentrations of **potassium**, **nitrogen** or **tricarboxylic acid**s (which interfere with the **absorption** of magnesium across the **rumen**). Magnesium concentrations in plasma, and especially cerebral spinal fluid, decrease from a normal value of 1–1.1 mM to < 0.5 mM, at which point normal nerve function can no longer be supported. This leads to uncontrollable muscle spasms (tetany) and tonic **convulsion**s, as a result of excessive release of acetyl **choline** at the neuromuscular junctions, hyperexcitability and rapid death. The syndrome is often accompanied by **hypocalcaemia** secondary to the low blood magnesium concentration.

Magnesium ions are absorbed mainly from the reticulorumen by **sodium**-linked active transport. The chief factor that affects this absorption is the potential difference across the ruminal epithelium. Active absorption of magnesium ions is reduced when this potential difference is increased by an increased concentration of potassium ions within the rumen. This can be the result of a high intake of potassium ions because of the ingestion of heavily fertilized grass, coupled with an increased potassium concentration in **saliva** in an attempt to correct a dietary **sodium** deficiency. A low dietary intake of **phosphorus** also reduces the absorption of **magnesium** ions. The condition is seen in older animals in which the skeletal reserves of magnesium are less available. Pregnant and heavily lactating cows are more susceptible to grass tetany because of their increased requirement for magnesium.

The onset of **hypomagnesaemia** in lactating cows is indicated

by nervousness, reduced **feed intake** and a stiff gait. In advanced cases the cow may bellow and gallop, and may have gone down with its head arched backwards, and convulsing (NRC, 1996). In the case of convulsing animals, treatment is by intravenous administration of magnesium and **calcium** salt solutions, though the results are often disappointing. In mild cases the animals can be treated with oral drenches containing magnesium salts. In housed animals, prevention is easily achieved by feeding higher amounts of magnesium (adding 20–30 g magnesium in a mineral form each day to the diet) but it can be difficult to ensure that grazing animals get sufficient supplemental magnesium. Prevention by oral **supplementation** of the concentrates with magnesium oxide to provide at least 60 g per day is recommended during periods of grazing rapidly growing grass, especially that treated with potassium and nitrogenous fertilizers. (ADC; JPG; GMcLD)

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Grazing

The consumption of **grass**, **legumes** and herbs in the field by

livestock. In temperate climates this will normally be growing **forage** consumed during the summer months. In the tropics it refers to the consumption of standing **hay** in the **dry season**, as well as of green material during the **wet season**.

In land that attracts little rainfall, trees may not be supported and vegetation is confined to perennial grasses that propagate by lateral growth. In a symbiotic relationship with **herbivore**s, quality is maintained by regular cropping, which prevents the pasture grasses from growing taller, for which they need to increase the fibre content to maintain structural stability. In ruminants the incisors are separated from the molars by a diastema, which enables them to continue **chewing** herbage at the same time as **harvesting** it. The lower incisors meet the upper palate, a pad on the upper jaw, against which they press herbage to tear it from the plant base. In cattle this cropping is by wrapping the tongue around the blades of grass and jerking the head backwards. Small herbivores with narrow mouthparts, such as sheep and deer, are more selective when grazing than large herbivores. This enables them to consume better-quality grass, but in smaller quantities than large herbivores. Selection during grazing may be horizontal, consuming only certain areas of pasture, or vertical, in which case only the upper layers of leaf and pseudostem are consumed. Horizontal selection may discriminate against grass that is contaminated with excreta, with rejection of this grass being initially a response to the smell and later because of its **maturity**. Darker green pastures are selected because of their higher **nitrogen** content. In mixed grazing of multiple species,

greater utilization of the pasture is attained because the rejection of herbage around excreta is usually species specific.

The stage of growth of a sward is a major determinant of its **nutritive value**. Cell wall contents increase markedly with age and protein concentration falls. This implies that regular defoliation, preventing flowering and seeding, ensures the highest-quality herbage, accepting a possible reduction in total yield of **dry matter**. The **digestibility** of young grass can be in excess of 0.8, falling below 0.5 in winter grazing or 'foggage' (in temperate regions) and well below this value in dry-season standing grazing in tropical natural grassland.

The amount of herbage available and the grazing behaviour of the animal dictate the amount of material the animal eats. These factors include bite mass, bite rate, length of time of the meal and the number of meals per day. Sheep graze the sward to a lower level than cattle and are more selective. Cattle digest fibre to a greater extent than either sheep or goats. Most grazing activity occurs during the hours of daylight, the other major activities in a 24 h period being ruminating, drinking, walking, grooming, lying and standing. Maximum use of the herbage available is often achieved by mixed-species grazing, as preferences and grazing behaviour vary between livestock species.

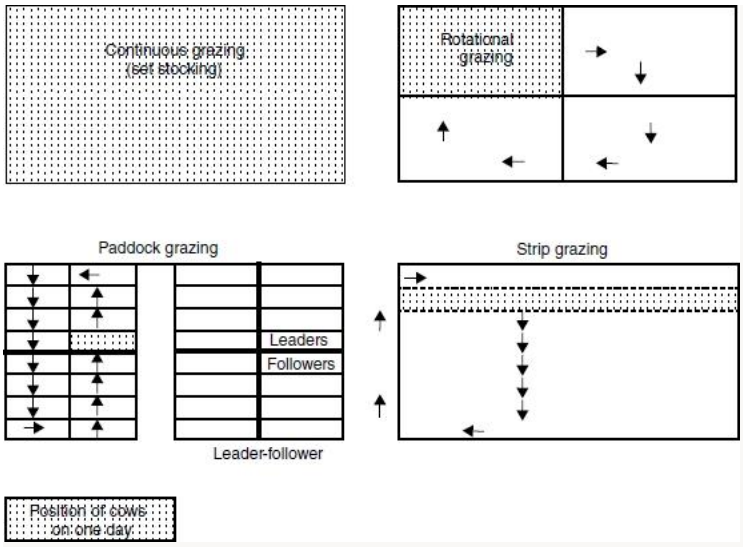
There are several systems of managing grazing. *Set stocking* involves a fixed number of livestock grazing a given area of land over a considerable time. It is often employed where factors such as the cost of fencing and provision of water preclude the use of small paddocks. It is suitable for areas of natural grazing but, if animal

numbers are high, the continuous grazing pressure and destruction of the natural habitat can lead to land degradation and erosion. This can be offset by feeding **supplement**s at grass. If numbers are low, insufficient grazing pressure in the growing season will lead to uneaten grass becoming rank. *Continuous grazing* differs from set stocking in that animal numbers and the land area available can be adjusted as the season advances. Frame (1992) used the term 'continuous stocking' and also described the 1.2.3 system, by which, in the early grazing season, one-third of the area is grazed and two-thirds cut for **silage**; the whole area is thereafter grazed. Systems based on removal of livestock at regular intervals have the advantages of allowing the application of fertilizer during the season and interspersing grazing with conservation, when regrowth is sufficient. However, they require more fencing and water points than in set stocking systems. ***Rotational grazing*** is when stock is moved to a fresh paddock at predetermined intervals and the recently grazed area is allowed a recovery period; the length of the periods can be from days to months. A simple example is the division of a large grazing area into four paddocks (e.g. 7 days grazing, 21 days rest). On a larger scale, *cell grazing* divides a **rangeland** property into large paddocks or cells and cattle are moved between cells on a regular basis. *Paddock grazing* is a form of rotational grazing in which the duration of grazing (often as brief as 1 day) depends on the number and size of the paddocks (normally a large number of small areas), the number of animals and the amount of herbage available; the period of rest will be calculated to match the expected recovery time of the sward.

Again, grazing can be replaced by conservation when the amount of regrowth allows. Both rotational and paddock grazing should aim to avoid undergrazing when herbage is plentiful and overgrazing when it is short. *Strip grazing*, or allocation of fresh material by moving an electric fence, is often used for intensively managed dairy cows, the intention being to keep a supply of fresh, untrodden grass in front of the animals at all times. *Creep grazing* (including leader/follower systems) describe systems in which young stock are allowed access to fresh herbage in front of their dams. This allows them maximum opportunity for selection, leading to improvement in intake of nutrients and growth rate.



Paddock grazing at a UK dairy farm, showing paddocks separated by electric fences. Photo courtesy of Phillips Halling. Licensed under CC BY SA 2.0.



Diagrammatic representations of the continuous, rotational, paddock and strip-grazing systems.

With all these grazing systems the land benefits from the direct application of manure. Dividing the land area may be by permanent or electric fences, or shock collars are being developed that control cattle to a specific area. However, there are instances, especially with dairy cows on wet land, where it is beneficial to move the grass to the livestock: this is called *cut-and-carry* or *zero-grazing*. This gives the farmer closer control of grassland and conserves **energy expenditure** in the stock, but it is labour and machinery intensive. For most farmers the disadvantages outweigh the advantages. *Tethering*, an extreme form of controlling grazing livestock, is used where grazing pressure is high. In many tropical areas it is most common in the **wet season** where arable crops cannot be adequately fenced. It also allows safe grazing of roadside verges. Animals often have access to limited grazing and cut feed. (TS; CJCP)

See also: Grass

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Green-crop fractionation:

see Fractionation, green-crop

Green feed

Plant material harvested for immediate use as animal feed, without preservation. (JMW)

Green tea

Crop derived from a plant with the scientific name *Camellia sinensis*, which is bushy and evergreen and has a strong vertical root and yellow and white flowers. In general, the young, light green leaves of the plant are used to produce **tea** for use in food/feed and medicine in the form of drinks and additives. Globally more than 5 million tonnes of green tea are produced annually, which indicates the strategic importance and extent of the use of this edible and medicinal plant. Green tea leaves contain **polyphenol**s (between 25% and 30% of the dry weight), which have potential beneficial effects on human and animal health.



Tea crop trials in Mealini Agricultural Station in Hawaii. Photo courtesy of Starr Environmental. Licensed under CC BY 2.0.

The bioactive and chemical compounds in the leaves depend on the time of **harvesting** and the type of processing, but the importance of green tea is mainly due to its **antioxidant** properties and the bioactive compounds (Liu and Chi, 2000). One of the most important and effective antioxidant compounds in green tea are the catechins (types of **flavonoid**). The catechin epigallocatechin-3-gallate is considered the most biologically active substance in green tea. Catechins also have **cholesterol**-lowering, anti-cancer, antibiotic and anti-inflammatory properties, as well as blood-fat-lowering, anti-diabetic, anti-**obesity**, Alzheimer's-preventing and antimicrobial properties in humans (Zhao *et al.*, 2022). Epigallocatechin-3-gallate is said to intervene in the dissolution of cholesterol in micelles and reduce cholesterol **absorption**, as well as regulating the expression of genes related

to **lipid metabolism** (Abunofal and Mohan, 2022). In addition to catechins and other flavonoids, green tea contains **caffeine**, **theobromine**, **theophylline** and gallic acid, with multiple biological effects. Caffeine is an **alkaloid** from the methylxanthine family that antagonizes all types of transmembrane receptors for adenosine (an inhibitory **neurotransmitter** that causes drowsiness) in the brain and increases alertness. Besides affecting the central nervous system, it has lipolytic properties. Other active components of green tea, such as theophylline and theobromine, have similar effects as caffeine. L-Theanine (an analogue of L-**glutamine**) is a unique amino acid that is found mostly in tea. It crosses the **blood**–brain barrier and increases alpha brain waves, which are involved in conscious relaxation (Ahmad *et al*., 1998). In addition, L-theanine increases the production of **nitric oxide** (NO; a major vasodilator) from L-**arginine** by endothelial cells (Yang *et al*., 2015), thereby improving cardiovascular function in animals.

Supplementing the diet of poultry (broilers, laying hens and quails) with green tea increases feed consumption, stimulating growth, and is potentially an alternative to antibiotics. Claimed benefits include potentially increasing the efficiency of nutrient utilization and strengthening the immune system against diseases such as **coccidiosis**, Newcastle disease and influenza. It also reduces low-density **lipoprotein** (LDL) in plasma, serum **cholesterol** and **meat** peroxidation, thereby reducing abdominal fat and yolk cholesterol. It improves **egg** yolk colour and α-**tocopherol** content, providing immunological and hepatic benefits, improving the atherogenic index (LDL/HDL) and

balancing the intestinal microbiota (*Lactobacillus* proliferation and a reduction of ***Escherichia coli*** population in **ileum** and **caecum**) (Seidavi *et al*., 2014, 2020; Liu *et al*., 2021). (AS; BH-G; CJCP; GW)

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Grinders

Machines used in feed processing to reduce **particle size** and especially to rupture cereal **grain**s. Two main types of grinder are used in the animal feed industry. The most common is the hammer mill, in which feed material is fed into a grinding chamber where it is shattered by the impact of 'hammers'; these are rectangular pieces of hardened steel attached to a shaft which rotates at high speed. Perforated metal screens around the periphery of the chamber retain coarse particles for further grinding and allow properly sized material to pass. Hammer mills are easy to operate and maintain, and the cost of wearing parts is low.

The other main type of grinder used for animal feed is the roller mill, in which feed material is passed between two or more counter-rotating, fluted rollers. Coarser material can be sifted after rolling and re-circulated for further reduction. Compared with hammer mills, roller mills are less noisy and dusty, more energy efficient and produce few finer and fewer oversize particles. (AMo)

Gross energy

The heat released when the carbon and hydrogen present in a substance are completely oxidized to **carbon dioxide** and water. Gross energy is synonymous with heat of combustion and is determined by burning a sample of the substance in a **bomb calorimeter**. (JAMcL)

Gross protein value (GPV)
A measure of the effectiveness of a 'protein' (usually a mixture of proteins) added to a diet containing a **cereal** base. The response to the test protein is compared with the response obtained when **casein**, as a standard, is used in place of the test protein. The response is in units of grams of body weight gain per unit of protein consumed when incorporated into the diet containing the cereal. GPV has no units; it is simply a ratio. It is not equally applicable to all species or ages of animal, because of differences in the pattern of their amino acid requirements. (NJB)

Groundnut (*Arachis hypogaea*)
Leguminous plant (also peanut) that is commonly grown in the tropics, primarily for its **oil**. The seeds are produced in pods beneath the ground and the oil (about 500 g kg^{-1}) is extracted by pressing either the shelled seeds or the whole pods. The residual meal, either decorticated or undecorticated, is used as a high-protein feedstuff for both ruminant and non-ruminant animals. It is susceptible to fungal contamination by *Aspergillus* spp. which produces **aflatoxin**s, potentially causing aflatoxicosis in animals. The protein content of decorticated groundnut meal is about 500 g kg^{-1}; for undecorticated meal it is about 300 g kg^{-1}.



Groundnut, a tropical nut of particular value for its oil. Photo courtesy of K.R. Harsha. Licensed under CC BY-SA 2.0.

The **crude fibre** content of undecorticated meal is about 300 g kg^{-1}, while the decorticated meal has about 100 g kg^{-1} (with neutral detergent fibre about 130 g kg^{-1}). The decorticated meal, which has an apparent **metabolizable energy** (AME) for poultry of 13–14 MJ kg^{-1}, is the more suitable for non-ruminants and the undecorticated for ruminants (AME about 10 MJ kg^{-1}). The ME depends on the content of residual oil. The **lysine** and **sulphur** amino acid contents of the **protein** are relatively low. The **forage** material can be fed to ruminants: it has a protein content of about 100 g kg^{-1} **dry matter**. (TA)

Groupers

Marine finfish belonging to the subfamily Epinephelinae, commonly known as groupers or rock **cod**. There are approximately 159 grouper species in 15 genera worldwide. The more popular cultured species belong to the genus *Epinephelus*. Groupers are coastal warm-water fish widely distributed in tropical and subtropical waters. Most are found in coral reefs and off rocky coasts but some species inhabit estuarine areas.



The dusky grouper (*Epinephelus marginatus*) at the Garaiau Nature Reserve, Madeira. Photo courtesy of B. Mal. Licensed under CC BY-ND 2.0.

By nature, groupers are predatory and are exclusively carnivorous – a major problem in **aquaculture** of this species. The bulk of groupers for human use comes mainly from the capture fisheries. Due to increasing consumer demand and depletion of wild fish stocks, the culture of hybrid groupers is expanding quickly in China and the Southeast Asian countries by using **extrusion** diets from a starter diet to one for a fish of marketable size. In 2020, the total aquaculture production of grouper in China was about 192,000 t, which is 84.9% of the world grouper production of 226,000 t (CFSY, 2021; FAO, 2022). (RMG; QS)

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Growth

The dynamic process by which animals change from a single newly fertilized cell into an adult. At its simplest, it means getting bigger and heavier. Growth of the whole animal or of one of its complex parts can be neatly divided into two aspects: increase in size and change in form.

Rates of **liveweight** gain are agriculturally important but, for genetic and nutritional studies, investigations may be made of the growth of particular components of the body. There are several approaches for measuring growth. Dissection allows measurements to be made of individual tissues (bone, **muscle** and **fat**), specific organs or parts of the body, individual cells or even an organelle. Numerical growth refers to changes in the number of units, ranging from population growth (whole animals) down to micro-populations such as the number of cells, the number of glands or the number of follicles. Growth may also be considered in terms of changes in linear dimensions such as height, width, length, girth and circumference. For certain studies, growth of areas of the body may be of interest, such as surface area of the whole animal, respiratory surface or absorptive surface of the gut. Chemical growth refers to changes in the mass of a chemically defined entity of the body, e.g. **protein**, **lysine**, **lipid**, **ash** or **calcium**.

At the cellular level, growth is usually considered as having two components: increase in number, described as hyperplasia; and an increase in the actual size or mass of the cell, called hypertrophy. As a general rule hyperplasia is a feature of early growth and hypertrophy of later growth. During normal metabolic activity, complex molecules are continually assembled and dismantled in a

process known as **turnover**. Growth itself can be considered as the balance between anabolism and **catabolism** or synthesis and degradation. This is also called net accretion.

Temporal growth

Growth rate is a measured unit of change over a given time interval. The mass of an animal, or that of one of its parts, when plotted in relation to time produces a characteristic sigmoid growth curve. Its appearance is that of a rather flattened italicized capital S. Over the life of the animal, the first part of the curve is often described as 'self-accelerating' and the second part as 'self-decelerating' until an asymptotic value is reached that is mature weight. Blaxter (1989) pointed out that the growth curve is closely related to **feed intake** and derived an equation to show the relationship. It is a matter of debate whether growth requirements drive feed intake or intake drives growth.

The condensation of animal growth curves into algebraic formulae has exercised mathematicians for many years. Such efforts vary from the merely empirical to those that attempt to model and integrate the intrinsic complex biological interactions that are involved. A relatively simple curve that models all phases of the growth curve is the so-called Gompertz equation. This produces a sigmoid curve with an inflection at about one-third of the mature size. Discussions and descriptions of **growth equations** are given by Lawrence and Fowler (2002) and Bakker and Koops (1978). Though growth equations have their place in biology, they are not always applicable. Seasonal shortages of feed and stresses imposed by disease and varying stocking density and

pregnancy can cause major perturbations to the curve.

Relative or allometric growth

Some animals grow without any obvious change in shape. Many aquatic or marine creatures, such as fish, tend to fall into this category. Such growth is called isometric, because each component increases by the same percentage increment over a period of time. However, most animals can be seen to be either 'mature' or 'immature' by changes in their conformation. For example, calves are not miniatures of adult cattle. Changes in proportion are a response to the changing physical and physiological needs of the animal as it increases in mass. As Brody (1945) pointed out, the strength of muscles is closely related to their cross-sectional area or the square of linear size. However, in land animals, weight, which has to be supported and moved, increases as the cube of linear size. The effect is that farm animals become more muscular with a more compact appearance as they grow larger. Baby animals tend to have large heads relative to the rest of their bodies and large eyes relative to the size of their heads. Limbs tend to be poorly muscled and spindly in the young but well-muscled and sturdy in the adult. These changes occur because the components are growing at different percentage growth rates. This is called allometric or differential growth.

Huxley (1932) was one of the first to show that most tissues and parts tend to grow in logarithmic relationship to each other and to the whole animal. He proposed the relationship

$$\log Y = \log a + b \log X$$

where Y = weight of part, a = the value of Y when log X = 0, and

X = weight of whole minus weight of part. Such a relationship implies a constant ratio between the percentage growth rates of X and Y. When the slope, b, is 1, the relationship is isometric; if $b < 1$ then growth of the part is slowing down relative to the whole (early maturing); and if $b > 1$ then the part is growing more quickly than the whole in percentage terms.

The tendency of animals to grow more rapidly in their distal regions when young and then broaden and thicken at the top of the legs and in the pelvic region is sometimes called centripetal growth (Hammond, 1932). Hammond and his school described those tissues or parts that went through their growth programme early in life as early maturing and those growing as the animal approached adulthood as late maturing. For tissues, the sequence in order of completion of the growth cycle from early to late maturing was: (1) nervous tissue, (2) bone, (3) muscle and (4) fatty tissue; and for regions the sequence was: (1) extremities or distal parts (e.g. metatarsals and metacarpals), (2) medial (tibia fibula, radius and ulna), (3) proximal (femur and power muscles at the top of the legs) and (4) axial (lumbar vertebrae and loin muscles and **adipose tissue**s).

Fluctuations in **nutrition** may disrupt some of these elegant patterns. Growth rates can be deflected and so can some of the inter-structural relationships. The most obvious example is the extreme flexibility of the adipose tissue depots. Comparing the proportions of tissues and organs on a fat-free basis (either chemical or dissectible fat) often reveals underlying relationships that are obscured if fat is included.

The changing relationship between parts and tissues during growth is of considerable interest, especially for agricultural purposes. Not all components of **liveweight** or **carcass** weight gain have equal economic value and a knowledge of growth patterns can greatly assist in optimizing strategies for economic production of **meat**. (VRF)

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Growth disorders

Growth disorders are usually assumed to mean reductions in **growth**, in particular dwarfism, which is detected in all the major species of farm animals. Often specific breeds have been developed with dwarf characteristics; for example, several breeds of cattle

have been developed, including the Dexter, Japanese Brown and dwarf zebu. The proportion of cattle within a breed that have dwarf characteristics is variable. The selection of dwarf animals has always been a feature of the domestication process, because they are easier to handle and have lower **maintenance** requirements than larger breeds of the species. However, in recent years the greater mechanization of livestock production has favoured the selection of larger farm animals, which are little handled by humans and are fed *ad libitum*. Thus the small cattle breeds that were developed in Britain over the past 200 years, for example, are not popular for intensive production systems.

In many breeds a proportion of the animals are particularly small. Affected cattle usually have limbs that are disproportionately short, compared with their trunk size, with wide **epiphyses** of the femurs and humeri. This may be due to incomplete maturation of carpal and tarsal bones and incomplete maturation and abnormal flaring of epiphyses of the short humeri and femurs. A short vertebral column is a feature of Dexter cattle.

The reasons for dwarfism are not only genetic. They include abnormal feeding of dams during pregnancy, **twinning**, **mineral deficiencies** (especially **iodine**, **zinc** and **manganese**) and infectious diseases (e.g. Akabane virus infection in pregnant ewes). One inherited characteristic that can produce dwarfism is inadequate IGF-1 production. Another possible cause is **heat stress**, which will prematurely terminate pregnancy, particularly in housed sheep. This leads to inadequate growth of brown fat reserves in the final stages of pregnancy.

Sometimes a congenital chondrodysplasia is lethal, causing **abortion** or neonatal mortality, but this may also occur with infectious agents. A number of severe, simply inherited growth disturbances have been identified in farm animals. These disorders are controlled by defective alleles at major loci referring to **hormone**s or hormone receptors, e.g. growth hormone receptor for the recessive sex-linked dwarfism in chickens.

Mineral deficiency may be a factor. In ruminants, the critical time for the most severe effects of **mineral deficiency** is the mid trimester, when the neurons of the cerebral cortex and basal ganglia are formed. At this time, an **iodine** deficiency could affect maternal thyroid function. There is now evidence indicating transfer of maternal thyroxine, with impaired fetal thyroid function following in the third trimester to augment the effect of reduced maternal thyroid function.

When caused by disease, dwarfism is often accompanied by skeletal deformation, for example the endemic osteoarthropathy Kashin-Beck disease in Chinese poultry.

Some growth disorders are potentially beneficial, such as double muscling in cattle and sheep, which increases the ratio of **muscle** to the inedible parts of the **carcass**. In the past 25 years a genetic mutation that increases the rate of muscle growth has appeared in the Belgian Blue breed of cattle and it is suspected to exist in other breeds. Double-muscled cattle have a considerably increased ratio of muscle to fat, particularly in the male, and they have smaller organ weights. The increase in size of the muscles is accompanied by an increase in tenderness, which enhances the

commercial value of the fore- and hindquarter cuts. The trait is controlled by a major gene, which was recognized in some sheep breeds long before its recent appearance in cattle. However, in Belgian Blue cattle the trait is associated with difficult calvings in pure-bred animals, which require specialist management to keep the number of Caesarean births to a minimum. The increased cost of care during calving may be financially justified by increased growth rate potential but the growth disorder raises concerns for the **welfare** of the cows. (CJCP)

Growth equations

A growth equation, or growth function, is a mathematical function describing the growth of an animal over time. The general form is

$$W\bar{o}=f\theta(t)$$

where W is **liveweight**, t is time and f is the growth function. The function f depends on parameters θ. Growth functions may also be used to model measures of growth other than liveweight, such as height, or weight of some body component of the animal.

General functional forms, such as polynomial or spline functions, may provide adequate fits to a single set of growth data over time. These functions tend to require many parameters, with no biological significance. A number of growth functions have been proposed that are derived from equations describing biological processes such as autocatalysis or senescence, and which require fewer, more meaningful parameters. We will describe the most well-known and important of those here: the exponential, logistic, Gompertz and Richards equations.

It is unrealistic, however, to expect to describe growth, the

result of complex genetic and environmental interactions, with any analytical function of a small number of parameters. These functions are most successful at describing growth in completely controlled environments, for example an 'unlimiting' environment in which an animal may meet its growth potential. More complex environments require more complex simulation models.

The exponential growth equation is derived from the assumption that, since the animal itself is the mechanism of growth, the rate of its growth is at any time proportional to its weight. This autocatalysis assumption implies the differential equation

dWdt=μW (Equation 1)

where $\mu > 0$ is the growth rate parameter. The resulting growth function is

W=W0eμt

Here W_0 is the initial, non-zero, weight. This function predicts an unlimited increase in weight over time, so it is only a realistic description of the initial phase of growth of an animal.

The logistic growth equation provides a correction to the exponential by restricting growth based on availability of a **substrate**, which is assumed to decrease as the animal grows. Assuming that growth is proportional both to W and to $W_m - W$, the amount of substrate left out of a fixed quantity W_m, we have

dWdt=μW(Wm−W), (Equation 2)

and

W=W0WmW0+(Wm−W0e−μt

The weight reaches a maximum W_m once the substrate is

exhausted.

Farm animals stop growing because they reach **maturity**, not usually because they run out of food. The Gompertz equation assumes exponential growth as in (1), but assumes that the rate of growth μ itself decreases exponentially over time:

$$\mu=\mu_0 e^{-Dt},$$

where $D > 0$ is a second parameter describing rate of senescence. Explicitly,

$$W=W_0 e^{\mu_0(1-e^{-Dt})/D}.$$

The mature weight, approached as t gets large, is

$$W_m=W_0 e^{\mu_0/D}.$$

The family of Richards growth equations have the form

$$W=W_0 W_m (W_{0n}+(W_{mn}-W_{0n})e^{-kt})^{1n}$$

Here W_0 and W_m are as before, and $n \geq 1$ and $k > 0$ are new parameters with no simple biological interpretation. The Richards equation specializes to the logistic when $n = 1$ and the Gompertz when $n = 0$. Richards equations are therefore a mixture of mechanistic models such as these, and empirical, non-biologically based models. (RG)

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Growth factors

Polypeptide **hormone**s that promote cell growth, proliferation and anabolic processes. Some well-recognized members of this group include the **insulin-like growth factor**s (IGFs), epidermal growth factor (EGF), transforming growth factors (TGFs), nerve growth factor (NGF) and fibroblast growth factor (FGF). Of particular importance are the IGFs (I and II). These hormones comprise a family structurally related to **insulin** with multifunctional metabolic and anabolic properties and may influence differentiation and be mitogenic in developing muscle. They exert their actions by occupation of membrane-bound receptors as well as interactions with soluble **binding protein**s. The IGFs are synthesized by various tissues and act by paracrine and autocrine mechanisms. Blood-borne IGFs, synthesized mainly in the **liver**, exhibit endocrine activity. Manipulation of muscle growth and mass by increasing expression or insertion of IGF genes is a possible future strategy. (MMit)

See also: Growth; Muscle

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Growth models

All animals and plants have the potential to grow at a rate determined by their **genotype**. This potential growth rate is often constrained by one or more of many environmental factors, such as disease, inadequate food supply, or too high an **environmental temperature**. In modelling growth, different approaches may be used, depending on whether the model is to predict the potential or

the constrained growth rate of the animal. Modelling, or predicting, potential growth is simple, but predicting the effects of the various constraining factors on potential growth, and the consequences on subsequent growth once the constraints are removed, is far more complex.

A number of **growth equations** may be used successfully to represent unconstrained growth. Such equations result in a smooth, sigmoidal curve of body weight (w) over time (t). Differentiating such equations results in a representation of weight gain over time (dw/dt), which reaches a maximum, and then declines to zero, when the animal reaches its mature body weight. In place of body weight, other characteristics of the animal may be used to represent growth, such as the degree of **maturity** (u) ($u = P/P_m$, where P and P_m are the **protein** weight and mature protein weight of the animal, respectively). In unconstrained conditions the **chemical composition** of the body may be predicted with the use of the allometric relationships that exist between different components of the body. Body protein weight may be used as the predictor (independent variable) and **body water**, body **ash** and body **lipid** as dependent variables. Whereas body lipid content varies between individuals and between species, the three remaining chemical components exhibit a fixed relationship with one another at maturity, even between most species. Nevertheless, the body lipid weight of a given animal is also allometrically related to the body protein weight under unconstrained conditions. As a result, once the growth of body protein has been modelled by means of a growth equation, the growth of the other chemical

components of the body may be predicted by allometry, and the sum of the four components would then result in a prediction of the body weight of an animal over time. The growth of any integuments, such as feathers or hair, may be modelled in the same manner.

Modelling constrained growth

Modelling the effects of constraining factors on the growth of an animal is more complex than modelling unconstrained growth. These constraints may influence the growth process in different ways, and theories should be developed to account for each of these effects before they can be modelled successfully. For example, the constraint might act at the level of food intake, which, if reduced either in quantity or through a change in quality, would result in a reduced growth rate. A reduction in food intake may have little to do with the **feed** composition, or the daily amount allocated, but may be due entirely to unfavourable environmental conditions, such as high temperatures. Conversely, a disease may influence the growth process, possibly through a reduction in the rate of metabolic processes in the body or by reducing the uptake of nutrients from the **small intestine**. The resultant growth constraint may or may not be the same as that due to a reduction in food intake. Of importance in modelling the effect of a given constraint on the growth of an animal is having a plausible understanding of how the limited supply of dietary nutrients would be partitioned between functions.

In order to describe growth, whether constrained or not, in terms of the supply of dietary nutrients, it is necessary to describe

the feed in terms that are relevant to the animal. In the successful growth models that have been developed, some of the dietary nutrients, such as digestible **amino acid**s, are considered to be resources, whereas others, such as **metabolizable energy** (ME), must be transformed into resources, using a set of rules, given that the ME scale does not take account of the contributions of the different chemical components of the feed to its energy content, nor does it effectively predict the heat increment associated with the **digestion** and **metabolism** of the given feed. Predicting the amount of heat produced by the animal in a given state, and consuming a given amount of a given feed, is critical in determining whether the animal will be successful in consuming the amount of food that is required for potential growth, or whether the environmental temperature is too hot to allow it to do so. The animal must retain its thermal balance, and if the animal is unable to dissipate the heat produced during digestion, metabolism, **maintenance** and growth it has no alternative but to reduce food intake. In modelling constrained growth through the prediction of **voluntary food intake**, therefore, the model must integrate information about the animal, the feed that it is being offered, and the environment in which it is kept.

Modelling compensatory growth

There are many reports in the literature claiming that animals are capable of catching up with their counterparts in weight after a period during which they did not grow to their potential, i.e. they were able to compensate for the growth lost by growing faster during the rehabilitation period. This would imply that, in addition

to growing faster, animals utilize their feed more efficiently during rehabilitation. In modelling such **compensatory growth**, care must be taken to identify which, if any, of the chemical and/or physical components of the body exhibit such growth during the period of rehabilitation.

Depending on the extent to which growth and **body composition** have been affected, the animal may, at the end of the period of abnormal growth, have a protein deficit (with an associated water deficit) and either a deficit or an excess of lipid relative to its ash weight in the empty body. In addition, it may have abnormally high or low weights of the food-processing organs and gut-fill compared with normal animals at the same ash weight. In other words, the chemical and physical composition of the animal at the end of the period of constraint is likely to be very different from that of an animal having grown normally. It may be assumed that the animal would attempt to rectify any insult to its growth, thereby regaining its genetically determined physical and chemical composition at a given ash weight. But the response in the growth of the different body components once the animal has been returned to a non-limiting environment will depend not only on its composition before the restriction was lifted but also on factors to do with the feed offered and the environment in which it is placed.

Growth models that are useful in real-world situations are those that attempt to predict both chemical and physical growth, under both unconstrained and constrained conditions. Because of the complex interactions between the animal, the feed that it is being offered, and the environment in which it is kept, such models of

growth must take account of all of these factors. (RG)

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Growth promotersHormones and antimicrobial substances that stimulate faster growth; they are principally used in cattle. In the European Union both synthetic and naturally occurring growth-promoting hormones were banned in 1986. The most potent growth promoters are the gonadal steroids, since rapid growth and sexual development coincide at **puberty**. Most powerful are the androgens, principally testosterone, produced predominantly in the testes and important in increasing the efficiency of growth by increasing the **nitrogen** incorporation into muscles. Androgens also cause epiphyseal plate fusion in bones, and exogenously administered androgens can reduce skeletal size. Exogenous androgens such as trenbalone **acetate**, if permitted, have their greatest effect in heifers or cull cows, due to the low level of natural male steroids in the female.

Oestrogens are also potent growth stimulators in young steers.

They increase growth hormone, leading to increased muscle production, decreased fat production and reduced losses of urinary nitrogen. In the older animal, oestrogens cause epiphyseal plate fusion in bones in the same way as androgens. Both synthetic oestrogen-mimicking agents, such as diethyl stilboestrol and zeranol, and naturally occurring female steroids, principally oestradiol, are most effective on steers, though combined-action trenbalone acetate and oestradiol implants are effective in stimulating growth in bulls, steers and calves. The efficacy of synthetic steroid use is greatest in cattle, intermediate in sheep and of limited value in pigs. Because of the stimulation of muscle growth by both oestrogenic and androgenic hormones or hormone-mimicking agents, it is often necessary to supply extra rumen-undegradable protein to implanted animals.

Other hormone mediators of growth include the β-agonists, which are synthetic analogues of adrenaline and noradrenaline, such as **clenbuterol** and **cimaterol**. These reduce intramuscular fat considerably, by up to 30%, with a corresponding increase in protein deposition of 10–15%. As a result the food conversion efficiency is often increased by a similar proportion (10–15%). The effects on weight gain and **feed intake** are variable, depending on the relative impact on fat and protein deposition. There is evidence that cattle treated with β-agonists are more susceptible to dark cutting, and the low level of muscle **glycogen** and **carcass** fat can give rise to cold shortening (cross-bonding between **actin** and **myosin** fibres) if the carcass is rapidly chilled post mortem to 10–15°C. The increase in carcass yield may be accompanied by smaller

non-carcass components. The action of β-agonists is not sex specific but all animals are susceptible to tachycardia (elevated heart rate) and increased **basal metabolism** rate, which may be perceived as reducing their **welfare**. The risk of residues is low as the β-agonists are rapidly metabolized, and after withdrawal of the substance from the feed the animal's nitrogen metabolism rapidly reverts to normal.

Surprisingly the administration of growth hormone to growing cattle does not result in large increases in muscle growth, perhaps because of the lack of additional receptors. However, immunization against somatostatin, which is the agonist of bovine **somatotrophin** (bST), can increase growth but it also tends to increase carcass fatness. Somatostatin inhibits other hormones, such as **insulin** and the thyroid hormones, which may explain its action.

Antimicrobial compounds are routinely used in some cattle production systems to modify the gut microflora. The most commonly used is monensin **sodium**, which was originally developed as a coccidiostat for poultry. In the **rumen** of cattle it is active in reducing the population of acetate- and hydrogen-producing bacteria, such as *Ruminococcus* spp. and *Bacteroides fibrisolvens*, allowing **propionate** producers such as *Selenemonas ruminatum* to flourish. This increases the efficiency of growth by about 5%, partly because **acetate** production is accompanied by **methane** loss via eructation. As a result of its mode of action, there are no effects of such growth promoters on carcass composition. The widespread use of monensin sodium was not

possible until it could be incorporated into **feed block**s that could be offered to the cattle when they were out at pasture. If cattle are offered feeds with added monensin sodium indoors and then turned out to pasture with no **supplement**, there is a considerable check to growth as the rumen microflora adapt.

There is increasing concern over the routine use of antimicrobial compounds in cattle production systems, principally because of the risk of transfer of resistant bacteria from animals to humans via the **food chain** and the possible transfer of resistant genes from animal bacteria to human pathogens. Currently within the EU, animal **feed additives** are only allowed if there is no known adverse effect on human or animal health, or the environment. Although there were originally ten licensed antimicrobial growth promoters, four of these (bacitracin **zinc**, spiramycin, tylosin phosphate and virginiamycin) were withdrawn in 1999 because of fears that human health would ultimately be compromised by their use. A human antibiotic similar to virginiamycin is currently being developed, which it is suspected could be rendered ineffective with continued use of virginiamycin in animal food. A further two antibiotics (olaquindox and carbadox) have been banned due to possible risks to human health during the manufacturing process, leaving only four that can legally be used (monensin **sodium**, salinomycin sodium, avilamycin and flavophospholipol).

Probiotics are an alternative to antibiotics when they are used therapeutically but are not very effective as growth promoters. They promote colonization of the gut by benign bacteria, such as

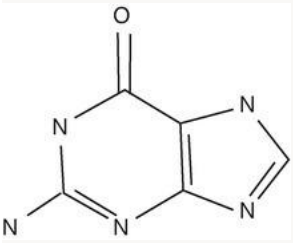
Lactobacillus spp., thereby excluding pathogenic bacteria by reducing nutrient availability or, in the case of lactobacilli, acidifying the gut contents with **lactic acid**. Their use in cattle is restricted to the pre-ruminant calf, where they may prevent ***Escherichia coli*** from colonizing the gut and causing scours. Photoperiodic manipulation of cattle growth can achieve desirable changes in composition but it is doubtful whether weight gain is increased. In autumn, ruminants in natural **photoperiod** naturally begin to divert nutrients from muscle to fat deposition, to give them a store of nutrients that can sustain them through the winter. This would have been of particular benefit to wild ruminants, although nowadays adequate conserved food is usually made available to prevent cattle losing weight in winter. Many wild **herbivore**s naturally lose weight in winter; for example, the bison catabolizes considerable amounts of fat tissue through the winter on the American plains. In intensive rearing of cattle, food is available in similar quantity and quality throughout the year but the animals still use the cue of declining photoperiod to start diverting more nutrients to fat deposition in autumn. By extending the photoperiod in autumn to 16 h of **light** daily, they will deposit lean tissue as if it were still summer. This could be useful if the animals are to be slaughtered in midwinter, as they will put on more muscle and less fat tissue. If they are being kept until the spring, photoperiodic manipulation will have no benefit, as cattle in natural photoperiod start to divert nutrients away from fat deposition to muscle growth in spring. (CJCP)

Guanidine

Iminourea, $(NH_2)_2{\cdot}C{=}NH$. It is related to **urea**. The guanidinium ion is a strong organic base at physiological pH. Naturally found in **turnip**s, **mushroom**s and other plant materials, it has also been identified in **urine**. (NJB)

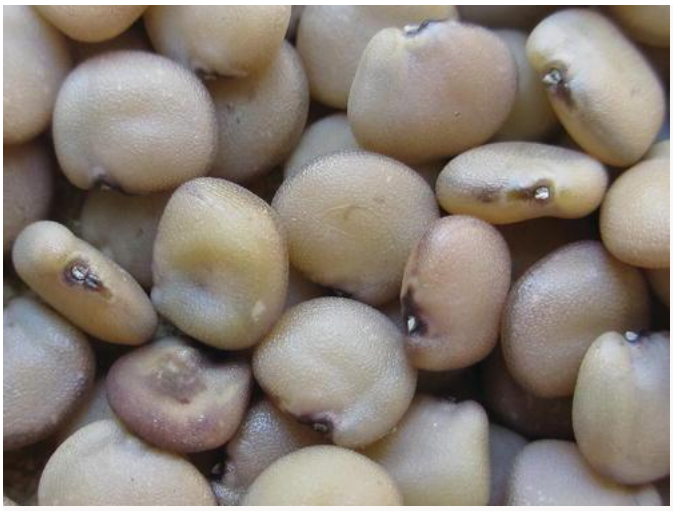
Guanine

A **purine**, $C_5H_5N_5O$, one of the purine **nucleic acid** bases. It is the base in the nucleoside guanosine and the **nucleotide** guanosine monophosphate. In DNA it pairs with **cytosine**, a **pyrimidine** base, to stabilize the helical structure of DNA. This same base pairing is found in the tertiary structure of some RNA. (NJB)



Guar

Also known as the clusterbean, guar (*Cyamopsis tetragonoloba*) is a **drought**-resistant, tall-growing annual **legume**. Within its comparatively large **endosperm** is a large proportion (19–43%) of **galactomannan** gum, which is the primary product of this crop. The refined **gum** is used for a variety of human nutritional products. The remaining guar meal, which contains approximately 35% protein, provides a palatable **protein supplement** feed for livestock when pelleted and toasted. (DA)



Guar seeds. Guar gum from the seeds is used as a thickener in the food industry (ice-cream, salad dressings and bakery mixes). The young green pods are used as a vegetable, mainly in Indian dishes. Photo courtesy of Ton Rulkens. Licensed under CC BY-SA 2.0.

Guinea fowl:
see Game birds, specialty birds and small mammals

Gums
Homo- and heteropolysaccharides, typically stem exudates or seed extractives, that are water soluble and usually viscous in aqueous solutions. Also known as mucilages, they are widely used as thickeners in industry. Common plant-derived gums are **arabinogalactans**, pectins and glycanoxylans; common examples include **guar**, **locust bean** and larch-wood gums, and gums arabic, ghatti, karaya and tragacanth. Microbially derived gums include xanthan gum, dextran and pullulan. Molecular weights are highly variable but generally the lower the molecular weight, the lower is the **viscosity**. (JAM)
See also: Carbohydrates; Dietary fibre; Galactomannans; Hemicelluloses; Storage polysaccharides

Gustation:*see* Taste

Gut:

See Gastrointestinal tract

H

Haemagglutinins

Agents that cause the agglutination, or clumping together, of red **blood** cells. They may be **antibodies**, viruses or plant **lectins**. Antibodies to erythrocytes of a different blood group can cause haemagglutination after a second blood transfusion. Viruses that can act as haemagglutinins include adenoviruses, parvovirus, togavirus, some coronaviruses, picornavirus and myxoviruses (e.g. influenza viruses).

Plant haemagglutinins (also called plant lectins or **phytohaemagglutinin**s) are heat-labile toxic factors that are found principally in some **legume** seeds or beans. Some are found in the tuber or sap. They are proteins with a specific affinity for **sugar** molecules and are found on cell surfaces. Though lectins can affect a range of cells, some show special affinity to red blood cells of different animal species. As well as causing agglutination of red blood cells, lectins may bind to intestinal epithelial cells, reducing the action of some digestive **enzymes** and thus decreasing the absorption of nutrients and reducing **growth** rates. They can cause death (consumption of as few as five castor **oil** beans have been recorded as fatal to humans). Legume seeds/beans

containing haemagglutinins are normally cooked and sometimes pre-soaked before human consumption. **Heat treatment** during **pelleting** may reduce haemagglutinin activity in animal feed, but usually the amount of leguminous seed protein that can be fed is limited. (EM)

Haematocrit

The proportion of **blood** volume that is made up by red cells. It is measured using centrifuged blood treated with an anticoagulant. Haematocrit values will depend on the number and size of red blood cells. Haematocrit varies between species, for example sheep 32, cattle 40, pig and horse 42, dog 45. (EM)

Haemochromatosis

An excessive **absorption** of **iron**, relative to requirements, usually due to impaired regulation of the absorption mechanism. Excretion of iron is limited, since excess iron is stored. Although hereditary haemochromatosis is quite common in humans, it is rarely detected in other animals. It has been observed in cattle and sheep exposed to high levels of iron in feed or water. High **molybdenum** concentrations in the diet may enhance iron absorption. Large amounts of iron are found in the **liver**, lymph nodes and **connective tissue**, where the excess iron is stored as **haemosiderin**, principally in lysosomes. These tissues are darkened and brown. An excess of stored iron can cause cell death. Late in the course of the disease the liver becomes cirrhotic and there may be myocardial disease. This is a chronic condition and should not be confused with acute iron toxicity, when excess iron is given, for example as an injectable or oral **supplement**. (EM)

Haemoglobin

The major functional component of the erythrocyte, transporting oxygen from the air in the lungs to body tissues. Haemoglobin is a coiled, folded and soluble combination of a porphyrin molecule, haem, which has an **iron** atom in the centre, and a protein, globin. It is found in two major forms: oxyhaemoglobin in arterial **blood**

and carboxyhaemoglobin in venous blood. Haemoglobin is measured as total haemoglobin in g dl^{-1} blood, or as the mean content of haemoglobin (MCH) per red blood cell or as the mean cell haemoglobin concentration (MCHC). Normal values range from 8 g to 14 g dl^{-1} in cattle and sheep and from 10 g to 14 g dl^{-1} in pigs.

Alpine cows increase haemoglobin concentration to cope with high altitude (Berry *et al.*, 2001), and ewes increase haemoglobin concentration in response to walking stress (Seijan *et al.*, 2012). Oxygen requirements for **metabolism** in the dairy cow are considerable and are increased by high **milk** yields (Sordillo, 2005). Because of this, **hypoxia** reduces productivity at high altitudes, at least before any **adaptation** (Leiber *et al.*, 2004). In the early-**lactation** cow, nutrient demands exceed the provision from intake, and mobilization of body tissues is essential to sustain high productivity. The hypertrophy in the viscera in response to these demands, in particular physiological changes in the splanchnic tissues, and increased hepatic artery flow, facilitate increased oxygen supply to the **liver** (Reynolds *et al.*, 2003). By 12 weeks post-partum, **oxygen consumption** by the splanchnic tissues has increased by more than supplied by **blood flow**, which may be due to increased haemoglobin concentrations in high-yielding cows. Haemoglobin **availability** may be a constraint to productivity in high-yielding dairy cows (Ramin *et al.*, 2022).

Haemoglobin production can be reduced if dietary intakes of protein (Wu, 2016), Fe (Zavalishina, 2018) and Cu (Yang *et al.*, 2007) are low. Haemoglobin concentration in the blood is increased by **heat stress** (Srikandakumar and Johnson, 2004), and hot **temperatures** can increase haemoglobin concentration in the blood of Holstein-Friesian cows, to support enhanced respiration rates (Marai *et al.*, 1999). (CJCP; EM)

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Haemosiderin

Haemosiderin is believed to be a degradation product of **ferritin** containing fragments of the ferritin protein associated with its mineral core. The assembled ferritin macromolecule forms a hollow sphere-like structure in which the walls are made of 24 copies of ferritin subunits. **Iron** is deposited in ferritin in a form that has similarities to the mineral ferrihydrite. Degradation of the protein shell may be required for iron release from ferritin. Haemosiderin accumulates in some tissues during iron overload. (RSE)

Hair

Hair follicles are generally present over almost the whole body, but follicle density varies to reflect the different needs for insulation. Thermal balance is influenced by the quantity and quality of hair and can be partly controlled by pilo-erection. Although hair serves an invaluable thermoregulatory function, its physical presence and its moderation of the thermal environment facilitate colonization by a number of obligate parasites, such as fleas and ticks.

Hair growth is affected by the seasons, determined mainly by **photoperiod** but also by nutrition. Photoperiod is used as a cue for weather and food availability, and the hair growth is greatest in spring and summer to prepare animals for harsh conditions later in the year. Many animals lose hair at the start of spring in preparation for new growth.



An animal's coat with lustrous hair indicates a high protein intake. Photo courtesy of Tony Alter. Licensed under CC BY 2.0.

The lustre of the hair of animals indicates whether the quality of nutrition is adequate. It can, for example, be used to distinguish calves that have been well fed on their mother's **milk** from undernourished, bucket-fed calves. High-quality protein is required for good hair growth, particularly in ruminants such as sheep or **cashmere goats** that are used primarily for **wool** or hair production. Specific amino acids, in particular **methionine** and **cysteine**, may be deficient and need to be provided in rumen-protected supplements. Hair mineral analysis can provide a useful index of exposure to some toxic **heavy metals**, such as **arsenic**, **cadmium** and **lead**, but not **zinc** or **copper**. External **contamination** must be carefully avoided. The adequacy of copper intake can be assessed by hair colour in farm animals, since low copper intakes reduce pigmentation because of the involvement of copper in the enzyme tyrosinase, the amino acid **tyrosine** being a precursor of the pigment melanin. Adequate zinc and **selenium** are also important for hair growth and quality. Residues of **growth promoter**s can be detected in hair and may be used for detection of illegal use. (CJCP)

Halal

Food permissible to be eaten by people adhering to Islamic teaching. The converse is foods classified as haram, such as **pork** and food from carnivorous animals, such as lions or birds of prey, which are forbidden to be eaten. (CJCP)

Halal foods

The Muslim faith prescribes in the Qur'an and Sunnah that only certain foods are considered lawful for Muslims to eat. This excludes any pig products, meat from carnivorous animals, such as crocodiles, and most insects. Methods of slaughter may be either mandatory, such as that the animal is not stunned before slaughter, or recommended, including that the slaughterer faces Mecca during the slaughter process. **Meat** must be prepared by a Muslim, using a sharp knife for a single cut to the throat that severs the oesophagus and jugular blood vessels. Stunning is allowed by some

but not all halal authorities. Multiple cuts to sever the jugular vein, carotid artery and windpipe should be avoided by the necessity to use a sharp knife, usually sharpened in between animals. Stunning of animals is sometimes permitted before the knife cut and is widely applied in major meat-exporting countries. It should not be the cause of death. Some countries forbid the sale of meat that has come from animals not stunned before slaughter. Consumption of alcohol is forbidden. (CJCP)

Halibut

The genus *Hippoglossus* is composed of two large, right-eyed **flatfish** species: the Atlantic (*Hippoglossus hippoglossus*) and Pacific (*H. stenolepis*) halibuts. The adults are long-lived, attaining weights of 200 kg, though 10–25 kg is the usual size of market fish. Both species are carnivorous and principally inhabit cold, boreal and subarctic oceans. Research into culture of both species began in the early 1980s, at a time of rapidly declining wild stocks. Much of the research focused on the difficult larval stages of hatchery production. Norway first marketed cultured halibut in 1993. Pacific halibut is mainly farmed in north China, kept in mono-cultures in greenhouses with **water temperature** controlled. (RHP; QS; CJCP)



Halibut may reach 200 kg, but the usual market weight is 10–25 kg. Photo courtesy of Ed Bierman. Licensed under CC BY 2.0.

Harvesting

The first process in the removal and conservation of **cereal** and **forage crop**s from the field in which they were grown. Weather conditions and stage of maturity of crops at time of harvest determine feed value and field losses. **Grass** and cereal crops need

to be harvested at optimum quality and quantity. Field losses due to poor weather conditions at harvest can exceed 5% of the total **dry matter** yield of the conserved crop. (RJ; CJCP)

Hatchery waste

Hatchery waste consists of infertile eggs, dead embryos, culled chicks and shells of hatched eggs. It can be processed into a protein-rich hatchery waste meal (HWM) by thorough maceration followed by **heat treatment** (100°C for 15 min to ensure freedom from pathogens), drying and grinding. The average nutrient content is shown in the table.

Average composition of hatchery waste meal.

Main analysis	Unit	Avg	SD	Min	Max
Dry matter	% as fed	99.3	0.8	96.4	99.9
Crude protein	% DM	22.9	4.1	18.1	37.2
Crude fibre	% DM	2.1	2.2	0.0	6.1
Ether extract	% DM	11.3	3.0	7.8	21.7
Ash	% DM	61.4	6.8	36.0	65.5
Gross energy	MJ kg^{-1} DM	9.8*			
Minerals	**Unit**	**Avg**	**SD**	**Min**	**Max**
Calcium	g kg^{-1} DM	191.4	25.6	155.0	221.1
Phosphorus	g kg^{-1} DM	3.1	1.8	1.2	6.5
Sodium	g kg^{-1} DM	2.4	0.1	2.2	2.6

Amino acids	Unit	Avg	SD	Min	Max
Arginine	% protein	4.8			
Cystine	% protein	1.1			
Glycine	% protein	5.5			
Histidine	% protein	2.0			
Isoleucine	% protein	3.6			
Leucine	% protein	6.1			
Lysine	% protein	4.2	0.4	3.6	4.8
Methionine	% protein	2.2	0.5	1.4	2.8
Phenylalanine	% protein	3.5			
Threonine	% protein	3.4			
Tryptophan	% protein	1.3			
Tyrosine	% protein	2.4			
Valine	% protein	5.0			
Pig nutritive values	**Unit**	**Avg**	**SD**	**Min**	**Max**

Energy digestibility, growing pig	%	86.7*
DE growing pig	MJ kg^{-1} DM	8.5*
MEn growing pig	MJ kg^{-1} DM	7.9*
NE growing pig	MJ kg^{-1} DM	5.7*

* Asterisk indicates that the average value was obtained by an equation. Avg, average; DE, digestible energy; DM, dry matter; MEn, metabolizable energy; Max, maximum; Min, minimum; NE, net energy

HWM can be used at low concentrations as a protein and mineral source in a range of diets for livestock, poultry, rabbits, mink and fish, the high content of Ca being a limiting factor. High concentrations may be toxic. Due to its nature it is unlikely for HWM to be approved in any country for use in the diets of food-producing livestock. Under the current European regulations (Regulation (EC) No 1774/20026 on animal **by-product**s), dead-in-shell chicks are designated by Article 5(1)(e) as Category 2 material. According to Article 5(2), animal by-products of Category 2 must not be used in the production of feed for farmed animals or in petfood. EFSA (2011) concluded that 'the risk associated with the use of dead-in-shell chicks, submitted to a conventional heat treatment to a minimum Fc value of 3 in a moist environment, for the production of canned petfood is negligible'.

Other egg waste products include dried raw eggs, which can be fed to animals but **biotin** deficiency may be induced by **avidin** contained in raw egg whites, leading to cracked hoofs, dry rough

skin and loss of hair in pigs fed at > 30% in the diet. Heating the eggs before drying can prevent this, since it destroys the avidin. About 10% of the egg is shell, containing 94% **calcium** carbonate, which can be sterilized, ground and used in pig and poultry diets. (RB)

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Hay

Field-**dried grass** or other **forage**. Haymaking produces a stable forage product of adequate **nutritive value** with minimum loss at a reasonable capital and labour cost. The method of conservation is to dry the mown forage to remove 70–95% of the water present, using wind and solar energy whilst the crop lies in a swath or windrow in the field. The final **dry matter** (DM) content of the hay needs to be 85–88%. Thus 3.5 t of water ha^{-1} have to be evaporated from an immature crop at 80% moisture to produce 1 t of 'dry' hay at 12% moisture content, compared with < 2.5 t of water when a more mature crop, containing only 75% of moisture, is dried down to the 15% at which it can be safely stored.



Hay making in Switzerland. Short field drying times are necessary in high rainfall areas and may be supplemented by barn drying. Photo courtesy of Dennis Jarvis. Licensed by CC BY SA 2.0.

Immature crops are generally more difficult to dry because they contain more leafy material, which packs together and reduces the movement of drying air through the crop. However, while a mature crop is easier to make into hay than an immature crop, the hay produced will be of lower feeding value. Thus, in deciding when each crop should be cut and which haymaking system should be adopted, a balance has to be struck between the ease and certainty of the making process and the likely feeding value of the hay that will be produced, and the amount of digestible dry matter that can be harvested.

When **forage crop**s are cut for hay, the plants continue to respire until the moisture content falls below 40%. Dry matter is lost during this process. The loss may be as high as 15% but is more usually about 5–6% of the total dry matter. When the moisture content of hay drying in the field reaches about 40%, further dry matter losses may occur during tedding, raking and baling. Losses from these operations may average 15%. Dry matter losses from these mechanical sources, called 'shattering', are especially severe because most of them come from the most valuable leafy part of the plant, especially if the forage is **lucerne** (alfalfa) or similar

legumes. Using hay crimpers and conditioners can reduce dry matter loss. Their use reduces drying time in the swath, exposure to the weather, leaf shattering and respiration losses.

The keys to keeping dry matter losses of hay to a minimum are to **bale** at a moisture level low enough to prevent excessive heating and to prevent infiltration of moisture into the hay after it has been baled. When hay is baled, its moisture content should not be higher than 18–22%. At higher levels of moisture, excessive heating and moulding will result in further dry matter losses. Moisture levels for safe storage of hay vary with size and density of the bale and type of hay. In general, hay in small rectangular bales should be baled at less than 22% moisture to keep moulding and heating to a minimum. Large round bales retain internal heat for much longer than conventional bales; therefore, hay in large bales should have less than 18% moisture.

The stage of **maturity** at time of harvest is one of the most important factors affecting forage quality. Most forages will have a 20% loss in **metabolizable energy** (ME) and a 40% loss in protein from a delay of only 10 days past the optimum stage of harvest. For instance, perennial ryegrass harvested at its optimum 66% **digestibility** will contain *c.* 15% protein and 16% soluble **sugar**. In contrast, 2 weeks later most of the crop will reach the seed-head stage with a protein content of 11%, which represents a 25% loss in the value of hay. Legume–**grass** mixtures should be harvested when the legume reaches the desired stage of maturity regardless of the growth stage of the grass. Overall losses due to late haymaking can reach staggering proportions. Shattering and **wilting** losses are always proportionately higher with late-cut than with early-cut forages. If hay is baled with a moisture content of 20–22% and covered during storage, it should not lose more than 5% of its original dry matter during the first year of storage. It will lose very little of its digestible nutrients during that time or in succeeding years. Hay may suffer some loss of carotene, the precursor of **vitamin A**, following prolonged storage.

Large bales stored outside will suffer variable losses, depending upon the moisture of the hay at baling time, the amount of rain

during the storage period, the space between the bales, the type of hay (grass or grass–legume), and the skill of the operator making the bales.

The weight loss in hay stored outdoors is quite variable. It depends on how tightly the hay is baled (tighter is better), the type of bale, and weather conditions. Losses of hay in round bales stored outside without cover can be as much as 30–50% of the hay dry matter. The second type of loss in outside storage is the loss in digestibility of the hay during feed-out. Some general guidelines can help to reduce outside storage losses:

Always store bales in a well-drained area.
Use a minimum of 1 m between bale rows for air circulation (the more space, the better).
If bales are stored side by side, leave at least 0.6 m between bales.
Avoid storing bales under trees and in the shade of buildings.
If space is available, store some of the bales inside, especially the higher-quality hays that should be used near the end of the feeding period.

Treatments designed to accelerate drying rates of forages reduce the potential for rain damage during field curing. Mechanical **conditioning** has long been used to accomplish this. Chemical drying agents have been proposed as an additional means of reducing the duration of field curing. Mechanical conditioning physically breaks the plant stem, while chemical conditioning breaks down the cuticle on the external surfaces of the epidermal cells. Both allow faster water loss so that the rates of water loss from the plant stem and the leaves is similar and the leaves do not get over-dried.

Potassium carbonate solutions are effective in increasing drying rates of lucerne (alfalfa) and combinations of potassium carbonate and emulsions of **fatty acid** esters are even more effective. Under favourable conditions drying agents are effective in reducing the time needed to cure hay by one-third to one-half. They are least

effective under cool, humid conditions. However, drying agents are of limited effectiveness with grass hay.

Several carbonate-based commercial formulations are available and have generally produced similar results when used on lucerne. The carbonate-based drying agents function by modifying the waxy cutin layer of the plant so that it is more permeable to water. The formulations are most effective when applied to stems at cutting. Commercially available applicator kits include a holding tank and pump, hoses, nozzles and deflector bar mounted in front of the header about 200–250 mm above the cutting level. This device pushes plant tops over so that the spray can be directed primarily at the stems. The use of solutions containing potassium carbonate alone is cost effective for lucerne except under cool, humid conditions. Because **sodium** carbonate is cheaper, solutions of one-half potassium carbonate and one-half sodium carbonate may further improve the cost effectiveness of this treatment.

The use of hay preservatives permits greater flexibility in haymaking operations. Hay can be baled at moisture levels of up to 35%, thereby reducing the time required for curing. This reduces the severe leaf-shattering losses associated with handling dry forage. Because moisture content is difficult to determine accurately in curing windrows, preservatives can ensure proper preservation when hay is baled at moisture levels of 20–35%.

Anhydrous **ammonia** has fungicidal properties and has been used successfully in the preservation of high-moisture hays. Use of 1% anhydrous ammonia has been shown to reduce storage dry matter losses and prevent heating and mould development in hays containing up to 32% moisture. Increased **crude protein** content is an additional benefit of ammonia preservation. However, this method of chemical preservation has not received wide acceptance, because of problems in applying the ammonia to large amounts of hay.

Recent work suggests that dry **urea** could be used as an alternative to anhydrous ammonia in preserving high-moisture hays and increasing the crude protein content of poor-quality hays. Application equipment has not yet been developed for this

material, although some urea products and an enzyme product produced as pellets are available in the UK. **Organic acid**s have been the most widely accepted hay preservatives. Materials such as **propionic acid** and ammonium isobutyrate act as fungicides to reduce mould development, heating and deterioration in hays baled at high moisture content. The most common commercial formulations consist of propionic acid and mixtures containing propionic acid and ammonium isobutyrate, acetic acid or **formaldehyde**. Flavouring ingredients have also been added to some of the commercial products. Organic acid preservatives must be applied at an appropriate rate as the hay is fed into the baler. Applicators consisting of a corrosion-resistant tank, a pump powered by the tractor's electrical system, spray nozzles and plastic tubing, which are commercially available, can be attached directly to most conventional balers. Recommended application rates are based on the moisture content of the hay. These rates are appropriate for propionic acid alone, mixtures of propionic acid and acetic acid (80:20) or formaldehyde (70:30) and ammonium isobutyrate. Although hays containing moisture levels > 35% can be effectively preserved with these materials, the practice is not recommended, because of preservative costs and difficulty in handling wet bales.

The **chemical composition**s of a range of hay crops are shown in the table.

Chemical composition of hay crops.

Crop	**DM** (%)	**ME**(MJ kg^{-1} DM)	**Crude protein** (% DM)	**Fibre** (% DM)
Grass hay				
High digestible	85.0	9.0	10.1	32.0
Low digestible	85.0	7.5	9.2	36.6

Crop	**DM** (%)	**ME**(MJ kg^{-1} DM)	**Crude protein** (% DM)	**Fibre** (% DM)
Lucerne hay				
Early flower	85.0	8.3	19.3	32.1
Full flower	85.0	7.7	17.1	35.3
Red clover hay	85.0	9.6	18.4	26.6
Vetch and oats	85.0	8.1	13.8	28.8

There is a highly significant relationship between **feed intake** and digestibility with crops conserved as hay or dehydrated forages (e.g. Mulligan *et al*., 2001). (RJ; GMcLD)

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Haylage

High dry matter (DM) **silage**. The point at which silage can be classified as haylage is arbitrary but a DM content of 50% or greater is often used as a guide. Haylage is made almost exclusively in big bales for use in feeding horses and sometimes sheep. The

high DM content results in a restricted **fermentation**, thus the pH is often 5.5. Typical ranges for haylage composition are: **crude protein** 90–120 g kg^{-1} DM; **crude fibre** 300 g kg^{-1} DM; **digestible energy** 6 MJ kg^{-1} DM. (DD)

Heat balance

It is axiomatic that the rate of metabolic **heat production** (M) must be matched by the rate of heat loss (H) or else heat storage in the body (S) occurs and the mean body **temperature** alters.

$$M=H+S \quad \text{(Equation 1)}$$

Most farm animals are homeothermic or warm-blooded, but their deep-body temperature does alter by approximately 1°C between cold and hot environmental conditions; deep-body temperature can also rise by a similar amount during exercise. Variations in the temperatures of the limbs and peripheral regions of the trunk are considerably greater. Poikilotherms, which include **fish**, are animals whose whole-body temperatures fluctuate, remaining close to that of their environment.

The rate of heat storage may theoretically be measured either by **calorimetry** (from M – H in Equation 1) or by thermometry (change in mean body temperature × weight × specific heat). Neither of these methods is practical for everyday use; the first because extremely precise calorimetry is needed, and the second because the different body regions are neither defined nor accessible for temperature measurement. Instead, an empirical formula has been developed with the form:

$$S=3.47\times W\times(aTb+(1-a)Ts) \quad \text{(Equation 2)}$$

where W is body mass, T_b and T_s are rates of change of deep-body and mean skin temperatures and 3.47 J g^{-1} represents the mean specific heat of body tissues. This formula has been validated for humans and cattle using prolonged simultaneous measurements by direct and **indirect calorimetry** and thermometry. In humans, values of the weighting factor, a, have been found ranging from 0.65 to 0.8. For cattle the value is higher, i.e. 0.86, which is probably because cattle have a higher proportion of their total body weight in the trunk than do humans. It is likely

that still higher values of a would be appropriate for sheep and poultry. T_S is itself an average of skin temperatures of different skin regions weighted according to their areas.

For most homeotherms the maximum change in heat stored in the body between night and day or due to muscular work is small; it seldom exceeds the amount of heat normally produced in an hour. An exception is the camel, which has the facility to allow its deep-body temperature to alter by up to 6°C between night and day. This unique **adaptation** to desert conditions gives the camel a heat storage capacity equivalent to 3 h of heat production and thus economizes on the use of water for evaporative cooling.

(JAMcL)

See also: Energy balance

Further reading

McLean, J.A. and Tobin, G. (1987) *Animal and Human Calorimetry*. Cambridge University Press, Cambridge, UK, pp. 181–183.

Heat increment of feeding

When an animal consumes food, its **heat production** is increased. The increase is known as the heat increment of feeding, which has been described as the **energy** wasted incident to the utilization of food. The underlying causes of the heat increment are numerous and still imperfectly understood. Contributing sources include the physical or muscular work associated with eating, **chewing** and swallowing food, propelling it through the digestive tract and excreting the waste, chemical energy for driving digestive reactions, secretions and **absorption** and for intracellular synthesis of **adenosine triphosphate (ATP)** and other temporary energy reserves. Another contribution is the increased heat of **fermentation**, especially in ruminants, though this is not strictly part of the **metabolizable energy** (ME = **gross energy** of food minus energy of excreta). Expressed as a proportion of ME, the heat increment of feeding is (1 – k), where k is the efficiency of utilization of the feed.

Heat increment can be measured as either (1) the extra heat produced in response to a single meal, or (2) the difference

between the mean levels of heat production resulting from two different feeding levels. Method (1) is difficult to perform in practice, because the rate of heat production rises immediately when food is eaten and subsides only slowly; the response to one meal is seldom complete before the time for the next one. Method (2) involves establishing the animal for several days at a fixed level of feeding before measuring the average heat production over 24 h in a **calorimeter**; the whole procedure must then be repeated at another feeding level.

The heat increment (1 – k) is the complement of the **efficiency of energy utilization** (k) (*see* Energy utilization). The values found by these methods depend not only on the type of food, but also on the level of feeding and the form in which energy is retained or expended. The heat increment, or wasted energy, per unit of ME intake is greater at the high levels of food intake needed to promote **growth**, **lactation**, pregnancy, egg-laying, etc., than that at the lower level needed for **maintenance**. It is also greater with **roughage** diets than with concentrates. The heat increment of feeding is thus a limiting factor in attaining adequate nutrient intakes in highly productive animals, especially in warm climates. On the other hand, the heat increment is useful to animals that must survive in extreme cold and on poor-quality **forage**. (JAMcL)

Further reading

Musharaf, N.A. and Latshaw, J.D. (1999) Heat increment as affected by protein and amino acid nutrition. *World's Poultry Science Journal* 55, 233–240. doi: 10.1079/WPS19990017

Weiss, W.P. (2019) *Energetics for the Practicing Nutritionist: 5. The Heat Increment*. Available at: https://dairy-cattle.extension.org/energetics-for-the-practicing-nutritionist/#The_Heat_Increment (accessed 22 May, 2023)

Zuidhof, M.J. (2019) A review of dietary metabolizable and net energy: uncoupling heat production and retained energy. *Journal of Applied Poultry Research* 28, 231–241. doi: 10.3382/japr/pfx062.

Heat processing:

see Heat treatment

Heat production

The heat generated by metabolic processes in the body. The rate of heat production is also known as the **metabolic rate** or the rate of **energy expenditure**. Heat production represents a large part of the total food energy and it derives from a complex chain of chemical reactions. Despite this, it can be estimated with remarkable accuracy by calculation from the rates of **oxygen consumption** and **carbon dioxide** production. This is possible because of a natural law first discovered by Germain Hess in 1838. Hess's law states that the heat produced in a chemical reaction is always the same regardless of whether it proceeds directly or via a number of intermediate steps. It means effectively that the heat of metabolizing a nutrient through the complex web of metabolic reactions that occur in the body may be estimated from measurement of the heat produced in burning the same nutrient in a **bomb calorimeter**.

The quantity of heat produced by an animal depends on many factors, including its size, the quantity and quality of food it consumes and its productive processes (**maintenance**, **growth**, **lactation**, etc.). It can only be estimated with any accuracy if all of these factors are known. The table gives a very crude guide to the rates of heat production of growing farm animals, expressed in kJ per day and in watts (W). The values given should be multiplied by approximately 1.5 for pregnant animals, by 1.75 for **laying hen**s and by 2 for lactating animals, or even by as much as 3 for a high-yielding cow. For maintenance conditions they should be reduced to about two-thirds. (JAMcL)

Rates of heat production.

	Chickens		Sheep		Pigs		Cattle	
Body weight	kJ day⁻¹	W	MJ day⁻¹	W	MJ day⁻¹	W	MJ day⁻¹	W
50 g	45	0.5						
70 g	65	0.7						
100 g	95	1.1						
150 g	140	1.6						
200 g	175	2.0						
300 g	215	2.5						
500 g	250	2.9						
700 g	335	3.9						
1 kg	410	4.7						
1.5 kg	560	6.5						
2 kg	670	7.7	1.2	14				
3 kg			1.5	17				
5 kg			1.8	21	1.6	20		
7 kg			2.1	24	2.1	25		
10 kg			2.6	30	3.0	35		
15 kg			3.5	40	4.2	50		
20 kg			4.5	50	6.0	65	5.0	60
30 kg			5.9	70	8.2	95	6.3	75

	Chickens		Sheep		Pigs		Cattle	
Body weight	kJ day^{-1}	W	MJ day^{-1}	W	MJ day^{-1}	W	MJ day^{-1}	W
50 kg			7.2	85	12.2	140	10.3	120
70 kg			10.0	120	13.5	160	13.0	150
100 kg					15.0	175	16.5	190
150 kg					17.5	200	21.0	245
200 kg					20.0	235	25.0	290
300 kg							31.5	360
500 kg							40.0	470

See also: Indirect calorimetry

Heat stress

A condition in which environmental conditions make it difficult for the animal to lose the heat it produces, so that body **temperature** tends to rise (**hyperthermia**). Heat stress may be caused by high **environmental temperature** alone or in conjunction with high humidity, which limits **evaporative heat loss**. Heat stress can be alleviated by shade, by increased air movement and, in non-sweating species, by the provision of sprinklers, wallows, etc. (MFF)

Heat stress and nutrition

Heat stress reduces **feed intake**, induces oxidative stress,

stimulates the secretion of **glucocorticoids** from **adrenal** glands, and impairs immune responses in animals. Thus, a **climate** change towards global warming can adversely affect animal productivity. Besides physical cooling methods to ameliorate heat stress (e.g. sprinklers, water baths and the shade of trees), nutritional strategies to mitigate heat stress in animals includes the following. First, dietary levels of **protein** should be reduced to minimize the loss of **body water** through the excretion of **ammonia** and **urea**, as well as heat increment, coupled with dietary **supplementation** with key amino acids (e.g. **arginine**, **glutamine**, **glycine**, **lysine**, **tryptophan** and threonine) and **betaine** involved in antioxidative and immune defences. Secondly, diets can be supplemented with saturated **fat** to increase the generation of metabolic water in the body, and with **vitamins** E and C to promote antioxidative responses. Thirdly, diets can be supplemented with the *Yucca schidigera extract that contains steroidal* ***saponin****s (*natural structural analogues of glucocorticoids) to antagonize the catabolic effects of glucocorticoids on stimulating muscle **protein degradation** and whole-body amino acid **oxidation**. (GW)

Further reading

Cardoso, D.M., Cardeal, P.C., Soares, K.R., Sousa, L.S., Castro, F.L.S., Araújo, I.C.S. and Lara, L.J.C. (2022) Feed form and nutritional level for rearing growing broilers in thermoneutral or heat stress environments. *Journal of Thermal Biology* 103, 103159.

Wu, G. (2018) *Principles of Animal Nutrition*. CRC Press, Boca Raton, Florida, 772 pp.

Heat treatment

Raw materials may be heated to dry them, to improve their nutritional value or to alter their structure. Heat may be applied directly, for example by the sun, by an oven or as steam, or indirectly, by passing material under pressure through an orifice. Under the correct conditions heat may improve the nutritional value of the material but if the conditions are incorrect heat can reduce the nutritional value or even make the material worthless. Heat is frequently used to dry raw materials (e.g. grass, blood,

skimmed milk). It may also be applied with pressure to break down complex **protein** or **carbohydrate** structures and make the nutrients, which would otherwise pass straight through the animal, available for **digestion**. Heat is used to gelatinize **starch**, making it more available to many non-ruminants. It also decreases the product's density: this is useful for **fish** food. Heat can break down some **antinutritional factor**s such as **trypsin inhibitor**s, making an otherwise unacceptable material usable. **Extrusion** is a process by which materials are forced under pressure through a small orifice, which increases their **temperature**. Steam may be added to increase the temperature further but overheating can denature heat-sensitive ingredients such as amino acids and vitamins, reducing their nutritional value. (MG)

See also: Pressing; Toasting

Heavy metals

A group of 66 elements usually defined as those with a **specific gravity** < 4.5 or 5 g cm^{-3}. This definition does not include some lighter elements, such as **cadmium**, that are nevertheless usually considered heavy metals by virtue of their position in the periodic table. Many heavy metals can be used in animal **metabolism** but essentiality it has only been demonstrated for a few (**iron**, **zinc**, **copper**, **manganese**, **cobalt**, **molybdenum**, **selenium**, **chromium**, tin, **vanadium**, **nickel** and **arsenic**) and for two in specific circumstances (**lead** and **rubidium**). Some of these are required in such small quantities that deficiencies are very rare or even unknown (see table).

Main symptoms of trace element deficiencies and excesses.

Element	Deficiency symptoms	Toxicity symptoms

Element	Deficiency symptoms	Toxicity symptoms
Arsenic	Reduced growth rate and milk yield, reproductive disorders, sudden death	Acute: restlessness, rapid breathing, muscular and visual disorders, inflammation of digestive tract, death Chronic: reduced growth rate, weakness, haemorrhages, muscular disorders, tissue inflammation
Cadmium	–	Kidney malfunction, gastric disorders, reproductive disorders, osteomalacia, reduced growth rate and feed conversion efficiency
Chromium	Impaired growth, decreased life expectancy, eye disorders	Depressed growth, liver and kidney damage, scouring, nervous degeneration

Element	Deficiency symptoms	Toxicity symptoms
Cobalt	Ruminants: anaemia, muscular atrophy, listlessness, loss of appetite, depressed growth, reduced viability of young	Blood disorders, anaemia, loss of appetite, impaired growth
Copper	Anaemia, impaired reproduction, depressed appetite and growth rate, ataxia, bone disorder, cardiovascular disorders, depigmentation, defective keratinization, scouring (cattle), swayback (sheep)	Retarded growth, weight loss, anorexia. Other symptoms vary with species. Terminal stage is haemolytic crisis
Iron	Anaemia, depressed growth, lethargy, lowered resistance to infection	Reduced feed intake and growth rate, weight loss, scouring, reduced milk yield Acute: diphasic shock, vascular congestion, anorexia, diarrhoea

Element	Deficiency symptoms	Toxicity symptoms
Lead	–	Vary according to species, e.g. stiff gait, fractures, osteoporosis, kidney disorders, impaired vision, reproductive disorders, neurological disorders Acute: blindness, excessive salivation, hyper-irritability, convulsions, death
Manganese	Impaired reproduction, depressed growth, skeletal disorders, ataxia	Anaemia, depressed growth rate, leg stiffness
Molybdenum	Not reported for grazing livestock	Secondary copper deficiency
Nickel	Not reported for grazing livestock. Laboratory animals show non-specific symptoms including retarded growth and anaemia	Kidney damage, hyperglycaemia, respiratory disorders, reduced growth rate, increased mortality
Selenium	Impaired reproduction, muscular dystrophy, ill-thrift	Chronic: anaemia, dullness, rough coat, hair and hoof loss, stiffness, lameness

Element	Deficiency symptoms	Toxicity symptoms
Silicon	Stunted growth and bone formation	Depressed digestibility, growth rate and reproductive performance, kidney stones
Tin	–	Ataxia, muscle weakness, anorexia
Vanadium	Impaired growth and reproduction, disturbed lipid metabolism, reduced milk yield and milk fat content	Chronic: depressed growth rate Acute: diarrhoea, dehydration, haemorrhage, emaciation, prostration
Zinc	Impaired reproduction, severe inappetence, depressed growth, skin abnormalities	Anaemia, depressed intake, reduced liveweight gain and feed conversion efficiency

Adapted from Smith, S.R. (1996) *Agricultural Recycling of Sewage Sludge and the Environment*. CAB International, Wallingford, UK, pp.101–103.

The heavy metals are principally used by the body for catalytic and regulatory purposes. The capacity of some heavy metals (particularly the transition elements Zn, Cu, Ni, Co, Fe, Mn, Cr and

V) for multiple valencies and their affinity for **oxygen**, **nitrogen** and **sulphur** ligands has rendered them invaluable as catalysts in enzyme and catalytic processes. Many of the heavy metals have been identified as essential components of **metalloenzyme**s, though competition between metals for binding sites indicates that the sites are not specific to one element. Toxicity may arise when metals that are present in only low concentrations in nature, such as cadmium and lead, are concentrated in plant material, soil or industrial waste that is consumed by farm animals. Typically, the toxic metal will replace an essential element in the animal's metabolism; for example, cadmium and lead have a strong affinity for zinc- and calcium-binding sites, respectively, leading to a failure in the processes controlled by these elements (see table).

Deficiency problems mainly occur when livestock that are not native to an area, and are not adapted to the local mineral concentrations, are introduced and often required to grow or reproduce rapidly as part of an intensive agricultural production system. Such deficiencies may not be due to a primary deficiency of an element but a secondary effect of high concentrations of an element with which it interacts. An example is the induction of **copper** deficiency in cattle by high concentrations of molybdenum in pasture.

Some heavy metals, therefore, play a vital role in animal **metabolism** and, even though they are only required in trace quantities, they can be deficient as a result of human manipulation of animal production on a global scale. Others are less likely to be deficient but may be toxic when human activity creates concentrations that would not normally be encountered. (CJCP)

Further reading

Suttle, N.F. (2010) *The Mineral Nutrition of Livestock*, 4th edn. CAB International, Wallingford, UK.

Hedyphagia

Selection of food or feeds that give the most pleasure to the consumer. Primarily this is presumed to be by association with the **taste** of the food or feed. Post-ingestive consequences, in

particular sickness and malaise, are also likely to play a part in rejection of some plant items. (CJCP)

Hemicelluloses

Mixtures of **xylan**s, glucomannoglycans, **arabinogalactans**, arabinans and **arabinoxylans**. They are primarily **structural polysaccharide**s in plant secondary cell walls and may be associated with **lignin**. Common in grasses, annuals, hardwoods, cereal grains, fruits and vegetables. Also present as the principal food reserve in several **algae**. (JAM)

See also: Carbohydrates; Dietary fibre; Gums; Storage polysaccharides

Hen:

see Domestic fowl

Hen feeding

All the nutrients the modern commercial layer, layer breeder or **broiler breeder** hen requires, for both **maintenance** and production, must come from the **compound feed**, in the daily **feed allowance**. The feed is normally provided in the physical form of a coarsely ground **mash** containing some whole **grain**s. This ensures that birds develop a normal **gizzard** to aid **digestion** and lower the pH at an early stage of digestion, thereby reducing the chance of infection from feed-borne sources. Feed may also be presented as a pellet or crumble but this normally leads to increased **feed intake**.

Commercial **laying hen**s are normally kept in one of three different types of production systems: cages, barn or free-range. The vast majority of birds, worldwide, are kept in wire mesh cages. These are constructed in banks, three to six cages high and of unspecified length. Each cage normally accommodates about five birds; however, the limiting criterion is to provide each bird with a minimum of 550 cm^2. Water is supplied via a nipple drinking system with two nipples per cage to ensure provision of normal **water intake** of about 200 ml per bird per day. If water intake is

affected, feed intake will decline and so will **egg production**. A **feed trough** at the front of the cage provides at least 10 cm of feeding space per bird from which to consume the normal daily allocation of between 110 and 120 g of feed. Feed intake increases with age as body size increases and hence **egg** size also increases. **Nutrient requirements** only change marginally during the adult life of the bird but different diets must be fed at different stages of life, because of changes in **appetite**. When the bird first starts to lay she is in a **net energy** deficit, because her appetite is low and her nutrient intake cannot meet her egg output. As a consequence she uses body reserves to lay. As appetite increases, she comes into surplus and can replenish her **fat** reserves. In later life the nutrient concentrations have to be reduced as appetite increases further, to avoid the hen laying too large an egg and compromising the shell quality. Throughout the 76 weeks of the bird's life she will be in lay for up to about 385 days, during which time she may lay 330 eggs. This equates to 85% production or six eggs every 7 days, with an average egg size of 63 g. This means that the hen has a total egg mass capacity in excess of 20 kg with a **feed conversion ratio** (FCR) of 2.15.

It is essential that the bird receives all her daily nutrient requirements within this feed allowance. In particular she must receive sufficient **calcium** carbonate to enable her to create approximately 3 g of **eggshell** each day. She also deposits about 6 g of fat in the yolk. All the materials used for egg production have to be digested, absorbed and then synthesized on a continuous basis by the hen. The hen needs to receive the daily nutrients shown in the table. Failure to do so will result in a rapid decline in egg production. However, hens are very adaptable and can recover quickly when the nutrient supply is restored.

Daily nutrient intake requirement of laying hens.

Crude protein (g)	19.6
Crude fat	3.5
Lysine (g)	0.85

Methionine (g)	0.43
M+C (g)	0.8
Threonine (g)	0.62
Tryptophan (g)	0.22
Calcium (g)	4.2
Available phosphorus (g)	0.42
Sodium (g)	0.16
Chloride (g)	0.17
Linoleic acid (g)	2.0
Energy (MJ kg^{-1})	11.5

Altering the proportion of **methionine** in the diet can directly affect egg size. However, as egg size increases shell thickness decreases, because the hen produces the same amount of shell on a daily basis. An increase in the **essential fatty acid** content of the feed can also increase egg size but body weight remains the single largest determinant of egg size.

Feed intake is increased in alternative laying systems, such as deep **litter** (also known as barn and free-range). This is due partly to increased maintenance requirement due to greater activity, as well as lower **environmental temperatures** depending on the **climate**, combined with large diurnal changes, requiring a higher expenditure for **thermoregulation**. As a consequence of the higher intake, nutrient density can be decreased but the total **energy intake** usually increases. In many cases the **amino acid** content is maintained on these systems to maximize egg size to meet market demand.

Feeding systems used for these production systems can be track feeders, using chain drag distribution, pan feeders or tube feeders. The birds have free access to feed and water and, as a consequence, tend to eat an average of 125–135 g a day, which can increase to 150 g in cold weather.

Both broiler breeder and layer breeder hens are kept in barns,

with the birds roaming freely within the confines of the house. This is to allow natural mating to occur for the production of hatching eggs. Males form < 10% of the population. Although the male does not require the same high **calcium** level in the feed, it is usual, for practical reasons, to provide only one feed.

Layer breeder diets are similar to commercial laying hen diets but with additional vitamins and without yolk pigmenters (*see* Yolk pigments). Broiler breeders are a case apart as their feed is restricted throughout life. Their average daily feed intake is > 150 g but they can have an **appetite** of > 200 g. It is important that not all the energy is from **carbohydrate**, such as **cereal starch**: a minimum **oil** concentration of 40 g kg^{-1} is recommended. These hens have a high requirement for vitamins. **Vitamin E** is often added above the requirement, as it is known to improve the immunocompetence of the bird and thus help to fight disease. (KF)

Hepatoma

A carcinoma derived from the parenchymal cells of the **liver**. It is a form of primary hepatic carcinoma whose cells organize into associations that resemble cells of the hepatic cords of the liver lobule. (NJB)

Herbicide residues

Herbicides are chemicals used to control or kill unwanted vegetation. Many are quite selective for specific plants and have low mammalian toxicity. Most problems with herbicide toxicity involve human error or accident, due to accidental ingestion of concentrates or sprays. Very rarely are herbicide-treated forages toxic to livestock. Most signs of herbicide toxicity are neurological, with incoordination and **convulsion**s. Most ingested herbicides are rapidly cleared in animals, with clearance times of a few hours. Glyphosphate ('Roundup'), one of the most common herbicides, has very low mammalian toxicity. Despite popular belief to the contrary, herbicide residues on feeds and foods are of very little toxicological concern. (PC)

Herbivore

Any animal obtaining its **nutrient requirement**s from plant material by **grazing** or **browsing**. Herbivores have various adaptations of the alimentary tract, facilitating the prehension (e.g. specialized lips and **teeth**) and **digestion** (e.g. **stomachs** of several compartments, or a **caecum**) of fibrous plant material. Domestic herbivores include cattle, sheep, goats, deer, horses and camelids. (AJFR)

Herbivorous fish

A fish (usually warmwater species) that feeds on plant material, whether it be macrophytes, **phytoplankton** or detritus. Cultured herbivorous fish include various Chinese and Indian carps, some **tilapia** species, mullets and **milkfish**. Chinese and Indian carps are usually reared as species mixes that occupy different herbivorous niches in culture ponds. Herbivorous fish are characterized by the presence of the enzyme **maltase** throughout the digestive tract, to utilize **maltose** generated by the digestion of **starch**. Digestion of **cellulose** depends on the presence of gut microflora. (RHP)

Further reading

Pillay, T.V.R. and Kutty, M.N. (2005) *Aquaculture: Principles and Practises*, 2nd edn. Blackwell Scientific Publications, London.

Herring:

see Fish products

Hexose

A **monosaccharide** with the elemental composition $C_6H_{12}O_6$. Aldohexoses have six-carbon **pyranose** rings whereas the ketohexose **fructose** has a five-carbon **furanose** ring. As single units they are referred to as monosaccharides; as polymers they are called **polysaccharide**s. In the open-chain form hexoses have four asymmetric carbon atoms; thus there are 16 possible **isomers**. Carbon 6 of the pyranose ring has two possible orientations, designated D and L. Within the D series there are eight isomers. Of

these eight isomers, three (**glucose**, **mannose** and **galactose**) are important in animal **metabolism**. (NJB)

Key reference

Mayes, P.A. (2021) The pentose phosphate pathway and other pathways of hexose metabolism. In: Kennelly, P.J., Botham, K.M., McGuinness, O., Rodwell, V.R. and Weil, P.A. (eds) *Harper's Biochemistry,* 32nd edn. Appleton and Lange, Stamford, Connecticut.

Hexuronic acids **Hexose** sugars with the general formula $C_6H_{10}O_7$, in which carbon 6 is oxidized to an acid. D-Glucuronic, D-mannuronic and D-**galacturonic acid**s are found in natural products. D-**Glucuronic acid** is a constituent of plant materials and a constituent of chondroitin and mucoitin **sulphate**s of glycoproteins. Some xenobiotics are glucoronidated and excreted as a means of **detoxification**. **Ascorbic acid** (**vitamin C**) was initially classified as hexuronic acid. Galacturonic acid is a component of pectins, plant **gums** and mucilages. D-Mannuronic acid as a polymer is alginic acid and is used as a thickener in the food industry. (NJB)

High-density lipoprotein (HDL)

One of the four major classes of plasma lipoproteins: **chylomicron**s, very-low-density, low-density and high-density lipoproteins. As the ratio of **lipid** to **protein** increases in these particles, their density decreases and they can be separated by use of an ultracentrifuge. Their density varies from 0.95 to 1.28 g ml^{-1}. HDLs are synthesized and secreted from both the **liver** and **small intestine**. Specific **apolipoprotein**s are associated with HDL particles and participate in the selected receptor-mediated endocytosis of the particle. Apolipoproteins most commonly associated with HDL are apo C, apo E and apo A. (NJB)

Highly unsaturated fatty acids (HUFAs) in fish

Fish are an important source of highly unsaturated fatty acids that are important for the health of humans. The alternative term, **polyunsaturated fatty acid** (PUFA), normally refers to **fatty**

acids with 18 or more carbon atoms and two or more double bonds (NRC, 1993). HUFAs mainly include eicosapentaenoic (EPA), docosahexaenoic (DHA) and arachidonic (ARA) fatty acids. These are also the main **essential fatty acid**s for **marine fish** and should be supplied in marine fish diets. (QS; CJCP)

Reference

NRC (National Research Council) (1993) *Nutrient Requirements of Fish*. National Academy Press, Washington, DC.

Hindgut:
see **Large intestine**

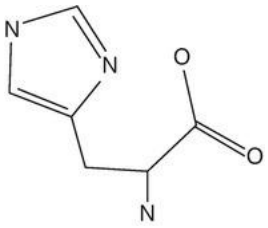
Hippuric acid
Benzoylglycine, $C_6H_5{\cdot}CO{\cdot}NH{\cdot}CH_2{\cdot}COOH$, containing a **peptide** bond between benzoate and **glycine**. **Liver** enzymes activate benzoate in a manner similar to **fatty acid**s, i.e. benzoate, $C_6H_5{\cdot}CO^-$ + ATP → benzoyl-AMP + P~P. Benzoyl-AMP reacts with glycine $H_2N{\cdot}CH_2{\cdot}COOH$ to become hippurate $C_6H_5{\cdot}CO{\cdot}NH{\cdot}CH_2{\cdot}COO^-$. **Benzoic acid** is not apparently catabolized but is conjugated with glycine and excreted in **urine** as hippuric acid. **Detoxification** of benzoate is one of the **liver function** tests. In **grazing** animals hippuric acid makes up a greater fraction of urinary **nitrogen** than that usually observed in non-ruminants. It was first identified in the urine of the horse. (NJB)

Histamine
A biogenic **amine** ($C_3N_2H_3{\cdot}CH_2CH_2{\cdot}NH_2$, molecular weight 111.15) formed by the **decarboxylation** of **histidine** in mast cells, enterochromaffin-like (ECL) cells and certain hypothalamic neurons. Outside the nervous system, histamine is released in response to physiological and inflammatory stimuli. It acts as a paracrine substance by diffusing to surrounding cells to exert its effects on target tissues. In the **stomach**, histamine is released from ECL cells in the lamina propria following hormonal and neural stimulation. It acts on specific H2 receptors of **parietal**

cells in the gastric **mucosa** to induce acid secretion. A number of pharmacological inhibitors to the H2 receptor have been developed, including cimetidine, ranitidine and famotidine. These agents antagonize histamine's effects on acid secretion in the stomach. Histamine is also released from mast cells and acts on H1 receptors in a variety of tissues. In general, it is a potent vasodilator but also stimulates **smooth muscle** contraction in various tissues. (GG)

Histidine

An amino acid ($C_3N_2H_3 \cdot CH_2CH \cdot NH_2 \cdot COOH$, molecular weight 155.2) found in protein. This essential amino acid can be decarboxylated to form **histamine**, a vasoactive **amine**. Also, free histidine can react in the body with β-**alanine** to form the **dipeptide**, **carnosine**, which is found free in muscle tissue. After being incorporated via **peptide** linkage into protein, some of the histidine may be methylated at the 1 position or the 3 position of the imidazole ring. The resulting 3-**methylhistidine** is found primarily in muscle **actin**: after its release during muscle **protein turnover**, it cannot be utilized for **protein synthesis** or metabolized in some species. Its excretion in the **urine** is therefore used as an index of muscle **protein catabolism**. However, in some species (e.g. pigs), 3-methylhistidine combines with β-**alanine** to form **balenine** (ophidine). Some animals can methylate **carnosine** at the 1 position of the imadazole ring, and this forms the dipeptide, anserine. Other animals may methylate carnosine at the 3 position, resulting in the dipeptide, balenine. Carnosine in feeds of animal origin is fully active as a source of histidine, but neither anserine nor balenine can be metabolized to histidine. Homocarnosine is another dipeptide that is synthesized (in brain tissue) from carnosine. The functions of carnosine, anserine, balenine and homocarnosine are not known. (DHB; GW)



History of nutritional sciences

Nutrition is an integrative science based mainly on chemistry, physiology, biochemistry, food science and medicine. It owes much to developments in chemistry, the foundations of which were laid by Joseph Priestley (1733–1804), Antoine Lavoisier (1743–1794) and Justus von Liebig (1803–1873) and to developments in the related sciences.

An important source of information on the history of nutritional sciences is the collection of papers presented at a Symposium organized by the American Society for Nutritional Sciences under the title of 'Experiments That Changed Nutritional Thinking' (Carpenter *et al*., 1997).

A comprehensive 'Short History of Nutritional Science' by Kenneth J. Carpenter (1923–2016) was published as a four-part series in the *Journal of Nutrition*, covering the period 1785–1985 and providing a very interesting perspective on the background to the discoveries made during that 200-year period (Carpenter, 2003a,b,c,d). His history covers the transition from the initial studies on food and nutrition to the identification of **micronutrient**s in the first half of the 20th century and then to the recognition of the role of foods and dietary patterns in the development of diet-related chronic diseases in humans in the second half of the 20th century. These developments were assisted by improvements in chemical techniques for the analysis of nutrients and their measurement in foods and feedstuffs, also to the identification of suitable animal models for the study of human **nutrient requirement**s.

The following article is a summary of the history of nutritional sciences based in part on the most important discoveries described by Carpenter *et al*. (1997) and Carpenter (2003 a,b,c,d) relating to the period 1785–1985. In addition the article describes other

important discoveries and developments in animal and **human nutrition** that were made in the period 1986–2021.

Carpenter was a British scientist with a PhD in Nutritional Science from Cambridge University. His first appointment was as a Scientific Officer at the Rowett Research Institute in Aberdeen, UK. After a year as a Kellogg Foundation Fellow at Harvard University he returned to Cambridge in 1956 as Lecturer at the School of Agriculture, eventually achieving the rank of Reader in Nutrition. In 1977 he was appointed Professor of Experimental Nutrition at the University of California, Berkeley, where he was active in teaching and research. One of his main contributions to nutritional knowledge was related to **pellagra**. Although pellagra was often prevalent in populations eating large quantities of **maize**, it was not common in Mexico. Carpenter showed that the traditional method of making tortillas – steeping the maize in limewater, neutralizing, and drying it – greatly increased the bioavailability of **niacin**. (As is described later in this article, pellagra is caused by a deficiency of niacin and **tryptophan** in the diet.) Carpenter also developed a micro method that made it possible to take serial measures of total **cholesterol** in small animals without killing them during the experiment.

Early concepts about foods

Although little was known by the Middle Ages about the nutritional properties of foods and what constituted an adequate diet, some nutritional facts were already known. For instance, the Greek physician Hippocrates was credited with stating that food should be thoroughly chewed before swallowing, and consumed in moderation to maintain good health, and (as noted by Carpenter, 2003a) prior to 1795 many scholars had published their ideas about how the food that humans ate was used in our bodies. It was only when the so-called ‘chemical revolution’ in France at the end of the 18th century, involving the identification of the main elements of foods and the development of methods of chemical analysis, that old and new ideas of food began to be tested in a quantitative, scientific way. One example was the important finding reported to the French Academy of Sciences in 1785 by Claude

Berthollet, namely that the vapour from decomposing animal matter was **ammonia**, and that this gas was composed of three volumes of **hydrogen** and one volume of **nitrogen**, or around 17% hydrogen and 83% nitrogen by weight (the modern values are 17.75 and 82.25%, respectively). This was very impressive work, especially considering the equipment available at that time. Other research confirmed the presence of nitrogen in animal matter and its absence from **sugars**, **starch** and **fats**.

Other key discoveries that laid the foundation for nutritional sciences were being made at the time in Europe. An example is a study by Antoine Lavoisier in France who measured human respiratory output of carbonic acid (**carbon dioxide**), both at rest and when lifting weights, and showed how it increased with activity. That was an important advance, because it had previously been supposed that the sole purpose of respiration was the cooling of the heart. Lavoisier also collaborated with the mathematician Pierre-Simon Laplace in comparing the heat produced by a guinea pig in its production of carbon dioxide with the heat produced by a lighted candle or charcoal. **Heat production** was measured in an ice **calorimeter**, in which the heat produced was related to the weight of water released from the melting of the ice surrounding the inner chamber where the animal or burning material was housed.

Other important discoveries related to nutritional chemistry that were made during this time included the atomic theory put forward by John Dalton, a British schoolmaster, in 1803. His theory proposed that matter is made up of atoms that are indivisible and indestructible; all atoms of an element are identical; atoms of different elements have different weights and different chemical properties; atoms of different elements combine in simple whole numbers to form compounds; atoms cannot be created or destroyed; and, when a compound decomposes, the atoms are recovered unchanged.

During this period some scientists began to question the prevailing assumptions about food. For instance, François Magendie in a report to the French Academy of Sciences in 1816

addressed the question of whether animals could use atmospheric nitrogen to 'animalize' ingested foods of low nitrogen content. His study was to take a single food that was accepted as being nutritious, even though it did not contain nitrogen, and feed it to dogs, a species that would eat both plant and animal foods. The foods tested included sugar, **olive oil**, **gum** or butter as the sole food. The result was the same with each food: none of the dogs survived beyond 50 days. It was clear that none of these foods provided a complete diet. As stated by Carpenter, his final conclusion was that 'diversity and multiplicity of aliments is an important rule of hygiene; which is, moreover, indicated to us by our instincts'. An important outcome of Magendie's work was that an animal species could be used as a model for humans.

This line of work was continued by Claude Bernard, following the death of Magendie in 1855, who discovered that the **liver** forms **glucose** and stores it as **glycogen** which, upon degradation, yields glucose.

More attention was paid to nitrogen as an important dietary factor following Magendie's report, resulting in J.-P. Boussingault proposing that the relative nutritional values of plant foods could be assessed from their contents of nitrogen. He was able to show that leguminous plants, but not cereals, were able to utilize atmospheric nitrogen during growth. In another trial carried out in 1839, he reported that a dairy cow was in positive **nitrogen balance** when her output in **milk** and excreta was compared with her input (a result not necessarily true in the 21st century high-yielding dairy cow). He conducted a further trial in 1845 to try to explain the observation that pigs would fatten when fed on **potato**es that were rich in starch, but contained only a negligible level of fat. The explanation appeared to be that animals must be able to convert **carbohydrates** to fat. He killed a young pig and analysed its **carcass**, while feeding a littermate of the same starting weight on measured amounts of feed for an additional 3 months. Carcass analysis of the second pig showed that it contained an additional 13.6 kg fat, whereas the feed it had eaten had contained only 6.8 kg.

Up until this time it had been recognized that so-called 'animal substances' came in different forms that were named **albumin**, **fibrin**, **casein**, etc., and that they differed in **solubility** and other physical properties. However, they all contained about 16% nitrogen. In 1839, it was suggested by a Dutch researcher, Gerrit Mulder, that these substances were all compounds of a common radical combined with different proportions of **phosphorus**, sulphur or both. The hypothetical radical was named '**protein**'.

Another line of research was the development of the concept of the conservation of **energy** in its different forms, an important contributor being James Joule, an English physicist, who in the 1840s showed that the various forms of energy – mechanical, electrical and heat – were basically the same and could be changed one into another. His concept formed the basis of the law of conservation of energy, the first law of thermodynamics that established a value for the mechanical equivalent of heat. This could then be used in **metabolism** studies to calculate the efficiency of muscular effort in relation to **heat production**. A standard unit of work was termed a **joule** (J), representing the work done by a force of one newton (1 N) acting over a distance of 1 m.

Prior to Joule developing his system of measuring heat production, a parallel system was developed in France, based on the **Calorie**. According to Hargrove (2006), Nicholas Clément introduced the term in lectures on heat engines that were given in Paris between 1819 and 1824. It defined the Calorie (kcal) as the heat required to raise the temperature of 1 kg of water from 0°C to 1°C, and was adopted in several countries as a system to evaluate the energy content of foods and feeds. It may have been introduced to the USA by W.O. Atwater, who became aware of the term during his earlier studies in Germany

An important contribution on the measurement of **energy expenditure** was made in 1866 by two Swiss scientists, Adolf Fick and Johannes Wislicenus, to test the prevailing theory of Justus Liebig that protein was the sole muscle fuel. They climbed a mountain in Switzerland while consuming a low-nitrogen diet.

Analysis of **urine** showed they had expended more than twice the energy that could have come from their breakdown of bodily protein. In collaboration with Edward Frankland, who was conducting research on the heat of **oxidation** of organic substances, they concluded that much of the fuel consumed must have come from other sources, presumably fat and/or carbohydrate. This conclusion was not immediately accepted by Liebig and others but was confirmed by other researchers.

Another prevailing assumption was that the **stomach** was the major site of **digestion**. However, in the 1850s, Claude Bernard discovered that the secretions into the **small intestine** from the **pancreas**, together with the emulsifying effect of the **bile**, were of the greatest importance for the digestion and **absorption** of fat.

Later discoveries

Prior to 1885 most of the nutritional studies had been carried out in Western Europe and involved mainly the requirements for energy and protein. These lines of investigation continued after 1885 but with scientists in other parts of the world making important contributions. One of these was W.O. Atwater, a professor of chemistry in the USA who had studied nitrogen balance procedures under Carl Voit in Germany.

Metabolism

Following the work of Lavoisier and Armand Seguin at the end of the 18th century, several researchers in France and Germany gradually improved the equipment for measuring the respiratory exchange of animals and their heat output under different conditions. In 1894, Max Rubner was able to demonstrate in a dog that its heat output matched exactly the heat of combustion of the food it was metabolizing, as measured by **urea** output and gaseous exchange.

One of Atwater's achievements was to construct a respiration calorimeter for humans that could also be used to measure heat output directly. The first aim was to confirm that the heat produced by the human body was the same as that produced outside the body (i.e. *in vitro*) by the combustion of the same quantity of nutrients. He and his team were able to do so, with considerable precision. In

1896 they established estimates for the **metabolizable energy** of the carbohydrates, protein and fat in mixed diets as 4, 4 and 9 kcal $^{-1}$g, respectively. These '**Atwater factor**s' were slightly different from those proposed by Rubner and are known to have limitations, but are still used at the present time as the basis of diet formulation in some systems for humans and food-producing animals.

The introduction of animal **calorimetry** and the determination of carbon/nitrogen balance allowed H.P. Armsby in the USA and Oskar Kellner in Germany in the early part of the 20th century to devise **energy system**s based on the NE (**net energy**) value of foods and feeds for application in animal feeding. Armsby expressed the NE values in terms of calories, whereas Kellner expressed the NE values relative to the NE value of starch in its relationship to fat production. Kellner's **starch equivalent** system was used mainly in Europe and remained in use as the basis of practical feeding system for livestock well into the 20th century. Armsby's system was used to some extent in North America, but the preferred system for practical use in animal nutrition was the **total digestible nutrients** (TDN) system. The total digestible nutrient content of a food was calculated as the combined weight in 100 kg of food of digestible **crude protein** and digestible carbohydrate (**crude fibre** plus **nitrogen-free extracts**), plus 2.25 times the weight of digestible **ether extract**. TDN values can be converted fairly easily into ME values and quite a number of feedstuffs detailed in feed composition tables have been calculated in this way. Both systems have largely been superseded by more accurate systems based on NE for animal feeding, but TDN is still used in beef cattle feeding in some countries. Another energy unit superseded by the NE system is the Scandinavian Feed Unit (SFU) system, one SFU being equivalent to the energy content of 1 kg **barley** (85% **dry matter**).

Other important factors allowing the introduction of the NE system were the development of more accurate procedures for the nutrient analysis of foods and feedstuffs by agencies such as AOAC International (Association of Official Analytical Collaboration International; originally the Association of Official Agricultural

Chemists, founded in 1884); the development of prediction equations for the estimation of energy content of foods and feeds from their chemical analysis; and the development of models of **energy utilization**.

Following the adoption of the International System of Units (SI) as the modern metric system of measurement in 1960, the preferred term for energy evaluation within the scientific community in Europe and some countries became the joule (J), whereas in North America and several countries the preferred term became the Calorie (kcal) (with an initial capital). In 1969 the International Union of Nutritional Sciences and the National Committee of the International Union of Physiological Sciences suggested the joule rather than the kcal as the unit of energy for use in nutritional, metabolic and physiological studies. One calorie is defined as exactly 4.184 J, and one Calorie (kilocalorie) is 4184 J.

Proteins

One of the early assumptions was that all proteins were of equal quality. Another was that proteins ingested in foods were absorbed almost intact and then modified, for example from 'fibrin' to 'albumin'. Related work on the physiology of digestion had shown the existence of a substance (**pepsin**), secreted by the stomach wall, that converted proteins into more soluble derivatives. Liebig regarded this as being a simple breakdown of aggregations of molecules, allowing them to pass through the gut more easily. However, it was later shown that the pancreas secreted another compound (**trypsin**) that further broke down the proteins to produce constituents that were non-coagulable, diffusible through parchment and included the products **tyrosine** and **leucine**. These compounds were first called 'amino-bodies' and then '**amino acid**s'. In 1806 the French chemists Louis-Nicolas Vauquelin and Pierre Jean Robiquet isolated a compound from asparagus that was subsequently named **asparagine**, a derivative of **aspartic acid**, and regarded as the first amino acid to be discovered.

Initially the amino acids were not considered of interest to nutritionists, because their isolation required treatment with

strong, boiling acids – conditions quite different from the mild conditions in the gut. Research in Germany and Denmark showed that **meat** proteins treated with pepsin and trypsin for long periods and free of intact protein served as nutritional substitutes when fed to adult dogs, but acid hydrolysates of protein did not. These findings strengthened the hypothesis that strong acid treatment destroyed some component of the protein, because proteins and even enzymic digests gave a colour reaction suggesting the presence of an **indole** derivative, but acid hydrolysates did not. In 1902, F.G. Hopkins and S.W. Cole at Cambridge University isolated the amino acid tryptophan, which contains an indole ring, from an enzymic digest and showed that it was destroyed by conditions of acid **hydrolysis**. Subsequently in 1906, the Hopkins group reported that mice receiving **zein** (which is devoid of tryptophan) as their sole **protein source** lived longer if they received a supplement of tryptophan. In support of these findings Emil Abderhalden in 1909 found that adult dogs could remain in nitrogen balance if the acid hydrolysates of protein that they were receiving were supplemented with this amino acid, indicating that tryptophan had some essential function.

Subsequent research investigated the relative value of different proteins using diets that included protein-free milk (skimmed milk acidified, heated and filtered). T.B. Osborne and L.B. Mendel had already found that gliadin, isolated from **wheat**, supported slower growth than was obtainable with **casein**. In 1914 they found that a diet with 18% zein (**maize** protein that is deficient in tryptophan and **lysine**) resulted in a failure of growth in rats unless the diet was supplemented with both these amino acids. It appeared, therefore, that certain amino acids are 'essential', i.e. they cannot be synthesized by the body or at least at a rate required for optimal utilization, and need to be provided in the diet. Further work showed that mixing proteins deficient in different amino acids could result in mutual **complementation**. **Digestibility** of the amino acids was also later found to be an important property.

In 1930 W.C. Rose and colleagues at the University of Illinois initiated research on amino acid mixtures that would support good

growth in rats. They began with 19 known amino acids, but the animals failed to grow. The list did not include **methionine**, discovered at Harvard in the 1920s as being required for the growth of certain bacteria. However, it was known that rats receiving casein as their sole protein would grow faster if **cystine** were added to the diet, suggesting that cystine was the sulphur-containing essential amino acid needed. Even with the inclusion of methionine, rats still failed to grow unless they received in addition the mix of amino acids obtained from an acid-hydrolysate of casein. Attempts to isolate an active factor from the hydrolysate indicated that it supplied two additional compounds, one of which was **isoleucine**. At that time there was no method for determining isoleucine separately from leucine. The second factor was identified as (2S,3R)-2-amino-3-hydroxybutanoic acid and named threonine. It was the last of the essential amino acids to be discovered. When it was included in the amino acid mix the rats grew well, an important finding. Rose then extended the research findings to humans and to establishing the minimum daily requirements of all amino acids for optimal growth.

The chemical methods of amino acid analysis were initially slow and subject to interference. Microbiological methods based on the requirements of lactobacilli were developed in the 1940s and allowed many more assays to be completed. From these it was possible to determine the '**chemical score**' of dietary proteins calculated as the lowest percentage value when the level of each essential amino acid was compared with that found in whole egg (taken as a provisional standard). These 'scores' were then found in most cases to correlate well with the relative values of the same foods as determined in **protein quality** tests with young rats, based either on weight gain or nitrogen balance.

In addition to their adoption in human nutrition, the concepts were also adopted in the feeding of food-producing animals. For instance, in **poultry feeding** the approach adopted was to formulate the diet in terms of **ideal protein** ratios (Elwinger *et al*., 2016). Knowledge of the amino acid composition of the main ingredients and the marketing of pure forms of several amino acids

allowed the practical feed mixtures to be formulated with an exact balance of amino acids, the crude protein level being determined by the most limiting amino acid provided from the feed proteins. Greater precision was achieved when measurement of digestibility in the distal **ileum** section of the digestive tract became adopted as the standard procedure for assessing the '**availability**' of dietary amino acids in poultry (as in other species). Supplementation with feed **enzymes**, particularly carbohydrases and **phytases**, was found to be beneficial in improving the digestibility of amino acids in various feed materials by eliminating **antinutritional factors**.

As well as these developments in poultry nutrition, in ruminants the main thrust of the research in the 1980s and 1990s was the development of rationing systems that divided ingested protein into that digested in the rumen and that digested post-ruminally, with the latter particularly required for very high-producing cows. Methods of measuring **rumen digestion** of **nitrogenous compound**s were devised (Dacron bags). Rationing systems were developed to supply both sources of amino acid.

Similarly the digestion of fibre was divided into that soluble in acid and neutral detergent fibre about this time. Later in the 1990s it was recognized that ruminants had to be fed to produce the required output of milk constituents, and it was recognized that there was no 'requirement' as such, but an input/output relationship.

Protein standards for humans

By the late 19th century the prevailing opinion of European researchers was that people with sufficient income would instinctively select a diet containing the amount of protein they needed to remain healthy and productive. Voit's estimate based on surveys was that the average German workman doing moderate physical work chose to eat 118 g **protein** per day, and this became his standard. Higher intakes would be necessary for heavy work. Atwater (who had studied under Voit) found that American workmen were generally better off and ate more: he set his standard in 1887 at 125 g per day. As Carpenter pointed out, there was very little questioning as to whether these amounts of an

expensive food ingredient were really required. The main thrust of Atwater's work in this period was to analyse foods by the proximate system (nitrogen, fibre, **ash**, **ether extract**, moisture and 'carbohydrate by difference') and to use these values to teach the poor how they could obtain their requirement for protein (the most expensive of their food needs), more economically. At this time, the purchase of food typically took about 50% of a working family's income (about 5% probably in western countries in 2021).

These standards and the way they had been developed were later challenged in the first decade of the 20th century by several researchers, mainly by R.H. Chittenden, who was a Professor of Physiological Chemistry at Yale University. By self-experimentation and three controlled trials using reduced-protein diets, he showed that he and three scientific colleagues remained healthy and in nitrogen balance for 6 months on daily diets containing an average of 62 g protein; that US soldiers remained in good health and physical condition with a standardized daily intake of 61 g protein; and that a group of seven Yale student athletes consuming 64 g protein per day maintained their levels of athletic performance and stated that they felt better for it. His conclusion was that the minimum protein requirement was 0.6–0.64 g kg^{-1} per day. Initially his findings were rejected by other scientists, partly on the grounds that they were based on short-term investigations and might lead to a lowered resistance to disease. Protein standards continued to be based on individual assessments but after a period of about 40 years they started to be based on recommendations of national and international committees. The League of Nations in 1936 published its recommendation of not less than 1g protein kg^{-1} body weight, but without scientific justification. That recommendation was modified to 0.6 g protein kg^{-1} per day by FAO/WHO/UNU in 1985 (WHO, 1985). It was clear that the metabolic approach used by Chittenden for the establishment of protein requirements was now accepted, rather than the dietary intake approach followed by Voit, Atwater and others.

A refinement to the concept of amino acid score in determining the completeness of the amino acid content in combination with

protein digestibility in determining the quality of a protein for humans was later recommended by FAO (2013), suggesting that DIAAS (digestible indispensable amino acid score) be adopted to replace the earlier measure of PDCAAS (protein digestibility-corrected amino acid score).

Nutritional adequacy of diets

By the early 20th century the known essential nutrients comprised protein, **sodium**, **potassium**, **calcium**, **phosphorus** and **iron** (Harper, 1997). Liebig's concept from the 1850s that a diet based on these nutrients and sources of energy constituted a nutritionally adequate diet was widely accepted, although there was some dissent. One sceptic of Liebig's claim that the physiological value of a diet could be predicted from its gross **chemical composition** was S.M. Babcock of the University of Wisconsin, who encouraged his successor E.B. Hart to investigate it. This led to the 'Wisconsin **grain** experiment' in 1907, involving the feeding of Shorthorn heifers from about 6 months of age to be grown to **maturity** and through two reproductive cycles on similar allowances of feed mixtures based on either maize, **oats** or wheat; or a mixture of the three. Each diet was formulated to be closely similar in gross composition and energy content. Initial results indicated that growth rate was not significantly affected by diet, but differences in appearance were noted by the end of the second year. Animals fed the maize diet had smooth coats, deep chests and appeared healthy. Animals on the wheat diet had rough coats, were of smaller girth and appeared gaunt. The other two groups were intermediate in these features. There were major differences in reproductive performance: calves born to cows on the maize diet were strong and vigorous and all lived, whereas those from the wheat-fed cows were weak and none lived beyond 12 days. Results from the other two groups were intermediate. Milk production was markedly reduced in the wheat-fed cows. Hart and his colleagues concluded that the **nutritive value** of a diet could not be predicted reliably from measurements of the contents of total nutrients and energy; however, they could not provide a definite explanation for the observed differences. Given current knowledge

it seems likely that the problems found were related to differences in the **carotenoid** content of the four diets, complicated in the case of the wheat-fed group by an inadequate intake of fat and a marginal intake of calcium and **magnesium**.

The importance of this research is that it provided the first clear evidence that the nutritive value of a diet depended on factors other than its content of protein, a few minerals, and **energy source**s. As Harper (1997) stated, it sounded the death-knell for Liebig and Voit's concept of what constituted a nutritionally adequate diet. It contributed, together with observations by European investigators on the inadequacies of purified or restricted diets for chickens, rats and guinea pigs, to a sharp change in the direction of thinking about the nutritional essentiality of constituents of foods. Undoubtedly it stimulated much of the later work that led to the discoveries of vitamins, amino acids and trace minerals.

E.V. (Elmer) McCollum, a chemist who had collaborated with Hart on the grain comparison trial, in collaboration with Marguerite Davis continued investigating the cause of the unexpected poor results obtained with the wheat diet. Rats were used as the test animals, because they required much smaller amounts of food and grew and reproduced rapidly. An initial finding in 1913 was the required presence of an organic complex in the purified diet used, and that it was extractable with ether. Other researchers around this time were making similar observations. F.G. Hopkins at Cambridge University in the UK proposed in 1906 that there were 'unsuspected dietetic factors' that were necessary for life and in 1912 showed that there were 'accessory factors' present in 'astonishingly small amounts' in milk that supported life. His two papers on the subject, in 1906 and 1912, are considered the first explanations of the concept of vitamins. This line of research later led to the discovery of other essential vitamins and trace minerals.

Mineral elements

As noted by Suttle (2010), all animal and plant tissues contain widely varying amounts and proportions of mineral elements,

which largely remain as oxides, carbonates, phosphates and sulphates in the ash after incineration. In the 1760s a Swedish chemist, Johan Gottlieb Gahn, had found **calcium phosphate** to be the major component of bone ash. In 1875, Sir Humphrey Davy identified the element potassium in the residues of incinerated wood and gave it the name 'pot ash'. The earliest indication of ash being of potential nutritional significance appears to be from Fordyce (1791), who showed that canaries on a seed diet required a supplement of 'calcareous earth' to remain healthy and produce eggs. Calcium supplements came into use for the prevention of rickets, and the discovery that iron was a characteristic component of **blood** led Frodisch (1832) (cited in Suttle, 2010) to link blood iron content with 'chlorosis' (**anaemia**) in humans. In livestock, Boussingault (1847) showed that cattle had a dietary need for common **salt**, and Babcock (1905) induced calcium deficiency in dairy cows by feeding diets low in calcium. A craving of sick cattle and sheep for the bones of dead animals on the South African veldt led to the identification of phosphorus deficiency in cattle (Theiler, 1912).

Nutritional diseases in humans

Several important nutritional diseases, namely scurvy, anaemia (chlorosis), beriberi, rickets and **goitre**, were investigated during the 18th and 19th centuries.

Scurvy

The earliest systematic work on nutrition appears to be a controlled clinical trial of the various therapies recommended for the disease of scurvy. This was a condition common on sailing ships, characterized by a loss of appetite, weight loss, fatigue, irritability and lethargy followed by spongy gums, loosening of the **teeth** and a bleeding into the skin and mucous membranes. The study was carried out in 1746 by James Lind on sailors at sea when Lind was a ship's surgeon in the British navy. He had no academic training but had a special interest in the problem of scurvy. According to the record he took 12 sailors, all similarly affected by the disease, divided them into pairs and for 2 weeks gave each pair one of several treatments that had been recommended for the condition.

He found that the pair receiving lemons and **oranges** had almost recovered after only 6 days, whereas those receiving either dilute sulphuric acid or vinegar showed no improvement after 2 weeks. As Carpenter (2003a) pointed out, although this was an important finding, it had been known for some 200 years that citric juice could prevent or cure scurvy, but that this knowledge could not always be made use of. Neither oranges, lemons nor fruit juice could be stored on long voyages before the days of refrigeration, because they went mouldy. Consequently the College of Physicians in London had reasoned that other acids could act as substitutes. Ships' surgeons were issued with sulphuric acid for many years without its actual value having been put to a critical test. A difficulty in applying Lind's findings was that since other acids could not replace lemon juice, and if lemons or their juice were too unstable for storage on long voyages, what was the answer? A practical solution, welcome to sailors, was to preserve the juice with a proportion of rum or brandy. Another approach was to extract **citric acid** from the juice and to issue that to ships. These approaches assumed that citric acid was the active factor, and it was much later before it became clear that pure citric acid was not anti-scorbutic.

Although Lind and others believed that scurvy was related to conditions at sea, the air causing poisons to accumulate in the skin, scurvy had been reported in land-based patients, for example in British prisons. The condition was exactly the same as that seen in affected sailors and was noticed to occur following the removal of potatoes from the diet. When these were added back to the diets, the disease disappeared. The importance of potatoes as anti-scorbutic was confirmed in the period from 1845 to 1848, when successive European potato harvests failed because of fungal attacks. As Carpenter (2003a) reported, land scurvy continued to be a problem in several countries whenever food was in limited supply. It occurred among prospectors during the California gold rush, soldiers during the Crimean War, prisoners in the American Civil War and ordinary civilians during the Siege of Paris in 1871. In every case, the problems were resolved when either fresh

vegetables or fruit juice became available again. It was known also that Eskimos managed to remain healthy in the far north without the use of fruit or fresh vegetables. Thus it became clear that a factor other than pure citric acid was the effective agent in preventing and curing scurvy. Identification of the actual factor was to come much later.

Anaemia

This condition had long been reported as a common problem among young women in their teens, their **blood** showing a decreased blood cell count and a reduced **haemoglobin** level. A common name for the condition was 'chlorosis' or the 'green sickness', referring to the greenish pallor seen in Caucasian patients. It was known that their condition responded to the oral administration of pills containing ferrous sulphate, but by 1885 it was not generally accepted that the response was the direct result of the iron being absorbed and incorporated into haemoglobin, since the process of synthesis was considered impossible in animals (Carpenter, 2003b). In addition, research in Germany had shown with dogs given a supplement of ferrous sulphate to their diet of meat that the additional iron recovered in the faeces was almost equal to that ingested. The conclusion was that inorganic iron was essentially indigestible. Another complication was that some people produced **hydrogen** sulphide in their **small intestine**, which reacted with iron and other elements and made it nutritionally unavailable. These conclusions were questioned in the 1890s when Ralph Stockman, a physician at Edinburgh University, found good responses in both red cell counts and haemoglobin levels in the blood of anaemic patients following subcutaneous injections of small quantities of ferrous citrate. Other patients received **keratin**-coated capsules containing ferrous sulphide, which also resulted in an improved blood picture. Stockman went on to investigate the assumption that there was always sufficient iron in the common human diets and found that the standard method of iron analysis at that time was faulty. His revised procedure showed that bread had only about 5 mg iron kg^{-1}, whereas meat had about 40 mg kg^{-1}. Analyses of five actual diets being consumed by

anaemic young women (mainly bread) showed an average intake of only 3 mg iron per day. In contrast, the more varied and abundant diets of healthy nurses were all found to provide 9–10 mg iron. He concluded that the combination of low iron intake and menstrual losses was sufficient to explain the occurrence of chlorotic anaemia in young women, also that when red blood corpuscles break down, most of the released iron is retained and re-utilized so that both the excretion and the requirement for the element are quite small. It took some time for the conclusions to be accepted by the medical community, since the prevalent opinion was that anaemia was associated with a neurotic condition, but eventually led to some countries such as the USA requiring white bread and breakfast **cereal**s to be fortified with inorganic iron as a preventive measure.

Beriberi

This disease, classified as a polyneuritis, was known to occur in parts of Asia, and by the 1880s was reported in the Japanese navy (Carpenter, 2003b). It was characterized by initial weakness and loss of feeling in the legs, then the development of heart failure and breathlessness together with oedema, in some cases followed by death. A naval surgeon named Kanehiro Takaki, who had received postgraduate training in England, was made responsible for eliminating the problem. The only difference he could find in the conditions of the Japanese sailors compared with those in European navies in which the problem did not exist was that their diet was considerably lower in protein content and well below the Voit standards accepted at that time. Altering the diet of the fleet to European standards by the inclusion of more meat, condensed milk, bread and vegetables at the expense of **rice** resulted in the problem virtually disappearing, except for cases in sailors who were unwilling to eat the supplemented rations. He concluded that beriberi resulted from a deficiency of protein.

In the same period, there was a similar problem of beriberi in a native army, recruited by the Dutch in their East Indian colony (now Indonesia). In response, the Dutch government sent a small team led by Cornelis Pekelharing, a bacteriologist, and later by Christiaan Eijkman, a young army physician, to investigate the

outbreak. Neither had any knowledge of Takaki's work at that time. Believing the initial diagnosis that the disease was the result of an unusual type of bacterial infection, Eijkman chose chickens as his test subjects since he required large numbers. He tried to infect them by injecting them with blood from hospital patients and after a few months began to see birds with an unsteady gait, somewhat similar to beriberi cases. However, the same condition was seen in uninjected birds kept in the same compound, which was considered to be due possibly to spread of infection. Further trials were conducted with the control birds separated further from the injected birds, but with the result this time that no birds in either of the groups developed the problem. Subsequent investigation by Eijkman discovered that the **leg weakness** occurred at a time when the birds had been fed leftover cooked rice from the hospital kitchen, whereas chickens fed either uncooked hospital rice or rough, feed-grade rice containing the **bran** layer remained healthy for the duration of the trial. There was no problem of nerve degeneration when the brown rice was consumed fresh but the army could not use it in feeding the troops because its high **oil** content resulted in it becoming rancid quickly under tropical conditions and unpalatable. His investigation lasted six years, the main conclusions at that time being summarized as follows. The disease in the birds appeared to be a type of peripheral polyneuritis. It was seen in birds fed uncooked white rice, although usually only after a longer period than with cooked white rice. There was no evidence of the involvement of pathogenic microorganisms or of toxins in causing the disease. Sick birds could be cured by switching them to a diet of brown rice. He therefore concentrated on what factor in the bran coat and present in brown rice could be responsible for its protective effect. Feeding ground bran was effective, but not ground husks.

These findings were later confirmed in human subjects when Adolphe Vorderman, the medical inspector of prisons in Java, found that the incidence of beriberi was much greater in prisons using mostly white rice. Less than one prisoner in 10,000 developed beriberi in the prisons using brown rice, whereas one in

39 were affected in the prisons using mostly white rice. Other research in Indonesia showed that several varieties of **beans** (e.g. mung beans) were even more effective than rice bran in preventing and curing the disease.

By 1905, the Dutch researchers in Indonesia had demonstrated that the disease was the result of white rice lacking some unknown, heat-labile component. However, this was not yet accepted in other parts of Asia in which the disease was a problem. Researchers at the Malaysian Institute for Medical Research found that adding alcoholic extracts from brown rice to a diet of white rice prevented the occurrence of polyneuritis in chickens, whereas feeding the brown rice remaining after alcoholic extraction induced the disease. These findings indicated that white rice was deficient in some factor (or factors), rather than being toxic. By this time, workers in Java and elsewhere were already attempting to concentrate and isolate the active factor from rice bran, with the aim of being able to identify and possibly synthesize it. It was discovered in Germany that pigeons, which were easier to house, could be used instead of chickens and showed a characteristic head retraction when deficient in the anti-beriberi factor. It now became easier for this problem to be pursued in established laboratories in the West. Since rice polishings had a relatively high concentration of phosphorus, a researcher in Germany tested phytin, phosphonucleic acids and other phosphorus-containing compounds for their potency. These were found to be inactive, but dried **yeast** was discovered to be highly active. In 1911, Kazimierz Funk, a Polish chemist working at the Lister Institute in London, was the first to claim to have isolated active crystals from rice polishings: they consisted of an organic base, and 50 mg was sufficient to cure a deficient pigeon. In the following year, a group of Japanese researchers obtained even more active material. It was later realized that these were both still mixtures and highly competitive attempts at purification continued for several more years.

Rickets

In the early years of the 20th century, rickets in young children was

becoming reported as a common problem in large cities in Western Europe and the USA. It was characterized by inadequate calcification of the bones, with bowed legs on walking and deformities of the ribs. An early conclusion was that it could not be the direct result of an inadequate intake of calcium salts because it was as common in areas where the drinking water had as high a concentration of 'lime' as elsewhere. It also occurred in well-to-do families in which the child was plump and well-fed. Walter Cheadle, a London physician, studied the problem, concluding that it was different from scurvy. A common factor was that the child had not been breast-fed, receiving either skimmed milk or newly patented 'artificial foods' that were high in starch but contained much less fat than breast milk. He referred also to the problem in London Zoo, where the lion cubs were ignored by their dams and had been dying of rickets until their diet of horse meat was supplemented with **cod liver oil** and ground bones. Theobald Palm, who had been a medical missionary in Japan, had been surprised at the complete absence of rickets there. He organized a worldwide survey by fellow missionaries of the incidence of the disease and concluded that it was always absent where people were in long hours of good sunlight, not blocked by industrial smoke. The work of the two researchers suggested that the disease appeared only when two conditions were met: sunlight was limited and the child was fed an inadequate substitute for breast milk.

In 1917 McCollum moved from Wisconsin to Johns Hopkins University in Baltimore. There, while conducting further rat experiments, he discovered that he had produced an experimental model of rickets. Research in the UK had shown in 1908 that puppies fed bread or oatmeal with whole milk developed rickets if kept indoors, but not if taken for outdoor walks. Subsequently Edward Mellanby reported in 1921 that he had produced rickets in puppies kept indoors by limiting their milk intake to 200 ml per day. He also reported that oatmeal had a rachitic effect.

Goitre

As described by Carpenter (2003a), **goitre**, characterized by a swelling in the front of the neck and cretinism in humans, had long

been recognized as endemic in certain areas, a traditional treatment being consumption of dried seaweed or sponges, or their ash. Discovery of the element **iodine** was made in 1812. Adolphe Chatin, during 1850–1854, linked environmental iodine deficiency to the incidence of endemic goitre in humans and animals (Suttle, 2010). This led French chemists to investigate the use of iodine for the treatment of goitre. However, it was frequently found to be toxic in the doses given and the treatment was largely abandoned, one medical conclusion being that goitre and cretinism should be included among the infective diseases. Later research showed that iodine was concentrated in the thyroid gland and that the enlarged thyroid in goitre patients had a low iodine content. The first **thyroid** hormone isolated, thyroxine, was also found to contain iodine in its molecule (Harington, 1926). One puzzle was that some observations on the incidence of goitre did not parallel the deficiency of iodine in local water and food supplies, leading to speculation that other factors were involved. In 1928 researchers at Johns Hopkins University discovered that **rabbits** fed mainly **cabbage** and being used for a study of infections developed goitre (Carpenter, 2003c). Studies with rats then showed that most **brassica** plants and also unprocessed soybeans possessed **goitrogen**ic activity that responded to higher intakes of iodide. However, feeding brassica seeds resulted in goitre that was reversed with thyroxine but not with iodide. Extension of these studies provided an explanation: goitre occurs when there is reduced thyroid hormone synthesis secondary to biosynthetic defects and/or iodine deficiency, leading to increased production of thyroid-stimulating hormone. This stimulates thyroid growth as a compensatory mechanism to counter the decreased hormone synthesis.

In 1917 David Marine organized a large-scale trial of iodine **supplementation** of schoolgirls in an area of Ohio where the disease was endemic, as outlined by Carpenter (2003c). Results showed that longer periods of treatment produced more complete freedom from the problem with no evidence of harm. After this report iodized **salt** began to be produced in many parts of the

world, with government approval.

Subsequent research on nutritional diseases showed that some did not have a simple aetiology and involved interactions of several nutrients. Examples include dermatitis (involving **niacin**, **vitamin A**, folic acid, **pantothenic acid** and **zinc**) and **perosis** (involving **choline**, vitamin B_{12}, folic acid and **manganese**).

Discovery of the vitamins

Some of the first evidence for the existence of vitamins emerged in the late 19th century with the work of Dutch physician and pathologist Christiaan Eijkman on beriberi (see above). In 1906–1907 British biochemist Sir Frederick Hopkins observed that animals cannot synthesize certain **amino acid**s and concluded that **macronutrient**s and salts could not by themselves support growth.

In the early years of the 20th century, the number of researchers engaged in nutritional work increased greatly and now included women. Because of all the important discoveries made it is often regarded as the Golden Age of Nutrition, or the Vitamin Era. A leader in this area was E.V. McCollum at the Wisconsin Agricultural Experiment Station. According to Carpenter (2003c), he was aware of the failure of European researchers to maintain small animals on purified diets, but was unaware of the report (in Dutch) of Pekelharing whose work (see above) had indicated that mice would not thrive on a simplified diet of casein, egg albumin, rice **flour** and **minerals**. Pekelharing's conclusion was that the mice were deficient in a factor or factors that could be provided in **whey**, but he could not identify the missing factor. Apparently McCollum was also unaware of the work of Eijkman and Gerrit Grijns in studying the disease produced by feeding chickens white rice and the conclusion by Grijns that it was caused by deficiency of a relatively unstable water-soluble **organic compound**.

As noted above, Osborne and Mendel in 1911 were primarily interested in comparing the nutritional value of a variety of isolated proteins tested in protein-free diets. The diet had to meet all the other nutritional needs of young rats, which led to their investigations on vitamins.

Kazimierz Funk in 1912 introduced the term 'vitamines', proposing that the anti-beriberi factor (and several other yet unidentified factors involved in nutritional diseases) must possess an organic base and therefore contain an **amine** group, i.e. they were vital amines. He later altered the term to 'vitamins', which was adopted by others. Research in this area became a major topic of nutritional research for the next 30 years. Initially most investigations started with a diet found to be associated with a particular disease, and later involved dietary mixtures based on pure forms of the major nutrients. Various sources and combinations of vitamins could then be included. Both approaches produced major findings, using in some cases rats, mice and birds as the test species.

By the 1940s, all of today's known vitamins had been identified, the last being **cobalamin** (vitamin B_{12}) which was isolated in 1948 in both the USA and UK. With the identification of vitamin B_{12} the so-called **animal protein** factor in liver, fish meal and in ruminant excreta was explained. After the detection, isolation and synthesis of the individual vitamins, a period of intensive research followed with the main object of establishing the requirements for humans and food-producing animals.

Fat-soluble vitamins

Vitamin A

One of McCollum's projects was to improve the mineral mix used in his research. As recorded by Carpenter (2003c), in 1913 he reported that rats fed diets containing 12–18% casein, 20% **lard**, 20% **lactose**, 6% minerals and starch, grew well for 8–14 weeks but then stopped growing and in some cases lost weight. Growth restarted if the rats were given a supplement of 1 g of ether extract of egg on alternate days. The need for a fat-soluble substance was confirmed by Osborne and Mendel, who also reported the high potency of cod liver oil. Contrary to the belief that all fats had similar nutritional value, in 1913 McCollum and Marguerite Davis showed that lard and olive oil were not equivalent to butter and egg yolk in supporting the growth and survival of rats. Osborne and Mendel at Yale University produced a similar report with rats fed

'the ether extract of egg or of butter'. Active foods included butter, egg yolk, whole milk, cod liver oil and several pigmented fruits and vegetables, whereas inactive foods included lard, olive oil and non-pigmented fruits and vegetables. Both reports were published in the same volume of the *Journal of Biochemistry* although the McCollum and Davis paper was submitted first. Consequently McCollum and Davis were credited with the discovery of the first accessory food substance to be recognized as a vitamin, which they called 'fat-soluble A'. 'Vitamin A' became the accepted name in 1920. Further research by the two American groups showed that rats needed both a fat-soluble 'Factor A' and a water-soluble 'Factor B' that was identical to the anti-beriberi factor related to the deficiency chickens and pigeons fed white rice. It was also noted that a deficiency of 'Factor A' resulted in severe ophthalmia, which could be prevented with cod liver oil. The next step was to identify the factor, which appeared to exist in at least two forms: a highly coloured form in leaves and **carrot**s and a colourless form in **animal fat**. Crystals of β-carotene, a polyunsaturated hydrocarbon, were obtained from carrots and found to be active. Carotene appeared to be a precursor of the final colourless vitamin, and this was confirmed when it was finally isolated from fish liver oils in 1939 and its structure identified. The vitamin (termed vitamin A) was an alcohol attached to a long unsaturated carbon chain linked in turn to a β-ionone ring and was named retinol. β-Carotene was subsequently shown to be two retinol molecules condensed through their alcohol groups.

Vitamin D

The discovery of this vitamin was made as a result of research to provide an explanation for the cause of rickets (Carpenter *et al*., 1997). Exposure of affected infants to sunlight was a traditional folk remedy in Northern Europe, and in 1919 exposure to ultraviolet **light** was also reported to be effective. As described by Carpenter, a research team led by Harriette Chick of the London Lister Institute went to Vienna where the Children's Hospital had many cases of rickets. They were able to report in 1922 that the use of either cod liver oil or irradiation with ultraviolet light cured the

condition, which otherwise developed even under the most hygienic conditions. By this time, the McCollum team had found that rats could be used as a model for rickets if the diet was severely imbalanced in ratio of calcium to phosphorus and that the disease was identical to the human form. Their next trial was to test whether vitamin A was responsible for healing rickets. They treated cod liver oil with oxygen to destroy the vitamin A and found that the preparation was no longer able to prevent **xerophthalmia** and vitamin A deficiency, but it still retained its ability to cure rickets. Their conclusion was that the factor responsible was a new vitamin, which they called **vitamin D**. Their subsequent finding in 1924 was puzzling, as recounted by Carpenter (2003c): not only did irradiation of rachitic rats with ultraviolet light have a curative effect, but so did irradiation of the **diet** that had induced the disease. As a follow-up, several groups then tried to determine what factor might be activated in this way. It was quickly traced to '**lipid**', then to the **sterol** fraction and finally to **ergosterol** and, in 1930, the compound was crystallized by F.A. Askew and colleagues at the National Institute for Medical Research in the UK. Application of this new knowledge allowed rickets to cease to be an important public health problem. It was later realized that there were two forms of the vitamin: the form identified by Askew *et al.* was ergosterol found in plants (vitamin D_2) and cholecholesterol found in animals and humans (vitamin D_3). The relative activity of these forms in humans and in animal and avian species was later shown to depend on the species involved.

As pointed out by Norman (2012), it is largely through historical accident that vitamin D became classified as a vitamin rather than as a steroid hormone, since it is itself biologically inert. There are no known essential biological actions or contributions that rely specifically on the vitamin D molecule. During the 1970s, through the work of Egon Kodicek in Cambridge and Hector F. Deluca in Wisconsin, the prevailing view that vitamin D acted directly to promote **intestinal absorption** of calcium and regulation of bone **metabolism** was shown to be in error. They discovered that vitamin D, through the combined actions of the liver and kidney,

was converted to a hormone that mediated the actions attributed to vitamin D. This represented a new concept: the action of a vitamin depending on its conversion to a hormone (DeLuca, 2014).

In addition, the active form of the vitamin can be produced in humans and animals by conversion of 7-dehydrocholesterol in the skin by exposure to ultraviolet light. Thus vitamin D becomes a true vitamin only when the animal or human does not have sufficient access to sunlight. Under normal physiological circumstances all mammals and birds can generate adequate quantities of vitamin D_3 in this way to meet their nutrition needs. It is now known that latitude and season affect both the quantity and quality of solar radiation reaching the earth's surface, especially in the ultraviolet band (UVB) region of the spectrum, affecting the conversion process. This can result in a 'vitamin D winter' in humans as well as in livestock housed outdoors in northern climes and it explains why over half the population of senior citizens in Germany are periodically deficient in vitamin D unless they are receiving a supplement (Rabenberg *et al*., 2015).

Vitamin E

In 1922 H.M. Evans and Katharine Bishop working at Berkeley found that a purified diet with vitamin supplements that supported good growth in female rats nevertheless failed to support normal **reproduction**; the embryos were being resorbed before the end of pregnancy. Lettuce was the first food found to prevent this problem, followed by wheat and, in particular, wheat germ oil. Cod liver oil seemed unexpectedly to increase the problem. The active factor was named '**vitamin E**' and following further investigations by many groups, it was isolated in 1935 and named '**tocopherol**'. Three years later the Swiss chemist Paul Karrer synthesized it. During this period there was a change in thinking about the effects of a deficiency of vitamin E. In rats, males showed testicular degeneration, but it was realized that in pregnancy it was the fetus that failed to develop rather than the dam being affected. It was also found that vitamin E deficiency in lambs and rabbits resulted in muscular degeneration rather than infertility and in chicks it resulted in **exudative diathesis** and/or encephalomalacia.

Vitamin K

Haemorrhaging in chicks, which responded to dosing with cabbage, was another disease that at one time was thought possibly to be caused by a deficiency of vitamin E. The Danish researcher Henrik Dam reported in 1935 that the condition was due to a deficiency of another **fat-soluble vitamin**, which he named '**vitamin K**' in recognition of its essential role in blood coagulation (*Koagulation* in Danish and German). It was discovered to occur naturally in modified forms in many plants and to be produced by bacterial growth in stored animal products. The vitamin also cured the haemorrhaging of patients with obstructive jaundice who lacked **bile** to aid absorption of the vitamin and of cattle that had been eating sweet clover **hay** that contained an anti-vitamin. The vitamin was found to occur naturally in various forms; **phylloquinone** (K_1) in plants and **menaquinone** (K_2), which is synthesized in the animal gut by microbes. A water-soluble form of the vitamin was later synthesized for dietary supplementation.

Water-soluble vitamins (B)

As the vitamins in this group were discovered they were initially named B_1, B_2, etc. (later the chemical names were used). The numbering is not quite consecutive, with some gaps such as B_4 and B_8, because the compounds in question failed to meet the definition of a vitamin, i.e. being essential in small quantities for the normal health, growth and nutritional needs in higher forms of animal life. In addition they had to be shown to be distinct from other biologically important compounds such as proteins, carbohydrates and lipid; and generally could not be synthesized in amounts sufficient to meet bodily needs and therefore had to be obtained from the diet or from a synthetic source.

In 1912 (the same year that Hopkins published his findings about the missing nutrients, which he described as 'accessory' factors or substances), Funk demonstrated that polyneuritis produced in pigeons fed on polished rice could be cured by supplementing the birds' diet with a concentrate made from rice bran, a component of the outer husk that was removed from rice during polishing. Funk proposed that the polyneuritis arose

because of a lack in the birds' diet of a vital factor (now known to be thiamin) that could be found in rice bran. Funk believed that some human diseases, particularly beriberi, scurvy and pellagra, also were caused by deficiencies of factors of the same chemical type.

In 1913 McCollum divided vitamins into two groups: 'fat-soluble A' and 'water-soluble B'. As claims for the discovery of other vitamins multiplied, researchers called the new substances C, D, and so on. Later it was realized that the water-soluble growth factor, vitamin B, was not a single entity but at least two – only one of which prevented polyneuritis in pigeons. The factor required by pigeons was called vitamin B_1, and the other factor, essential for rats, was designated vitamin B_2. As chemical structures of the vitamins became known, they were also given chemical names, for example thiamin for vitamin B_1 and **riboflavin** for vitamin B_2.

Thiamin (B_1)

McCollum and others had produced signs of polyneuritis in rats using purified diets with a source of vitamin A and had characterized the 'anti-beriberi factor' as vitamin B. It was then realized that autoclaved **yeast**, although it had lost its 'anti-neuritis' activity, still promoted growth in rats so that it must contain a second factor; these were then called B_1 and B_2, respectively. The isolation of B_1 was achieved in 1926 by Dutch scientists in Java and a biologically active compound synthesized in 1936. It was named thiamin(e) as 'the vitamin containing sulfur' (*thios*, Greek). Meanwhile R.A. Peters at Oxford was investigating the function of the vitamin. It was known that deficient subjects maintained unusually high levels of pyruvic or **lactic acid** in their blood after exercise, and his group obtained evidence that thiamin pyrophosphate served as a co-factor for the enzyme **pyruvate** de**carboxylase**. He introduced the term 'bio chemical lesion' to describe the effect of its deficiency. This was the first of a long series of findings that B-vitamins generally serve as part of **coenzyme**s concerned with different aspects of metabolism.

Riboflavin (B_2)

Interest in accessory food factors began in the latter half of the 19th

century with the discovery of the first vitamin, thiamin. Soon researchers realized that there were one or more additional water-soluble factors in foods such as milk, whole wheat, yeast and liver. As outlined by Northrop-Clewes and Thurnham (2012) the first observation of a pigment in milk with yellow-green fluorescence can be traced to the English chemist Alexander Wynter Blyth in 1872. It was not until 1933 that the substance was isolated and identified as riboflavin by Richard Kuhn and Paul György in Germany. Kuhn also developed a synthetic process for riboflavin in 1935. The essential nature of the vitamin as a food constituent for humans was shown in 1939. It was also found that human patients with pellagra who continued to show cheilosis (lesions around the mouth) after being treated with niacin responded rapidly to riboflavin. This finding suggested that most patients with signs of pellagra were also at least marginally deficient in riboflavin in addition to being deficient in niacin. In other species it was found that some dogs suffering from a condition known as 'blacktongue' could be cured by a dietary supplement of riboflavin.

Niacin (B_3)

The name 'niacin' is an abbreviation of 'nicotinic acid'. This vitamin was discovered due to its involvement in the human disease known as pellagra (Lanska, 2012). The name 'pellagra' is derived from the Italian *pelle agra*, meaning sour or rough skin. It was first described by the physician Gaspar Casal in Spain in 1735, soon after the introduction of **maize** into Europe. It is a condition characterized by dermatitis, **diarrhoea**, dementia and, if untreated, death. After 1900 pellagra became a significant health problem in the USA, particularly in the south where maize was an important food crop. It occurred following the introduction of a new **grain** processing method that involved fine grinding and sieving of maize in place of the coarse grinding method used previously.

Nicotinic acid was synthesized in 1867 by **oxidation** of nicotine and widely used in photography. It was not considered to have nutritive properties until German scientists demonstrated that it was present in yeast and in rice polishings. It was isolated by Funk

in 1912, while he was trying to find a cure for another disease – beriberi. In 1915 Joseph Goldberger, an American physician, conducted a series of experiments on 11 healthy volunteer prisoners in a Mississippi jail and found that he could induce pellagra by altering their diets. He concluded that the disease was caused by the absence of some factor that was lacking in maize but was present in meat and milk. He named it the P-P (for pellagra-preventive) factor.

The chemical structure of that factor was subsequently discovered in 1937 by the American biochemist Conrad Elvehjem. He induced a black-tongue condition in dogs by feeding them the Goldberger diet, and then cured the disease by supplementing their diet with niacin. He also isolated the P-P factor from active liver extracts, showing that this factor was actually niacin.

As outlined by Carpenter (2003c), by 1945 it was considered that pellagra might not be the result of a simple deficiency of niacin. Using a newly developed method of analysis for niacin, it had been found that simple rice diets from India (where pellagra was not a problem) contained less niacin than Rumanian maize-based diets, where it was a problem. In addition, rats fed a standard purified diet with 15% casein as the **protein source** thrived without any source of the vitamin, and excreted niacin and a methylated derivative in their **urine**. It was then found that rats would become niacin deficient if their purified diet was diluted with 40% maize meal, the food that had traditionally been associated with the disease in Europe. Furthermore, growth could be restored if the diet was supplemented with 0.05% of the amino acid, **tryptophan**, that is present at a lower level in maize than in other grains. It was then shown that tryptophan could also be used to treat humans afflicted with pellagra, with some of the amino acid being converted to niacin. Cats showed no conversion, and dogs much less than rats because they would become niacin deficient on diets containing relatively well-balanced protein. Among food-producing animals, ducks were found to be particularly dependent on a satisfactory level of niacin in their diet (about twice that required by chickens) due in part to their inability to convert

tryptophan to niacin. A deficiency of the vitamin in this species is typically manifested as bowed legs and/or enlarged hock joints.



Girl suffering from chronic pellagra in a London asylum. Photo courtesy of Welcome Foundation. Licensed under CC BY 4.0.

According to Carpenter (2003c), there are still problems in understanding pellagra. No animal model of niacin deficiency has shown the sun-induced areas of dermatitis seen in pellagrins. It is now realized that Goldberger's trial with convicts had actually produced riboflavin deficiency and a later attempt to induce niacin deficiency specifically in men failed.

Pantothenic acid (B_5)

This vitamin was first recognized as a microbial **growth factor** (Lanska, 2012). It was discovered in 1931 by chemist Roger J. Williams during his studies of the vitamin B complex when he found that an acidic substance was required for growth by certain strains of yeast. In 1933 he named the substance **pantothenic acid** (from the Greek word *pantothen* meaning 'from everywhere'), because small quantities of pantothenic acid are ubiquitous in food. In 1936 Thomas Jukes discovered a substance in liver and rice bran that was not absorbed by Fuller's earth from an acid solution, which he named 'filtrate factor'. Lack of this substance caused dermatitis in chicks and impaired the growth of rats. The initial isolation of pantothenic acid was achieved by Williams and colleagues in 1939, and synthesis achieved in 1940 by Karl Folkers

and colleagues at Merck and Company in the USA. One of the active forms of pantothenic acid, coenzyme A (CoA), was discovered by Fritz Lipmann and Nathan Kaplan in 1946 as an essential co-factor in the acetylation of **choline**, in the synthesis of citrate and acetoacetate, and in **pyruvate** and **fatty acid metabolism**. The second active form of pantothenic acid, the acyl carrier protein (a component of the fatty-acid synthase complex), was described by Salih Wakil and colleagues in 1964.

Pyridoxine (B_6)

In the 1930s Rudolf Peters showed that young rats kept on a **semi-purified diet** with added thiamin and riboflavin but no other supplement developed 'rat acrodynia', a condition characterized by severe cutaneous lesions (Rosenberg, 2012). In 1934, Paul György showed that the factor which cured 'rat acrodynia' was vitamin B_6. Other studies later showed that vitamin B_6 deficiency produced **convulsion**s in rats, pigs and dogs, and a microcytic anaemia in certain animals. Samuel Lepkovsky isolated and crystallized vitamin B_6 in 1938. The following year, Leslie Harris and Karl Folkers, and Richard Kuhn and his associates independently, showed that vitamin B_6 was a pyridine derivative, 3-hydroxy-4,5-dihydroxy-methyl-2-methyl-pyridine. György proposed the term **pyridoxine** for this derivative. Esmond Snell developed a microbiological growth assay in 1942 that led to the characterization of pyridoxamine, an active product of pyridoxine, and pyridoxal, the formyl derivative of pyridoxine. Further studies showed that pyridoxal, pyridoxamine and pyridoxine have largely equal activity in animals and owe their vitamin activity to the ability of the organism to convert them into the enzymatically active form pyridoxal-5-phosphate.

Biotin (B_7)

Like pantothenic acid, **biotin** was originally recognized as a microbial **growth factor**. In 1901, Eugene Wildiers reported that yeast requires an organic accessory substance which he named 'Bios' (from the Greek word meaning 'life'). In 1933, Allison and colleagues at the US Department of Agriculture in Washington, DC, described an accessory growth factor that they had isolated from

egg yolk and found to be essential for the growth of *Rhizobium*, a **nitrogen**-fixing bacterium found in leguminous plants. They called this factor 'coenzyme R' because they believed it furnished a co-factor for 'respiration'. In 1936, Frit Kögl and his graduate student Benno Tönnis at Utrecht University isolated a crystalline substance from boiled duck egg yolks, which they named 'biotin' because they believed it was one of the components of the 'Bios' factor.

Several scientists collaborated in determining the chemical nature of biotin. By 1940, György, Vincent du Vigneaud and colleagues established the equivalence of biotin, vitamin H and coenzyme R, and succeeded in isolating biotin from liver extracts and from milk. In 1942 du Vigneaud and colleagues reported the structural formula of biotin. The following year, S.A. Harris and co-workers at Merck and Company in the USA synthesized the vitamin. In 1959, Feodor Lynen and his group at the Max-Planck Gesellschaft in Munich began to establish the biochemical functions of biotin, recognizing its role as a co-factor in **gluconeogenesis**, **fatty acid synthesis** and **branched-chain amino acid catabolism**. These metabolic functions were discovered in experimental studies of microorganisms and rats, and by recognition of problems of biotin metabolism in humans. In human infants a spontaneous deficiency could be observed as a seborrheic dermatitis, due to a low content of the vitamin in breast milk or to malabsorption (e.g. because of persistent diarrhoea). Biotin deficiency was also seen in patients with biotinidase deficiency (who are unable to reutilize and recycle biotin), in severely malnourished children in developing countries, and in individuals who consumed large quantities of raw eggs (resulting in biotin in the intestine becoming bound by an **egg protein** named **avidin** and rendered biologically unavailable). Explanation of the causes for the occurrence of fatty liver and kidney syndrome in chickens and the involvement of biotin was established by researchers at the ARC Poultry Research Centre, Roslin, UK. Their studies showed a low bioavailability of this vitamin in some common feed ingredients (e.g. wheat) which contributed to the problem and

multidisciplinary studies established the full aetiology of the disorder (Whitehead, 2000).

Choline

The **chemical composition** of living tissues was an active area of research in the middle of the 19th century, and in 1850 Theodore Gobley in France isolated a substance from brain tissue and carp eggs that he described as '*matière phosphorée*'. He named it 'lecithine'. Adolph Strecker at the University of Tübingen noted in 1862 that when **lecithin** from boiled pig and ox bile was heated, it generated a new nitrogenous chemical that he named '**choline**'. Lecithin was eventually identified chemically as **phosphatidylcholine**.

Although choline is not by strict definition a vitamin, it is an essential nutrient and usually included with the B vitamins because of its functions. Unlike the other B vitamins, choline is not a metabolic catalyst but forms an essential structural component of bodily tissues (**phospholipid**s). The role of choline as part of the neurotransmitter, **acetylcholine**, was established by Otto Loewi at the University of Graz and Sir Henry Dale at the University of London (1836). In the early 1930s, Charles Best and colleagues at the University of Toronto reported that a fatty liver condition in rats on a special diet and diabetic dogs could be prevented by supplementation with lecithin. In addition, choline has been found to act as a donor of methyl groups in transmethylation reactions that involve folic acid or vitamin B_{12}. Although other compounds, such as **methionine** and **betaine**, can also act as methyl donors they cannot replace choline in its other functions.

Subsequent research showed that animals synthesize choline but this process is often inefficient, especially in the young, making supplementation advisable. Good dietary sources include fish solubles, fish meal, **soybean** meal and distillers' solubles. Along with **manganese**, folic acid, nicotinic acid and biotin, choline is necessary for the prevention of **perosis** (slipped tendon) in young chicks and turkey poults. A lack of choline also results in retarded growth and poor feed utilization. Humans can synthesize it in small amounts, but choline must be included in the diet to maintain

health. The importance of choline as an essential nutrient for human health was determined in the 1990s through controlled feeding studies in humans, and in 1998 the US National Academy of Medicine reported their first recommendations for choline in the human diet.

Folacin (folic acid, B_9)

In the 1930s, Lucy Wills identified a 'new haemopoietic factor' in yeast and liver which cured tropical macrocytic anaemia in humans and experimental anaemia in monkeys. Janet Watson and William B. Castle named the unknown substance 'Wills' factor'. Further studies with this unknown substance showed that it was active against nutritional pancytopenia in monkeys and experimental anaemia in chicks, leading to various designations such as vitamin M (monkey) and vitamin Bc (chick). Other factors with growth-promoting activity for microorganisms such as *Lactobacillus casei* were given interim names, including folic acid, in recognition of their presence in extracts of leafy greens. Several pharmaceutical research groups headed by Robert Stokstad at Lederle Laboratories and Joseph Pfiffner at Parke-Davis Research Laboratory in the USA isolated factors possessing the biological properties of Wills' factor and other unknown related factors, including folic acid from bacterial cultures, yeast and liver. The vitamin then was crystallized, chemically identified and synthesized as **pteroylglutamic acid** and named folic acid between 1943 and 1945.

Following absorption it was found that folic acid is reduced to tetrahydrofolic acid (THFA) and also methylated (MeTH4F). It was later shown that humans and animals can use all these forms, with intestinal enzymes removing excess glutamates before absorption, but that some microorganisms require the mono-**glutamate** specifically. A clinical link between folic acid intake of mothers and the incidence of neural tube defects (NTD) (spina bifida, etc.) in babies that was reported in the UK was the subject of serious concern by 1985 (Imbard *et al.*, 2013). As a result, in 1991 the UK Medical Research Council published the results from a large multi-centre double-blind randomized trial. This study is to date the

largest and most important randomized trial comparing the effect of 4 mg folic acid per day supplementation versus a multivitamin supplement (with or without folic acid) and versus a placebo, in a large cohort of women that had a history of delivering NTD-affected children. The folic acid-supplemented group (with or without multivitamins) had a decrease of 72% in the number of NTDs compared with the placebo, while the multivitamin supplement without folic acid did not result in any significant protective effect. Timing was regarded as being important, because NTDs are known to occur within the first 21 days of conception. A consequence of the findings was that in 1996 the US Food and Drug Administration authorized food fortification with folic acid, and this became mandatory in 1998. Grains and cereals were enriched with folic acid at a concentration of 1.4 mg kg^{-1} in order to increase the average consumption of women of reproductive age by around 0.1 mg per day. Many other countries, including all North America countries, Australia and the majority of South American countries, established similar policies. The fact that a similar policy was not implemented by the 28 members of the European Union in 2019 is regarded by some in the medical community as a public health failure.

The positive action taken in some countries on food supplementation with this vitamin was strengthened by another possible benefit of higher folic acid intakes on the health of adults, namely reducing the level of **homocysteine** circulating in the bloodstream and in stimulating red cell production in pernicious anaemia patients.

Cobalamin (Vitamin B_{12})

By the 19th century, clinical reports were being received in the UK of a disease called pernicious anaemia. It was different from simple iron-deficiency anaemia in that it caused severe neuropathy leading to paralysis and death, while post-mortem reports showed spinal cord demyelination. A characteristic was that the bone marrow produced unusually large, structurally abnormal, immature red blood cells (megaloblasts) that were relatively short-lived. These symptoms were first described in 1822 by physician

James Combe in the Transactions of the Medico-Chirurgical Society of Edinburgh. Providing an answer to the puzzle took many years and a large number of investigations, mostly on human subjects since no animal model of the disease was available.

One of the earliest investigations was in 1849 by British physician Thomas Addison, from which the disease acquired the common name of Addison's anaemia. In 1907, Richard Cabot reported on a series of 1200 patients with the disease and found that their average survival was between one and three years. William Castle performed an experiment in which he ingested raw hamburger meat and regurgitated it after an hour, and subsequently fed it to a group of 10 patients. Untreated raw hamburger meat was fed to the control group. The former group showed a disease response, whereas the control group did not. This study indicated the existence of an 'intrinsic factor' in gastric juice. Many years later, the intrinsic factor was found to be a glycoprotein that formed a complex with vitamin B_{12}, promoting its absorption through ileal receptors.

George Whipple suggested raw liver as a treatment following experiments in which he bled dogs to make them anaemic, then fed them various foods to see which would make them recover most rapidly. Ingesting large amounts of liver seemed to cure anaemia from blood loss, therefore liver ingestion was tried as a treatment for pernicious anaemia with some success, as reported in 1920. In 1926, a team of physicians from Harvard University reported that eating half a pound of liver every day would prevent pernicious anaemia in most patients. George Minot and William Murphy then attempted to isolate the curative property in liver, and in 1926 showed it was contained in raw liver juice. Their work also showed that it was the iron in liver tissue, not the soluble factor in liver juice, that cured the anaemia from bleeding in dogs.

Other researchers made important contributions to the problem of pernicious anaemia (Carpenter, 2003d). Karl Folkers at the Merck Laboratories in the US worked with Randolph West of Columbia University to find patients willing to participate and fed them various liver extractions. When Folkers learned that Mary

Shorb, a microbiologist formerly with the US Department of Agriculture, had identified a bacterium that responded to liver extracts, he realized that the bacterium could be used as a model for human subjects and Shorb joined the Merck Laboratories to assist in the research. The active ingredient in liver remained unknown until 1948, when it was isolated as a cobalamin and named vitamin B_{12} by two chemists, Folkers in the USA and Alexander Todd in the UK. Analysis of the crystalline isolate by the UK group indicated the presence of a trace metal – **cobalt**. The vitamin then received the alternative name '**cobalamin**'. It proved active in extraordinarily small quantities and was effective also when injected into muscle. When tested on a patient suffering from pernicious anaemia, it provided a cure. Pernicious anaemia was subsequently treated with either injections or oral doses of B_{12}. Whipple, Minot and Murphy shared the 1934 Nobel Prize in Medicine for their discoveries.

Eventually the various biochemical roles of vitamin B_{12} were elucidated, including its important interaction with **folate** and their common link with megaloblastic anaemia. An effect of the deficiency of either folic acid or B_{12} was shown as an increase in the concentration of **homocysteine** in the blood. This was another matter of concern, because people with very high levels of this compound in the blood as result of a genetic effect are particularly subject to early-onset arteriosclerosis. This resulted in the topic becoming an active field of research in the latter years of the 20th century.

An important conclusion from the work on vitamin B_{12} was that microbiological assays had indicated that no plants synthesized the vitamin, only certain microorganisms. Thus for the first time it was realized that animals (including humans) required a substance that can only be obtained from microbial synthesis. As described above, cobalt was known to be required by cattle, but a similar response to cobalt supplementation had not been shown in other species, such as rats or chicks. An explanation for these findings could then be proposed. The microbes in the rumen of cattle and sheep are known to be particularly active. This explained why these animals

benefited from a supply of inorganic cobalt salts; the **fermentation** occurred ahead of the process of digestion and absorption in the stomach and **small intestine**, and this made the microbial cobalamin available for utilization by the host animal. In humans, pigs and poultry, on the other hand, the cobalamin produced by the microflora in the **large intestine** is not absorbed efficiently into the bloodstream and is instead voided in the excreta. It had already been found that intensively farmed chickens would not thrive indefinitely on a purely plant diet, and there had been studies of their need for an '**animal protein** factor' known to be supplied by fish meal, and also by dried cow manure. Poultry and pigs allowed access to outdoor conditions appeared to obtain sufficient cobalamin from soil organisms, worms and faecal residues. When these species were housed indoors, however, and with access to faecal matter prevented, dietary supplementation with vitamin B_{12} became routine.

*Vitamin C (**ascorbic acid**)*

As noted above, research on the cause of scurvy among sailors on long sea voyages and in other populations restricted in their food supply showed that the disease was cured when fresh vegetables or certain types of fruit juice became available. However, the antiscorbutic factor responsible could not be identified. In 1907 the Norwegian scientists Axel Holst and Theodor Frohlich produced a condition in guinea pigs similar to human scurvy by feeding them a **cereal** diet and eliminating fresh animal and vegetable foods. Addition of the restricted foods to the diet provided a cure. The name 'water-soluble C' was initially proposed by Sir William Drummond of the Lister Institute in London in 1919 for the antiscorbutic factor. Albert Szent-Györgyi isolated this factor in 1928 as a substance from **adrenal** glands that he called '**hexuronic acid**' and four years later Charles King isolated vitamin C and concluded that it was the same as 'hexuronic acid'. Norman Haworth derived the chemical structure of vitamin C in 1933 and renamed it **ascorbic acid**.

To date no further compounds have been identified as meeting the criteria for acceptance as vitamins and being defined by the

Joint International Union of Pure and Applied Chemistry (IUPAC)–International Union of Biochemistry (IUB) Commission on Biochemical Nomenclature. Nevertheless, several compounds have been suggested as vitamins, such as '**vitamin** B_{17}' (amygdalin, a cyanogenic **glycoside**) present in apricot kernels and linked to unsubstantiated claims of anti-**carcinogen**ic activitity (Williams, 2016). Amygdalin and a derivative, laetrile, are now banned as medicinal agents in several countries due to the risk of **cyanide poisoning**.

Essential fatty acids

In 1929 George and Mildred Burr at the University of Minnesota found that rats fed purified diets that were completely fat-free for several months failed to reach their normal mature weight, lost fur and their tails became inflamed and scaly (Lanska, 2012). They also reported that at autopsy the kidneys and urinary tracts showed significant signs of damage. A subsequent investigation showed that giving the animals small quantities of lard, but not **butterfat** or added vitamins, prevented the condition. Their work indicated that **linoleic acid** provided by the lard was an **essential fatty acid** that was needed in only small amounts to support health. Later α-**linolenic acid** was discovered to be another essential fatty acid (Holman and Johnson, 1982). These fatty acids were found to form part of various membranes and play a role in lipid transport and certain **lipoprotein** enzymes. In addition, they were found to be the source materials for the synthesis of the **eicosanoid**s. Other **polyunsaturated fatty acid**s such **arachidonic acid** were later shown to be required but could be synthesized in most species from linoleic or linolenic acids and were not specified as dietary requirements. Cats were different in that they required arachidonic acid in their diet since they lacked the enzymes needed to lengthen and desaturate linoleic acid. Work with **fish** showed that these species required n-3 acids for normal growth. Other work showed that when animals were limited in the supply of **linoleic acid** there was a greater synthesis of eicosotrienoic acid 20:3(n-9) from the non-essential **oleic acid** 18:1(n-9). This work indicated that the eicosotrienoic:arachidonic ratio in the blood could be used as an

indicator of linoleic acid deficiency in rats, pigs and humans, even before the appearance of clinical symptoms.

Initially it was believed that linoleic acid was the only fatty acid required to be added to infant formula. It was only in the mid-1990s that the World Health Organization recommended that infant formula should have a fatty acid content more similar to human milk, which contains other long-chain polyunsaturated fatty acids as well such as omega-3 and omega-6 fatty acids DHA and arachidonic acid.

Discovery of more mineral elements

At the beginning of the 20th century, more minerals were discovered. Between 1928 and 1931 novel studies at the University of Wisconsin with rats given specially purified diets showed that **copper**, **manganese** and **zinc** were each essential for health (Suttle, 2010). The 1930s saw the extension of such studies to livestock and, in the field, animals were shown to suffer from deficiencies of copper and **cobalt** in North America, Australia and Europe. Further studies with rats maintained in plastic isolators to exclude atmospheric **contamination** extended the list of essential minerals to include **selenium**, an element previously known for its toxicity at certain levels to livestock.

By 1981, 22 mineral elements were believed to be essential for animal life: seven major or **macronutrient** minerals (calcium, phosphorus, **potassium**, **sodium**, chlorine, **magnesium** and sulphur) and 15 trace or **micronutrient** mineral elements (**iron**, **iodine**, **zinc**, copper, manganese, cobalt, **molybdenum**, selenium, **chromium**, tin, **vanadium**, **fluorine**, **silicon**, **nickel** and **arsenic)** (Suttle, 2010). Subsequently, dietary supplements of **aluminium**, **boron**, **cadmium**, **lithium**, **lead** and **rubidium** were shown to improve growth or health in rats, goats, pigs or poultry reared in highly specialized conditions, without inducing specific abnormalities or being associated with breakdown along metabolic pathways where they have specific functions. **Fluoride** ions were recognized in the 1930s as being toxic for livestock in areas where fluoride-rich ash was scattered as a result of mining or smoke from the manufacture of aluminium, with animals becoming

stiff and lame and without appetite. In the same period it was realized that mottling of the enamel of human **teeth** in particular areas was associated with a relatively high fluorine content of the local water supply. On the other hand, it was known that children growing up in areas where the water was low in fluoride had more dental caries. This led to the fluoridation of water supplies low in fluoride as a public heath measure in some areas.

All animal tissues contain a further 20–30 mineral elements, mostly in small and variable concentrations. These are probably adventitious constituents, arising from contact with a chemically diverse environment (Suttle, 2010).

An important aspect of the mineral supply was found to be its bioavailability during digestion and absorption. It had become clear with certain minerals such as zinc and phosphorus that simple analysis of the total concentration of a nutrient in the diet was not an adequate measure of nutritional value. In addition, there was evidence that increasing the intake of one mineral could result in impaired absorption of others. Also, for selenium, chromium and niacin (as well as other B vitamins), availability was influenced by the chemical forms or combinations in which the nutrient was present. These factors had therefore to be taken into account in diet formulation.

Studies during the 1990s on the calcium metabolism of dairy cows provided a method of reducing the incidence of so-called '**milk fever**', which occurs commonly in dairy herds at calving time in developed countries. The condition relates to a need for dairy cows to mobilize 20–30 g of calcium in the production of colostrum and milk in the early stages of lactation, the process causing serum calcium level to decline from a normal of 8.5–10 mg dl^{-1} to < 7.5 mg dl^{-1}. The result is hyperexcitability of the nervous system and reduced strength of muscle contractions, resulting in both **tetany** and paresis. **Parturient paresis** may occur in cows of any age but is most common in high-producing dairy cows entering their third or later lactations, especially in Channel Island breeds. Goff (2008) and other researchers showed that the use of diets fed prior to parturition that result in an acidic response in the

animal reduced the risk for milk fever, while diets that result in an alkaline response tend to cause milk fever. Metabolic **alkalosis** is common in herbivores, since they consume **forage**-based diets that are often high in potassium. The condition impairs tissue responsiveness to **parathyroid hormone** (PTH) and increases the risk for milk fever. Diets may be made acidogenic (lowered DCAD) by selecting feed ingredients that are naturally acidogenic, by feeding anionic salts, or by adding mineral acids to the diet. DCAD is defined as the dietary cation–anion difference, usually calculated as the milliequivalents of dietary cations (sodium + potassium) minus the milliequivalents of dietary anions (chloride + sulphur). Typical diets (without supplemental anions) fed to dry dairy cows in confinement dairies in the USA have a DCAD of about +250 to +350 meq kg^{-1} dietary dry matter (DM), whereas pasture diets typically have a DCAD of about +350 to +750 meq kg^{-1} dietary DM.

Related work showed that the condition known as 'grass staggers' or '**grass tetany**' in ruminants was not due to **hypomagnesaemia** caused by a simple dietary deficiency of Mg but to a reduced availability of this mineral from the diet (Martens *et al*., 2018). Among the dietary factors shown to influence the absorption of Mg in the rumen were a high content of potassium, which had a deleterious effect, and the ruminal production of **short-chain fatty acid**s, which had a beneficial effect.

New directions after World War II

The affluent diet

An increased food supply in several countries following the war led to new avenues of research for nutritionists. One was the shortcomings of the affluent diet now enjoyed by many humans. As Carpenter (2003d) pointed out, a surprising finding was that during the war, when supplies of food and particularly of animal foods in European countries were severely restricted, the incidence of some diseases had been reduced. Now it was realized from epidemiological studies that the most affluent countries did not have the best health records and that their dietary patterns were conducive to chronic, non-infective diseases of middle age. The

first aspects of the affluent diet to come under suspicion were the high levels of saturated fat and the low levels of fibre. The high intake of sugar was another concern.

One important cause of death in Western countries was found to be coronary heart disease (CHD). A characteristic of most Western diets was that a high proportion of energy came from fat, much of it animal. Initially it was considered that the CHD problem resulted from ingesting too much cholesterol found only in animal foods. Feeding cholesterol to guinea pigs, and to other herbivores that did not intake it in their normal diet, had been found to result in increased levels of serum cholesterol and in the formation of plaques. However, as outlined by Carpenter (2003d), human studies showed that the feeding of different types of fat did not affect serum cholesterol levels in proportion to the contribution of cholesterol ingested, although the level of dietary cholesterol did have some effect.

During the 1950s, Ancel Keys at the University of Minnesota and collaborators in several different countries studied several aspects of the CHD epidemic in the USA and different parts of Europe (Carpenter, 2003d). Data from Naples showed that the amount of dietary energy from fat was only half of that in the USA (20% vs. 40%) and that the death rate of men aged 30–50 years from degenerative heart disease was only one-third or less. Serum cholesterol levels did not rise in middle age in Naples to the same extent as in the USA or the UK, and it seemed that total fat intake was the determining factor and much more important than either physical activity or degree of **obesity**. In 1954 it was reported by the Rockefeller Foundation in New York that a mix of plant fats resulted in a lower level of serum **cholesterol** than the same diet with fat from animal sources (1.55 vs. 1.96 g l^{-1}).

As documented by Carpenter (2003d), cholesterol is carried in the blood in combination with proteins and in 1950 a research team at UC Berkeley that had devised a method of separating different classes of serum **lipoprotein**s suggested that high levels of the low density (LDL) or beta-fraction might indicate an increased risk of **atherosclerosis**. In 1959 Robert Olson

presented additional evidence for the importance of this fraction. Subsequently in 1977 it was reported from the NIH's large Framingham study in the USA that an analysis of 79 coronary heart disease deaths showed that the greatest risk was among those with the lowest levels of blood cholesterol in the form of HDL or α-lipoproteins. Of those with 44 mg 100 ml^{-1} or less the incidence was 105/1000, and among those with more it was 48/1000. Thus it appeared that HDL was a beneficial form of cholesterol. However, cholesterol in this combination made up only a small proportion of the total, so that earlier studies in which total cholesterol only was measured still had value. A subsequent study found that in a comparison of diets with different fats from plants and land animals, the resulting cholesterol levels were lowest with fats of higher iodine value (i.e. more unsaturated), regardless of origin. It was reported in 1959 that when published national CHD death rates were compared with different dietary characteristics, the closest correlation was with 'the percentage of energy coming from saturated fat'.

However, the lipid/cholesterol theory was not accepted by some scientists, one criticism being the omission of data from France and West Germany, whose populations had low rates of heart disease despite a diet high in saturated fat. Another critic was John Yudkin of Queen Elizabeth College London and a leading human nutritionist in Britain at the time, based on his findings that sugar and carbohydrates – not fat — raised blood levels of triglycerides and increased the risk for heart disease in rodents, chickens, rabbits, pigs and students. Sugar also raised **insulin** levels, linking it directly to type-2 **diabetes**, also **tooth** decay, cavities, obesity, **liver disease** and some forms of cancer. A powerful sugar industry backlash muted Yudkin's criticisms and ensured that the cholesterol theory remained to be accepted as the leading cause of CHD. In defence of the Yudkin theory it should be noted that over the past 200 or so years, the average annual intake of added sugars in the USA has increased from about 1.5 kg to over 70 kg (DiNicolantonio and Okeefe, 2017). These authors point out that sugar is even more rewarding than cocaine in animal studies, and

in humans added sugar is arguably the most widely consumed addictive substance around the world. According to their review, a diet high in added sugars for just a few weeks has been found to produce numerous abnormalities found in patients with CHD, including elevated insulin levels and insulin resistance. More importantly, a diet low in added sugars and refined carbohydrates has been found to reverse all of these metabolic defects. They concluded that there is compelling evidence that the overconsumption of added sugars (high-**fructose** corn syrup and **sucrose**) is a principal driver of CHD.

Genetic influences in CHD incidence have been studied by comparing the health records of emigrants with those of people who had not emigrated, in order to eliminate possible racial differences in susceptibility. In one study it was found that Japanese men who had migrated to California and had at least partially Americanized their diet showed approximately three times the low incidence of CHD of a corresponding population group in Japan (Carpenter, 2003d).

A 1977 US Senate committee report 'Dietary Goals for the United States' recommended low-fat, low-cholesterol diets for the American public. However, this was not without controversy and in 1980 the US National Academy of Sciences Food and Nutrition Board reviewed the data and concluded that insufficient evidence existed to limit total fat, saturated fat and dietary cholesterol for the general population.

The findings described above resulted in a recommendation in several countries for the public to adopt diets such as the '**Mediterranean diet**' with an increased intake of fruit, vegetables, whole grains, legumes, nuts and seeds, moderate amounts of dairy products, moderate amounts of red wine, low to moderate amounts of fish and poultry, and low amounts of red meat, with **olive oil** as the principal source of fat. One aspect of such diets that was not understood by 1985 was whether the Mediterranean-type diets were 'protective or simply nontoxic' (Carpenter, 2003d), also whether the more affluent diets were worsened by the presence of ***trans* fatty acid**s from hydrogenated

oils or a lack of **antioxidant**s from leafy vegetables.

The complexity of the problem was later exemplified in a review of Milanlouei *et al*. (2020) listing 16 food items and 37 nutrients showing statistically significant association with CHD incidence. Research in this area continues, in an attempt to clarify the exact role of dietary factors on the incidence of cardiovascular disease. This probably explains why agencies such as the American Heart Association and the American College of Cardiology have opted not to issue explicit guidelines on dietary cholesterol (Carson *et al*., 2020). The view of these agencies is that meta-analyses of intervention studies differ in their findings and most associate intakes of cholesterol that exceed current average levels with elevated total or low-density **lipoprotein cholesterol** (LDL) concentrations. Their recommendation is therefore that dietary guidance should focus on healthy dietary patterns (e.g. Mediterranean-style and DASH (Dietary Approaches to Stop **Hypertension**)-style diets) that are inherently relatively low in cholesterol. These patterns emphasize fruit, vegetables, whole grains, low-fat or fat-free dairy products, lean **protein source**s, nuts, seeds and liquid vegetable oils.

Dietary changes of this type also promoted research interest into **dietary fibre**, prebiotics and **probiotic**s in relation to human health (including obesity and type 2 diabetes) and the health and productivity of food-producing animals. As documented by Carpenter (2003d), evidence strengthened showing that communities consuming a Western-type diet were more subject to several non-infective adult diseases. It was also observed that, within Western communities, **vegetarian**s had a lower risk of IHD (ischaemic heart disease) than others, but it was uncertain whether the advantage could be attributed to their higher fruit and vegetable (and thus fibre) intakes or the lower intakes of **animal fat**. Although dietary fibre continued to be valued for its laxative action, it seemed to remain unproven that the lack of it was the specific factor directly responsible for the high incidence of bowel cancer in Western populations. Also, in South Africa it was noted that Africans who had moved to townships and adopted a more

Western diet of lower fibre content continued to have a very low incidence of **colon** cancer.

Another aspect of the affluent diet that was researched during the post-war period related to a connection between diet restriction and lifespan, especially since the rate of obesity and associated measures of ill-health began to increase dramatically. Much of the research in the 20th century was concentrated on promoting maximum growth rates in young food-producing animals. However, Clive McCay and colleagues at Cornell University had reported in 1935 that by placing rats on a very low-calorie diet their lifespan could be extended from three years to four, confirming previous findings. However (as documented by Carpenter 2003d), they also had to report that when the heating failed in the animal room it was only the skinny ones that succumbed. One aspect of the research carried out by McKay *et al*. was the uniqueness of its design, in that retarded growth was achieved through a reduction of calories only. This avoided the complication of interpreting the results of experiments involving a total reduction in food intake and reductions in the intake of a range of nutrients. By 1945 the findings had been confirmed by other researchers and their possible application to humans was being considered. In view of the difficulties associated with a reduction in the caloric intake in humans, Carlson and Hoelzel (1946) suggested that a more realistic method of calorie reduction would be intermittent fasting. The hypothesis was tested in rats using various feeding:food deprivation ratios and was found to be beneficial in terms of an extended lifespan and a reduced incidence of spontaneous tumours compared with rats fed daily. The practice of intermittent fasting has been adopted by some human populations. Based on subsequent research, it can be concluded that the health benefits of maintained caloric restriction resulting in lifespan extension are well established in many short-lived species, but that the effects in humans and other primates remain controversial.

The world protein problem

In contrast to the relative affluence in Western societies, the situation was quite different in some African countries with

recurring food shortages being the norm. Initially the view of global GM agencies such as FAO was that 'deficiency of protein in the diet is the most serious and widespread problem in the world' (Carpenter, 2003d). This conclusion was based on the finding that a serious disease, called 'kwashiorkor' in West Africa and recognized by flaky dermatitis, hair changes, oedema and apathy, was also common among 1–4-year-old children in other parts of the developing world. It was found to respond to concentrated high-protein nutritional supplements such as skimmed milk powder. Kwashiorkor was also characterized by liver damage and, because **cirrhosis** of the liver was common among adults in Africa, it was initially suspected that the African diet remained protein-deficient throughout life, and that the same might be true throughout the developing world. Milk and milk powder were expensive and in short supply, and it was urged that substitutes needed to be developed. In 1968 the United Nations published a paper entitled 'International Action to Avert the Impending Protein Crisis'. By then, several projects had been set up, with substantial funding (some from governments and foundations), to develop processes and machinery in advanced countries for the preparation of stable, solvent-extracted high-protein powders from fish (fish **protein concentrate** (FPC)) and other materials. This was encouraged by several international conferences, even though the original idea had been to devise new crops or simple methods of food processing that could be adopted in underdeveloped villages. As Carpenter (2003d) concluded, this is an episode in history that nutritional scientists would probably like to forget, but that a lesson of history is to allow us to learn from our mistakes and not to repeat them. It was brought to an end by the realization that most kwashiorkor patients had been receiving diets that were as deficient in energy as they were in protein, and too bulky for youngsters to ingest in sufficient amounts. It was especially difficult to improve diets based on roots such as **cassava** that are very bulky as well as being low in protein. The general need was to provide more concentrated foods and correct **electrolyte** deficiencies rather than concentrate just on protein.

Intensification of animal production systems

Until the 1950s, food-producing livestock and poultry in developed countries were raised by fairly traditional methods that generally involved keeping animals outdoors, at least for part of the production cycle. After World War II intensive systems began to be introduced and became predominant in developed countries for poultry and pigs that were largely fed on grain and other concentrated feed. Later it was reported that inadequate diets and conditions that were too intensive caused stereotypic behaviours in pigs (**bar biting**) and chickens (**feather pecking**). **Free range** systems were developed partly in response to this, to provide chickens with the opportunity for more normal behaviour. The shift towards confinement was much less pronounced for ruminant animals raised mainly on pasture and forage. An accompanying change to intensification of poultry and pig farms was a reduction in the number of smaller farms and an increase in average farm size, assisted by the introduction of automated systems of housing, feeding, watering and manure removal which allowed a reduction in labour requirement.

An example of the extent of this change was reported by Gilbert *et al*. (2015); between 1960 and 2010 the annual meat output per animal increased from 1.7 to 4.0 kg per bird for chickens, and from 60.9 to 111.2 kg per head for pigs, resulting in the global production of chicken and **pig meat** increasing by factors of 11.5 and 4.3, respectively. Over the same period, the human population rose by a lower factor of 2.3, from 3.0 to 6.9 billion. This massive growth in chicken and pig meat production was attributed largely to intensifying production through increasing animal densities, constructing larger production units, increasing efficiency of the processing infrastructure, using more concentrated feeds, increasing mechanization and the widespread use of pharmaceutical products such as antimicrobials and vaccination to control diseases. The growth was accompanied by the development of a network of feed-manufacturing mills to provide the feed mixes no longer being capable of being produced on-farm.

However, in the latter part of the 20th century several

scientists, members of the veterinary profession and members of the general public began to raise concerns about the **welfare** of the animals under intensive conditions. It led to changes (some voluntary and some mandatory) to improve animal welfare on farms, leading to the introduction of animal production systems that allowed the animals to express more of their natural behaviours. This included allowing the animals to have access to outdoor pastures and the expansion of organic-based systems of production. It also involved a change in the feeding of food-producing livestock, to allow for their increased **energy expenditure**s on pasture and exposure to outdoor conditions in relation to animal health, an increasing interest in the composition and quality of meat and eggs produced under pasture-based systems, and an environmental interest in the contribution of production systems to nitrogen and phosphorus pollution and greenhouse **gas production**. The importance of good nutrition in ensuring an adequate standard of welfare for farm animals was outlined by Phillips (2016).

An adverse effect resulting from the use of antimicrobials to control diseases and improve the productivity of food-producing animals in confinement housing was an increase in antimicrobial resistance (AMR) to the same antimicrobial when used to treat diseases in humans. As a result, many countries in the 1990s began to curtail or ban their routine use on farms and required veterinary prescriptions for their use, which resulted in a decrease in usage on-farm, at least in Europe. According to a 2021 report published jointly by the European Food Safety Authority (EFSA), the European Medicines Agency (EMA) and the European Centre for Disease Prevention and Control (ECDC), reduction in the use of antibiotics decreased over the period 2016–2018 and was now lower in food-producing animals than in humans. For instance, use of a class of antibiotics termed polymyxins, which includes colistin, nearly halved between 2016 and 2018 in food-producing animals, a positive development since polymyxins are also used in hospitals to treat patients infected with multidrug-resistant bacteria. The report showed that the use of carbapenems, 3rd- and 4th-generation

cephalosporins and quinolones in humans is associated with resistance to these antibiotics in *E. coli* infections in humans. Similar associations were found for food-producing animals. The report also identified links between antimicrobial consumption in animals and AMR in bacteria from food-producing animals, which in turn was associated with AMR in bacteria from humans. The ban on routine use of antimicrobials for use with food-producing animal resulted in an active area of research worldwide aimed at finding suitable alternative strategies. Modulating the gut microflora in livestock by the use of **probiotic**s, prebiotics, synbiotics, phage therapy and enzymes has been shown to be an effective alternative strategy to reduce infections in poultry and pigs, combined with vaccination and dietary and husbandry measures to enhance **immunity**.

Technological developments following World War II

Among important technological developments following World War II was the industrial production of amino acids and enzyme products such as **phytases** as dietary supplements, providing benefits in particular to the nutrition of food-producing animals. Other technical developments having an impact on the nutrition of humans and animals included the feeding of food-producing animals to provide nutritionally enhanced meat and eggs (for example, with increased PUFA content) and the industrial production of novel foods such as insect products and cell-based meat.

During the latter half of the 20th century there were several successful developments in improving crops for animal feeding, using conventional breeding techniques. Canola and **lupin** are notable examples. Canola was developed from industrial rapeseed by plant breeders in Canada during the 1960s, providing a food-grade oil and an improved high-protein meal for animal feeding. Previously rapeseed oil was high in **erucic acid**, which was used as a slip agent, and the meal remaining after oil extraction contained high levels of **glucosinolate**s, sulphur-containing compounds that have a bitter flavour, which reduced the **palatability** of the meal as food or feed and caused thyroid

dysfunction in humans and animals. Canola became the main type of rapeseed grown in North America and since 1991 virtually all rapeseed production in the EU has shifted to rapeseed 00 (double zero), i.e. similar to canola with a low content of erucic acid and a low content of glucosinolates. The development of low-**alkaloid** (sweet) cultivars of lupins in Germany in the 1920s and subsequently in Australia allowed the seed to be used as animal feed. Prior to that time the seed was unsuitable for animal feeding because of a high content of toxic alkaloids.

In the 1980s, Europe, and the UK in particular, suffered one of its worst food crises following the report in 1986 of a new progressive neurological condition in a cow. It was named **bovine spongiform encephalopathy** (BSE) (Doherr, 2003). Other transmissible spongiform encephalopathies (TSE) had been described before the occurrence of BSE, such as scrapie in sheep and goats. The media and an alarmed public named the disease 'mad cow disease'. Further alarm ensued in late 1994 when a number of people in the UK began to show symptoms of a somewhat similar condition, a neuro-degenerative disease similar to Creutzfeldt-Jackob disease (CJD), for which there was no known cure. By 1996 there had been eight reported cases of the condition. CJD is a fatal disorder that occurs naturally in a low percentage of people, though usually only later in life. This new form of the disease was subsequently identified as variant CJD (vCJD). Initially the UK government concluded that there was 'insufficient evidence' to link BSE and vCJD, but in 1996 announced that vCJD was caused by eating BSE-infected meat. The result of that announcement was a sharp fall in the confidence of the safety of beef among UK consumers, a reduction in beef consumption of 18%, and a complete loss of the export market for beef products. By 2019, 232 people worldwide (178 in the UK) were known to have become afflicted with vCJD, and unfortunately all died. In order to control the problem, the main decisions taken in the UK were to ban the inclusion of meat and **bone meal** (abattoir meat **by-product**) in ruminant feed since the infectious agent suspected of being the cause of the disease is found in brain and spinal cord

tissue, and to order the compulsory slaughter and disposal of cattle (over 4 million) suspected of carrying the disease. According to the official enquiry into the problem (Phillips *et al*., 2000), BSE may have originated from a novel source early in the 1970s, possibly a cow or other animal that developed the disease as a consequence of a genetic mutation or that a mutant strain of the scrapie agent was transmitted to one or more cows. The report concluded that the origin of the disease will probably never be known with certainty and that the theory that BSE resulted from changes in meat **rendering** methods has no validity: rendering methods have never been shown to be capable of completely inactivating TSEs.

In retrospect, the BSE outbreak is regarded as one of the worst public policy crises the British government has experienced during the postwar era. It led to the slaughter of 3.3 million cattle as a precautionary measure and estimated economic losses of UK£4–6 billion. In administrative terms, the crisis brought about the dissolution of the Ministry of Agriculture, Fisheries and Food. Apart from a major depressing effect on the whole British economy and a worldwide loss of confidence in the quality and safety of British food, it resulted in a severe economic blow to the farming, meat-processing, meat by-products rendering and feed manufacturing industries and a revision of their operating procedures. A major overhaul of the governmental agencies involved in handling the BSE outbreak (agriculture, food, veterinary, medical) also took place in the UK to better coordinate the handling of food crises. Beef consumption eventually recovered to some extent in the UK, but it is likely that the whole experience led consumers in the UK and several other countries to be attracted to foods perceived to safer, such as organic foods, and to be suspicious of foods derived from **genetically modified (GM) crops** and other organisms. The effect on the nutrition of consumers by a reduction in or an avoidance of beef products is less clear. Reports of BSE in the popular media resulted in a reduction in beef intake by consumers (particularly women) in several European countries as well as the UK. For instance, in Switzerland the proportion of women non-beef eaters was 7.7% in

1993–1995 and rose to 14.6% in 1996 (Morabia *et al.*, 1999). In men, the proportion of non-beef eaters remained constant (5%). There was a sharp increase in the number of women who did not eat liver (+14.7%) and a decrease most markedly in the intake of retinol from 417 to 340 μg per day and smaller decreases in the intake of energy, animal protein, total fat, saturated fatty acids and iron.

As described in the entry for GM foods and food products, a very important technological development in food production was the introduction in 1996 of grain and fruit crops for human and animal feeding that had improved traits such as resistance to viruses, insects, fungi and herbicides by the use of genetic modification (GM). All had been subjected to safety evaluations under special regulatory procedures before being approved for food use. Most of the crops were intended for feeding to food-producing animals, but some, such as cantaloupe, eggplant, plums and papaya, **lucerne** (alfalfa), **pineapple**, **safflower**, squash, **sugarbeet**, sweetcorn (maize), rice (golden) and **tomato**es, one apple cultivar and one animal (salmon), were intended for human consumption, together with a range of microorganisms, such as those used in beer and wine production. Within a few years a controversy arose based on claims from two scientists involved in GM crop research that GM foods were injurious to health, even causing cancer. These claims were spread worldwide by the popular media to an alarmed public, but were later shown to be erroneous and the controversy unfounded. As a result of the controversy not all countries and regions adopted **biotechnology** to improve the quality and yield of food crops, particularly in Europe. According to assessments by leading European scientists, this can be attributed to a policy which discriminates against the cultivation of GM crops (e.g. Masip *et al.*, 2013), based on a stated uncertainty of the technology and the public attitude to GM foods.

In spite of that controversy, since their initial introduction the global area devoted to GM crops increased from 1.7 million hectares in 1996 to over 175 million hectares in 2013. Thus, biotech crops are considered to be the fastest adopted crop technology in

the history of modern agriculture. In 2019, the 24th year of commercialization of biotech crops, 190.4 million hectares of biotech crops were planted by up to 17 million farmers in 29 countries (ISAAA, 2019), a main reason for the expansion being that their cultivation was more profitable. Also, a result of this development in GM technology was that it became more practical to use insulin produced by GM microbes rather than from the **pancreas** of slaughtered pigs, the original source of insulin. Similarly, microbially produced **trypsin** and chymosin came into use as alternatives to harvested trypsin or rennet from animal sources such as pigs and cows; and cheese began to be made mainly with chymosin (the active milk protein-coagulating enzyme in rennet) produced with GM organisms, instead of harvesting the enzyme from calf stomachs. Other examples of GM products that came into use in the 21st century for food and feed use include vitamins, amino acids, food enzymes, functional proteins (e.g. texturants), nutritional proteins, **oligosaccharide**s, flavours and sweeteners. Plant-based burgers containing haem from fermented GM **yeast** to simulate the look and taste of bleeding meat became mainstream.

Based on the findings of regulatory agencies, independent scientists and respected scientific agencies in many countries (including the European Academies Science Advisory Council), a broad scientific consensus developed that all approved foods and feeds derived from GM crops and organisms are as safe to eat as similar foods derived from organisms modified by conventional improvement techniques (Blair and Regenstein, 2020). A declaration by more than 100 Nobel Laureates, together with other scientists, called upon biotech critics to cease and desist opposition to GM crops, and for governments around the world to reject campaigns against biotech crops. In a 2021 report the Council for Agricultural Science and Technology (CAST) of the USA released a report that without GM crops as a part of the global cropping systems and food production, the second of the 17 Sustainable Development Goals of the United Nations to end **hunger**, achieve food security and improved **nutrition** and promote sustainable

agriculture would be compromised. A consistent conclusion from the evidence relating to human health is that much, or all, of the transgenic DNA from GM food products is degraded in the gastrointestinal tract of the human or animal consumer and that none is absorbed actively into the tissues (Blair and Regenstein, 2020). Van Eenennaam and Young (2014) assessed the scientific evidence on the health and productivity over the period 1996–2011 of animals consuming feed containing GM ingredients and the composition of products derived from them, since on a global basis food-producing animals consume 70–90% of the biomass of GM crops. These datasets, representing over 100 billion animals, did not show any unfavorable trends of concern. Also, the researchers found that no study had shown any differences in the nutritional profile of animal products derived from GM-fed animals. Although some consumers expressed concerns about the safety of GM foods, this was attributed largely to the fact that they had not been made aware of the extensive database of favourable findings, a very unfortunate aspect of the introduction of GM foods and food products. The introduction of GM crops has had demonstrable human health benefits (Blair and Regenstein, 2020; Smyth, 2020), attributed to reductions in chemical use, increased crop yields and improved farm profits, resulting, for instance, in an improvement in financial well-being and a reduction in suicides among Indian cotton farmers. Grain quality has also been improved and, importantly, dangerous mould and **mycotoxin** contamination decreased as a result of prevention of insect damage to crops. As outlined by Smyth (2020), small landholder farmers in developing countries gain most of the human health benefits, because they generally lack the mechanized systems of **pesticide** application and the necessary protective clothing used in developed countries.

As the journal *Nature Biotechnology* (Anonymous, 2013) stated in an editorial:

> Three decades after transgenes were first introduced into plants, why do so many consumers remain so negative about genetically modified (GM) food? … It does not matter that no adverse health effects have been recorded from eating them. Nor does it matter that august agencies, such as the World Health Organization, the US National Academy of Sciences, the European Commission or the American Medical Association, have come out with ringing endorsements of their safety. The fact is, negative attitudes remain entrenched and widespread. And changing them will require a concerted and long-term effort to

develop GM foods that clearly provide convincing benefits to consumers and something that seed companies have conspicuously failed to do over the past decade.'

In its analysis, the editorial outlined various factors that have contributed to the situation. One is that reports claiming negative effects on health are seized upon by anti-GM activists 'no matter how flimsy the evidence or flawed the study design' and that 'All too often, an uncritical and sensationalist media leaps upon negative findings, continuing the cycle of scares, urban myths, and downright mistruths about GM food, all of which serve to stoke consumer paranoia.' The editorial found also that the public mistrusts most mainstream sources of data on GM foods, including large corporations, regulators, governments and even scientists. In addition, European regulators have deepened the existing prejudices 'by creating a regulatory system that singles out GM products as sufficiently threatening to merit special attention'.

As a result of the controversy regarding GM foods and food products, several countries introduced special **labelling** requirements, since no internationally-agreed policy had been agreed.

Conclusions

Much has been learned of nutritional science in the period from the late 18th century to the present day. Initially little was known of how food was utilized in the bodies of humans or farm livestock and what constituted an appropriate diet. According to the published record the initial experiments on nutrition were related mainly to determining the main constituents of diets and their function in the nutrition of humans and animals. Another main avenue of research was in studying the role of diet in relation to diseases that could not be cured or prevented by prevailing medical treatments. These two main avenues of research led to the identification of what are regarded as all of the essential nutrients required by humans, as well as food-producing and companion animals, and a better understanding of what constitutes an appropriate diet for these species. An accompanying measure by some governments was the fortification of certain foods with important nutrients to ensure their adequacy in the diets of

vulnerable populations.

An initial aim in many parts of the world was to provide sufficient food for expanding populations, especially with the growth of cities and the need to transport food from its source of production. That aim persisted well into the 20th century but after World War II it changed in Western countries when it became clear that a food-insufficiency situation had changed to a food-surfeit situation, with accompanying health problems. Although food insufficiency remains a problem in some developing countries, the food-surfeit situation led to a reappraisal of the optimal diets for humans and to the role of nutrition in promoting good health.

In food-producing animals the initial aim was to maximize productivity. Later that changed to developing nutritional strategies that optimized the quality of the food products for human consumption, and subsequently to minimizing environmental pollution from the wastes produced on-farm (particularly N and P).

A necessary development in many countries was the introduction of food safety measures to control the levels of microbial, mycotoxin and chemical residues in foods; content of certain vitamins and minerals in foods; possible risks related to the introduction of novel sources of foods for humans and food-producing animals, such as new cultivars of vegetable and fruit crops (GMOs); and food scares such as 'mad cow' disease. One result of these food scares and a realization that the welfare of food-producing livestock was often compromised in some confinement systems was a move to so-called 'organic' systems of food production.

It is clear from the ways in which consumers came to learn about the possible risks related to introduction of these novel foods and to food scares, also the misinformation provided by a scientific minority and the popular media, that in the future consumers deserve to be better informed on the correct facts related to further developments in novel food production. One such development is the production of cell-based meat, which seems likely to become an important new food source for an increasing world population.

This type of meat is produced from animal cells using a combination of biotechnology, tissue engineering, molecular biology and synthetic processes. It is projected that about one-third of all meat consumed globally by 2040 may be cultured – resulting in benefits such as reduced greenhouse-gas emissions, antimicrobial usage and in costs compared with conventional **meat production** from farmed poultry, pigs and cattle. (RB)

See also: Human nutrition, essential nutrients

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Hog

In the USA, a synonym for pig; but elsewhere in the English-speaking world the term refers only to a castrated male pig. Also refers to a yearling sheep (but more usually hogg or **hogget**). (MFF)

Hogget

A yearling sheep not yet shorn (sometimes hog or hogg). (MFF)

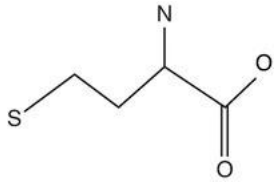
Homeostasis

The maintenance of a steady state in the cellular environment of an organism. It may require a coordinated physiological response

involving the brain, nerves, heart, lungs, kidneys and spleen. Take the example of the buffering capacity of the **body fluid**s: this requires coordination of changes in urinary excretion by the kidney and altered respiratory rates by the lungs to adjust excess acid or alkali. At a cellular level homeostasis requires control of individual steps in uptake, transport and **enzyme** activities such that components are altered to maintain cellular concentration gradients and **substrate** fluxes so that a physiological steady state can be maintained. (NJB)

Homocysteine

A **sulphur**-containing amino acid ($HS{\cdot}CH_2{\cdot}CH_2{\cdot}CH{\cdot}NH_2{\cdot}COOH$, molecular weight 135.2) not found in protein. It is synthesized as an intermediate in the *trans*-sulphuration pathway of **methionine** catabolism. The compound can exist in either reduced (homocysteine) or oxidized (homocystine) form, and some tissue homocysteine may be bound and some free. About half of the homocysteine formed in **metabolism** is methylated back to methionine, using either **betaine** or **5-methyltetrahydrofolate** as a methyl donor. The remaining homocysteine reacts with **serine** to form cystathionine, and this compound is subsequently degraded to α-ketobutyrate and **cysteine**. This is the *trans*-sulphuration pathway of cysteine synthesis. High levels of plasma homocysteine are thought to be a risk factor in cardiovascular disease in humans. (DHB)



See also: Non-protein amino acids

Homocystine:

see Homocysteine

Honey bees, nutrition

Honey bees for the most part obtain their nutrients from natural resources: nectar from flowers, extrafloral nectaries, or insect secretions; pollen from flowers, water from the environment.



Honey bees get most of their nutrients from flowers and other natural sources. Photo courtesy of Lucas Zallio. Licensed under CC BY 2.0.

When there is a dearth of supply from these sources, beekeepers provide **sugar** syrup or pollen to bee colonies. Sugar is presented to bees in a 50% syrup in the springtime and this foodstuff serves as the main **energy source**, while stimulating the queen to lay **eggs** because it simulates a nectar flow. In the autumn, if all honey is removed or if there is not enough honey for wintering (for example, in Michigan about 35 kg of honey is required per colony for it to survive the long winter), it is recommended to use 67% sugar syrup. This higher concentration reduces the work that the bees have to do, because they have to reduce the water content down to about 18% before they can seal the honey cells with wax (capping). For small-scale operations, beekeepers can 'trap' pollen by using a piece of metal or plastic with holes of around 6 mesh in front of the hive entrance, a method that allows foragers to enter the hive but scrapes off the pollen pellets on their hind legs. Pollen can also be frozen and fed back to colonies during a dearth of natural supply (for example, in Michigan, this commonly occurs around August/September). For large-scale beekeepers, this will not be possible because of the quantities required and so pollen substitutes are used. There are currently many types of pollen substitutes available in the US

market, including Bee-Pro (sold by Mann Lake), Megabee (Pierco), Ultra Bee (Pierco) and AP23 (Dadant). However, none of the pollen substitutes can truly replace the natural pollen collected by honey bees. Pollen substitutes should have adequate protein content, be attractive to honey bees (ensuring that they will readily consume them) and also should contain a high amount of **fat**. Substitutes on the market currently tend not to have as high a ratio of fat to protein (1.25:1.00, g/g) as is present in flowers and insect secretions.

Important nutrients for bees are: water; carbohydrates; proteins and amino acids; lipids; minerals; and vitamins.

Water

Water is an essential nutrient for honey bees. Water is used to dilute honey so that this food can be fed to larvae during active brood rearing (raising of new bees from larvae and pupae), or used to reduce the hive temperature via evaporative cooling. In the winter, metabolic water is available to the bee cluster. In the summer, beekeepers are recommended to provide a clean water source with 1% **salt** so that bees do not visit swimming pools for water.

Carbohydrates

Carbohydrates provide **energy** for honey bees. Honey bees are unusual in that they cannot convert **glycogen** or fat into energy in a short time period. Therefore, foragers without food in their honey crop will die within 2–6 h. The natural diet of honey bees is honey, which consists of mainly **glucose** and **fructose**. The honey is formed from **sucrose**, the main type of **sugar** in plants. Sucrose and high-fructose **corn** syrup have both been widely used to as **supplement**al feeding for honey bees. However, recent studies suggest that honey activates various gene-expression pathways that might be more beneficial to honey bees. The main concern of using either high-fructose corn syrup or old honey to feed bees is the possible presence of a high amount of hydroxymethylfurfural (5-HMF), which is toxic to both honey bees and humans. HMF is formed in honey and occurs in high-fructose corn syrup (HFCS) at elevated temperatures (during storage or transportation) due to the

acid-catalysed **dehydration** of **hexose** sugars. HMF above 30 ppm (parts per million) is toxic to honey bees. Stachyos (found in **soybean**s) is also toxic to honey bees. Honey bees cannot digest **starch**. It probably causes no harm to them in the summer; but, during the winter, starch will cause problems in cold areas because healthy honey bees can hold their waste for about 3 months. Starch in the diet can induce more frequent defecation, which is not possible in cold areas. Other sugars that are known to be toxic to honey bees include **arabinose**, **mannose**, **rhamnose** and **xylose**.

Proteins and amino acids

Honey bees need the same ten nutritionally essential amino acids as other animals: **arginine**, **histidine**, **isoleucine**, **leucine**, **lysine**, **methionine**, **phenylalanine**, threonine, **tryptophan** and **valine**. The ideal pollen for honey bees would be high in **crude protein** and should have the correct proportion of these ten amino acids. Little is known about dietary requirements of honey bees for the other ten proteinogenic amino acids that are synthesized *de novo* in the body. Different plant pollens have varying ability to enhance honey bee longevity in cages. Pollens that are harmful to bees (decreasing their lifespan) include ragweeds *(Ambrosia* spp.), a rust spore (*Uromyces* spp.), cattails (*Typha* spp.) and Mexican poppy (*Kallstroemia grandiflora*). Those that slightly improve worker longevity include turpentine bush (*Haplopappus laricifolius*), desert broom (*Baccharis sarothroides*) and dandelion (*Taraxacum* spp.). The best pollens are those from Mormon **tea** (*Ephedra* spp.), mesquite (*Prosopis* spp.), blackberry (*Rubus* spp.), rapeseed/canola (*Brassica napus*), almond (*Prunus amygdalus*) and cottonwood (*Populus* spp.). However, mixed bee-collected pollen is always as good as, or outperforms, pollen from a single plant in either cage or field studies, perhaps because of a better amino acid balance or due to more balanced ratios of **fatty acid**s, as well as an adequate supply of minerals and vitamins.

Lipids

A **sterol**, 24-methylene **cholesterol**, is common in pollen and is

the major sterol source for honey bees. Nearly all insects need to obtain sterols from their diet, because they are unable to synthesize them. Sterol is the precursor for important **hormone**s such as moulting hormone, which regulates growth and is required at the time of each moult. It is not clear what other **lipids** are required by honey bees, but most likely normal consumption of pollen meets all the lipid requirements. Pollen with low fat content is less likely to be consumed by honey bees, but can be made more attractive to bees with the addition of lipids.

Minerals

The **mineral** requirements of honey bees are poorly understood. High amounts of **potassium**, phosphate and **magnesium** are required by all other insects, and so presumably by honey bees as well. Excessive levels of **sodium**, as **sodium chloride**, and **calcium** have been shown to be toxic to honey bees. Again, all the required minerals can be obtained from pollen, although nectar also contains minerals. Dark honey contains higher levels of minerals. The optimal **ash** concentration for maximum brood rearing seems to be at 0.5–1%. Pollen with more than 2% ash inhibits brood production.

Vitamins

Nurse bees are thought to need the following **B-complex vitamins** for brood rearing: **thiamine**, **riboflavin**, nicotinamide, **pyridoxine**, **pantothenic acid**, folic acid and **biotin**. **Ascorbic acid** (**vitamin C**) also appears to be nutritionally essential for brood rearing. Like sterols and other lipids, the needs of a honey bee colony for vitamins are satisfied if either pollen stores are abundant in the hive or fresh pollen is being brought into the colony. It is not known whether microorganisms naturally present in the alimentary canal of bees may play a role in providing vitamins and other essential substances. (ZH)

Further reading

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Hooves

Hoof disorders with a nutritional aetiology include **laminitis** in horses, and laminitis, sole **ulcer** and white line disease in cattle (penetration of the junction of the wall and the sole by dirt or other small particles). Laminitis in horses is most common in overweight ponies on **grass**, but also occurs after systemic illnesses, including severe metritis, **colic**, **cereal** overeating, and overwork on hard ground. The horse shows **lameness** in several feet and is reluctant to move, standing with the legs placed forward. There is heat and pulsation in the feet and the horse may **sweat**. Treatment is contentious, but non-steroidal anti-inflammatory drugs (NSAIDs) are widely used, with removal of the original cause. Corticosteroids are regarded as harmful. Acute laminitis is rare in cattle, but can follow excess feeding of starchy feeds, with limited intake of fibre. Treatment is usually administration of NSAIDs. Sub-acute laminitis in cattle is said to be common in dairy cows fed large amounts of concentrates and living in uncomfortable cubicles so that lying times are reduced. It is thought to be a predisposing factor in the aetiology of sole ulcers and white line disease. Sole ulcers are the most common foot lesion in dairy cows in some surveys, followed by white line disease. Causative factors may include excessive starchy or high-protein **concentrate**s and feeding grass **silage** with low dry-matter concentration. The strength of hooves in pigs and horses is improved by a high concentration of **biotin** in the diet; evidence for a similar effect in ruminants is less clear.

(WRW)

See also: Foot diseases

Hormone

A compound produced by one tissue that is released from the organ into the **blood** and travels to another organ where, after

binding to a specific receptor (**binding protein**), it initiates a chain of events that alters some aspect of cell function. An example is the action of **insulin** in stimulating **glucose** uptake by **skeletal muscle**. Hormones fall into two general classes: **lipid**-soluble, such as steroid hormones (e.g. **glucocorticoids**); and water-soluble, such as proteins, peptides and **amino acid** derivatives. In general, steroid hormones regulate sexual development and function (**oestrogen**, testosterone), **electrolyte** balance (**aldosterone**) and stress responses (glucocorticoids). Polypeptide hormones regulate a multitude of cellular functions, including gastrointestinal function, **metabolism** and cell growth. Hormones may act on the same cell that secretes the hormone (autocrine), on nearby cells (paracrine) or on cells in a distant organ (endocrine). (RSE; GG)

See also: Epinephrine; Gastrin; Gastrointestinal hormones; Glucagon; Gonadotrophin; Gonadotrophin-releasing hormone; Insulin-like growth factor; Motilin; Nor-epinephrine; Pancreatic hormones; Plant oestrogens; Parathyroid; Progesterone; Prolactin; Thyroid; Vasoactive intestinal polypeptide; and individual hormones.

Horse and donkey meat, effects of nutrition

Horse and donkey **meat composition** and characteristics can be influenced by different aspects such as age at slaughter, sex, breed and the **muscle** or cut considered. All things being equal, nutrition represents an important parameter able to affect horse and donkey **meat production** capacity and its **chemical composition**. However, few papers have been published focusing on feeding strategies and their effect on horse and donkey meat.

Carcass features

Currently, there is a paucity of literature which reports results regarding nutrition effects on **carcass** characteristics and **meat yield** of horses or donkeys. In a study of Italian heavy draught horses (De Palo *et al*., 2014), it was observed that a higher nutritive level (from 150% to 200%) did not affect the **dressing percentage** at slaughter, but the weight of the forequarter was

proportionally increased. Moreover, young and growing Italian heavy draught horses (11 months old) fed with the lower nutritive level showed a higher incidence of lean and a lower incidence of **fat**. It is expected that younger foals will convert more **energy** into muscle, compared with older horses, whereas older horses will tend to convert more energy into **adipose tissue**.

Chemical composition

The chemical composition of horse meat exhibits great variability, probably due to the differences in breed, age at slaughter and muscles investigated. However, the feeding system can also affect these parameters. Horsemeat has very low levels of intramuscular fat (IMF), ranging from 0.15 g 100 g^{-1} of meat to over 6 g 100 g^{-1} of meat, and this reflects the pattern of fat deposition which in horses is predominantly observed in the subcutaneous and visceral areas and not in the intramuscular depot (Fig. 1). However, increased energy supply in horses has been reported to increase the IMF concentration by up to 400% (Franco *et al*., 2011, 2013). Similarly in donkeys it has been shown that artificial **suckling** results in a greater **energy intake**, which increases the IMF concentration in the meat for animals slaughtered at 12 months of age (Fig. 1), although this difference did not persist to slaughter at 18 months of age.

Physicochemical properties

Meat tenderness and colour are the most important characteristics affecting consumers' choice and purchasing habits. These physical characteristics are heavily dependent on ageing time and muscle type; however, few studies have explored dietary effects on these parameters. Warner-Bratzler shear force seems to be affected more by the production system than the diet (Fig. 2). In fact, it has been observed that if animals undertake significant walking this can change the physicochemical structure of their muscles, inducing higher meat shear force and firmness values. In donkeys, dietary effects on shear force have not been reported to date. Myoglobin is one of the major pigments that affect colour, and horse meat is rich in myoglobin. It has been observed that higher energy intake results in lighter and yellower horsemeat (Franco *et al*., 2013),

suggesting that this results from the higher IMF concentration that a finishing diet can induce, although other studies have not found this effect (Tateo *et al*., 2013). Because of the tendency of horses to concentrate adipogenesis in the subcutaneous depot, higher energy intake does not usually correspond to higher IMF content, consequently colorimetric parameters are influenced not only by IMF content but also by its composition and quality. There is no evidence currently that diet impacts directly on the tenderness of horse or donkey meat.

Fatty acid profile

Consumer demand for healthier food fits well with horse and donkey meat as it is characterized by a low fat and **cholesterol** content. Moreover, the **fatty acid** profile is characterized by high proportions of **unsaturated fatty acid**s, particularly of **essential fatty acid**s such as **linoleic acid** and α-**linolenic acid**. The most abundant fatty acids in horse meat are palmitic and **oleic acid**, and together they often account for over 50% of the total fatty acids. Feeding systems impact on horse meat fatty acids profiles (Fig. 3), with one study showing γ-linolenic acid increasing and **lauric acid** decreasing, respectively, as the feeding level increases, but with no effect on the total saturated and unsaturated fatty acid levels (De Palo *et al*., 2013). Other studies have, by contrast, reported that higher energy intake induced modification of the concentration of most of the fatty acids in meat, and in particular led to an increase in the concentration of mono-unsaturated fatty acids (MUFAs) with a decrease of poly-unsaturated fatty acids (PUFAs) (both n-3 and n-6), with no effect on the **saturated fatty acid** (SFA) concentrations (Franco *et al*., 2013; Lorenzo *et al*., 2014; Franco and Lorenzo, 2014; Belaunzaran *et al*., 2018). Overall, the evidence indicates that lower levels of finishing diets lead to a higher n-3 and n-6 concentration in horse meat. In donkeys fed with artificial **milk** the composition of the milk is one of the main factors affecting fatty acid composition, although it only lasts up to 6 months of age. In fact, compared with naturally suckled donkeys, the most abundant fatty acids (palmitic and oleic) decrease and linoleic acid increases in artificially suckled

donkeys (De Palo *et al.*, 2017). (PDP; AM)

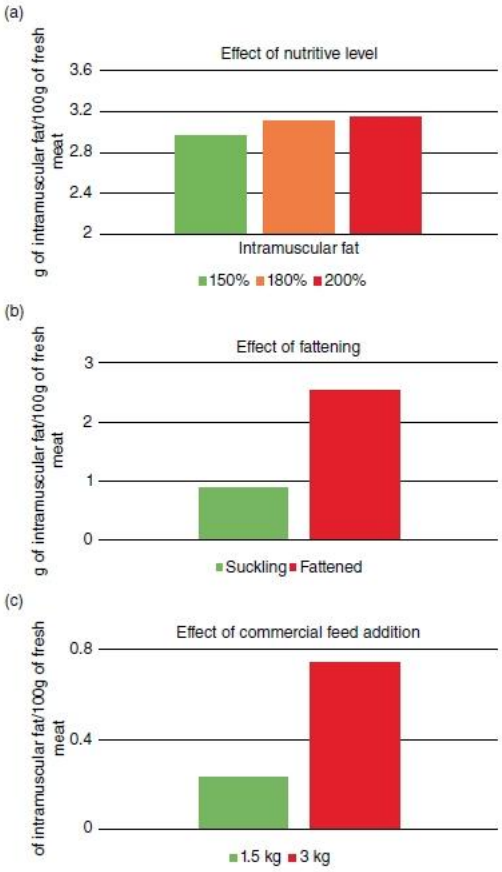


Fig. 1. Effect of different feeding systems/energy intake on horsemeat intramuscular fat (IMF) values. Adapted from: (a) De Palo *et al.*, 2014 ('Effect of different nutritive level on foals slaughtered at 11 months'); (b) Belaunzaran *et al.*, 2018 ('Differences between suckled and fattened foals slaughtered at 12 months'); and (c) Franco and Lorenzo, 2014 ('Effect of different finishing diets (1.5 and 3 kg of commercial feeding) in foals slaughtered at 15 months').

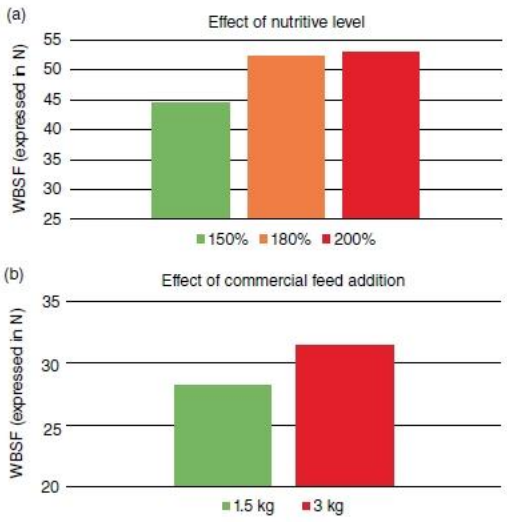


Fig. 2. Effect of different feeding systems/energy intake on horsemeat Warner Bratzler shear force (WBSF) values. Adapted from: (a) De Palo *et al.*, 2014 ('Effect of different nutritive level (150%, 180% and 200% of maintenance requirements) on foals slaughtered at 11 months'); and (b) Franco and Lorenzo, 2014 ('Effect of different finishing diets (1.5 and 3 kg of commercial feeding; crude protein 15.1 %, crude fibre 6.7%, ashes 5.5%, and fat 4.5%) in foals slaughtered at 15 months').

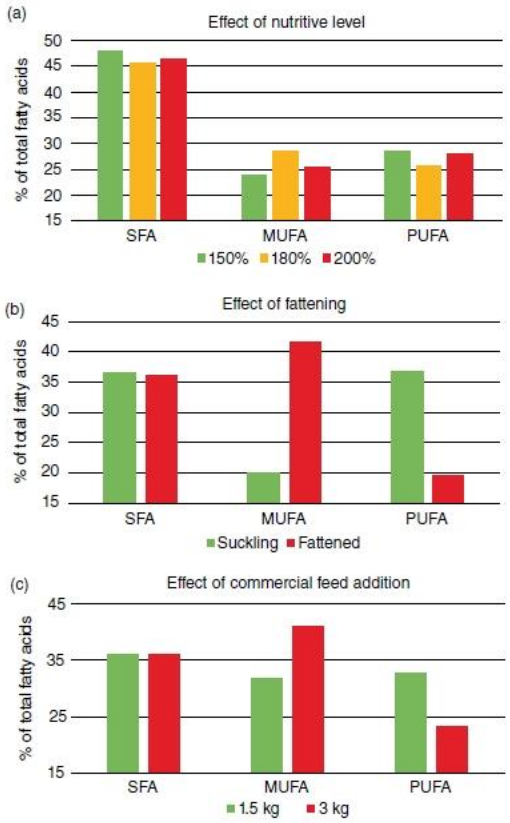


Fig. 3. Effect of different feeding systems/energy intake on horse meat fatty acids groups content. Adapted from: (a) De Palo *et al.*, 2014 ('Effect of different nutritive level on foals slaughtered at 11 months'); (b) Belaunzaran *et al.*, 2018 ('Differences between suckled and fattened foals slaughtered at 12 months'); and (c) Franco and Lorenzo, 2014 ('Effect of different finishing diets (1.5 and 3 kg of commercial feeding; crude protein 15.1 %, crude fibre 6.7%, ashes 5.5%, and fat 4.5%) in foals slaughtered at 15 months'). MUFA, monounsaturated fatty acids; PUFA, polyunsaturated fatty acids; SFA, saturated fatty acids

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Horse feeding

Horses have widely varying individual needs, particularly in respect of specific feeds that are accepted and eaten. Needs are also affected by such characteristics as age and dental health. Thus, horses should be fed as individuals, making allowance for apparent differences in **energy** needs, irrespective of body weight, and differences in performance capability, muscular strength and activity. The nutrient and feed requirements given in Tables 1, 2

and 3 are satisfactory for perhaps 95% of the population of healthy animals of each type and age in an equable environment.



Przewalski's horse grazing. These wild horses are endangered and live in the central Aisan steppe. Photo courtesy of Tambako. Licensed under CC BY-ND 2.0.

The horse is a selective **grazing** and **browsing** non-ruminant **herbivore** that uses soluble and insoluble dietary **carbohydrates** as its primary **energy source**. Pastures grazed exclusively by horses decline in value owing to the spread of ungrazed weed species and the build-up of intestinal parasitic worms. Mixed grazing with ruminants aids the **maintenance** of satisfactory plant species and the containment of a worm burden in the grazing sward. **Forage** preserved as **hay**, **silage** or **haylage** should be free from contamination by mould and by soil, as soil increases, particularly, the risk of **botulism** transmission. Haylage should have a **dry matter** content of at least 50%.

Horses use their lips, tongue and **teeth** in the prehension and ingestion of feed. The adult horse has 40–42 teeth. Forage is sheared off by the 12 incisors and taken in with use of the lips. Grinding by 24–26 molars and premolars reduces feed to a **particle size** suitable for swallowing, when it is mixed with **saliva**. Thus, for horses with sound teeth, large cereal **grain**s such as **barley** and **oats** need not be crushed or ground but small grains, such as **millet** and grain **sorghum**, should be rolled, cracked or coarsely ground before feeding. Rough **rice** (i.e. the

grain before removal of the hull) and dehulled rice are reasonably satisfactory but rice **bran** is unsuitable for feeding on its own. **Maize** grain is frequently very hard and should be cracked before feeding, especially for older horses or those with poor teeth.

Many **by-product**s are suitable for horse feeding, including **wheat** bran, oil-extracted rice bran, dried **sugarbeet** pulp, citrus pulp, **dried grass**, **dried lucerne** (alfalfa), good-quality **fats** and mould-free chopped **carrot**s. Other cut root vegetables can be used with care. **Potato** tubers must not be green. Satisfactory proteinaceous by-products include meals of **soybean**, **sunflower** seed, **cottonseed** (low in **gossypol**), **groundnut** (**aflatoxin**-free), rapeseed (low in goitrogenic **glucosinolate**s), cooked **linseed**, **peas** and field **beans**. All concentrate feeds should be free from mould and pathogenic bacterial contamination.

The adult horse's **stomach** holds only 8–9 l (for a 550 kg Thoroughbred mare). A probable consequence of this is that the grazing horse takes many small feeds distributed throughout a 24 h period. Horses given a large daily allowance of cereal grain should receive this in several small meals, otherwise the stomach contents achieve too high a proportion and amount of dry matter. The **small intestine** of a 450 kg horse is approximately 20–25 m in length. Most of the **digestion** occurs in this organ. The **large intestine** is made up of a blind dilated pouch, the **caecum**, having a volume of 25–35 l in a 500 kg horse, the ventral and dorsal **colon**, with a capacity of approximately 70 l, and the **rectum**. In the large intestine, undigested forage and other feed residues are held for many hours. During this time microbial **fermentation** occurs, with the production and **absorption** principally of **volatile fatty acids**, water and gas.

Whereas the wild horse subsists on leafy browsed and grazed forage, the higher **energy requirement** and restricted feeding time of the domesticated working horse require that forage is supplemented with more energy-dense feed, such as cereal grain. This may introduce a risk to health, if **starch** in excess of 0.4% of body weight is given at each meal. A large daily allowance of cereals requires that this is divided into three to five meals and that

any increase in daily intake is no more than 200 g daily for a 500 kg horse. An excessive starch intake may lead to gastric ailments and result in sufficient starch reaching the large intestine to cause an explosive fermentation, a rise in L-(+)-**lactic acid** content of the lumen of the caecum and ventral colon, with the risk of metabolic acidosis.

Water that does not come from piped mains should be demonstrably free from pathogenic microbial and chemical pollution before being supplied to horses. It is good husbandry to provide a source of safe drinking water for all horses. Nevertheless, horses that are maintained entirely on high-quality pastures in temperate latitudes can subsist without a supply of free water, unless they are lactating or heavily worked, or the ambient daylight **temperature** persists above 25–30°C. For the maintenance of an adult horse in an equable environment, the total water requirement is approximately 2 l kg^{-1} dry matter intake. Horses that are managed on air-dry concentrates, or are lactating or are worked in tropical and subtropical regions should preferably have *ad libitum* access to water. (Asses can survive without a source of free water for long periods.) Heavily worked horses should be offered water frequently during hours of work to avoid excessive intakes at any one time.

Horses have a metabolic requirement for all the recognized vitamins and minerals. If adult horses receive a diet of cereal grain and high-quality forage, adequate quantities of **ascorbic acid** are synthesized in the tissues and adequate amounts of the other **water-soluble vitamins** (apart from **biotin** and possibly **thiamine**), as well as **vitamin K**, are synthesized by the gut microflora and are absorbed. Thus, the dietary requirements are for vitamins A, D and E, biotin and possibly thiamine.

Cereals and forage for horses should be produced under conditions of good husbandry, harvested without microbial and other damage, stored soundly and be no more than 2–3 years old. If horses are to subsist on root vegetables and poor-quality forage, other vitamins will be needed in the diet for optimum performance.

Young foals need a dietary source of cyanocobalamin (B_{12}), normally obtained from the milk of their dam, and early-weaned foals should be given a supplementary source of all the B vitamins. **Vitamin A supplementation** is necessary for all horses if the forage contains insufficient amounts of β-carotene. The horse converts the mixed carotenes of grass and clover to vitamin A relatively inefficiently (approximately 40 μg carotene μg^{-1} vitamin A produced). **Vitamin D_2** or D_3 supplementation will be needed if the forage has been artificially dried, or if horses are housed for long periods. Outside the temperate latitudes, or in high temperate latitudes, vitamin D supplementation is necessary. The minerals **calcium** (Ca), **phosphorus** (P), **magnesium** (Mg), **sodium** (Na), **potassium** (K), **chloride** (Cl), **sulphur** (S), **copper** (Cu), **cobalt** (Co), **fluorine** (F), **iodine** (I), **iron** (Fe), **manganese** (Mn), **selenium** (Se), **zinc** (Zn) and probably **silicon** (Si) and **chromium** (Cr) are required in the diet. Horses given tropical forage that contains significant amounts of **oxalates** (more than 5 g total oxalates kg^{-1} with a Ca:oxalate ratio of less than 0.5:1) will require further supplements of Ca in their diet. If mineral problems are suspected, the dietary amounts of digestible Ca and P are the minerals most likely to be in error. Horses that receive at least half the dry matter of their diet as good-quality leafy forage grown in temperate latitudes, with cereal grain, may need no mineral supplementation. An exception to this is where horses are heavily worked, especially in hot weather, when they will require additional **sodium chloride**. In some places soils, forages and other crops contain inadequate copper, selenium or iodine and supplements of these will be required. The soil in a few regions contains toxic amounts of selenium and crops grown on such soils should not be used for horses. Some pasture species absorb certain **heavy metals** (e.g. **cadmium**) through their roots. Such grazing areas and herbage can become harmful.

The daily **digestible energy** (DE, in MJ per day) requirement for **maintenance** can be estimated from Equations 1 and 2. This requirement is directly proportional to body weight and for horses ranging in size from 125 kg to 600 kg the requirement is in

accordance with the relationship (where w is the weight (kg) of the horse):

DE=5.9+0.13 (Equation 1)

For horses exceeding 600 kg body weight, physical activity is generally less and the relationship is:

DE=7.61+0.1602w−0.000063w2(NRC, 1989) (Equation 2)

The energy needs for **growth**, work, etc., are given in Table 1. Dietary protein, Ca and P requirements are given in Table 2 and the dietary requirements for other minerals and the vitamins are given in Table 3. The dietary requirement for protein assumes that the protein is derived from forage of adequate **digestibility**, cereal grain and **protein concentrate** meals of reasonably high **biological value** (BV). With this assumption the BV of the mix should be adequate. If root vegetables are used, with protein concentrates of poorer indispensable **amino acid** balance, the **lysine** and possibly the threonine content of the diet will limit performance. In this situation higher concentrations of dietary protein, or synthetic supplements of lysine-HCl, will be needed for optimum performance. (DLF)

Table 1. Digestible energy (DE) (MJ per day) requirements of horses and ponies for various functions[a].

	Mature weight			
	200 kg	**400 kg**	**500 kg**	**600 kg**
Mature horse maintenance	31.0	56.1	68.6	81.2
Mare				
Last 90 days gestation	35.6	64.9	79.5	94.5
Lactating mare				

	Mature weight			
	200 kg	**400 kg**	**500 kg**	**600 kg**
1st 3 months	64.0	101.2	122.3	141.0
3 months to weaning	51.0	82.4	102.0	120.9
Stallion				
Breeding	38.9	70.3	85.8	101.7
Non-breeding	35.0	62.0	75.0	89.0
Weanling				
6 months old	35.0	57.3	67.4	75.7
Yearling				
12 months old	39.7	68.2	84.1	100.0
Long yearling				
18 months old	37.5	69.0	87.9	104.6
Two-year-old				
Excluding work	33.0	64.0	78.7	98.3
Maintenance plus 1 h moderate work	47.7	90.0	110.1	135.1

[a] The required daily intake (kg) of air-dry feed may be estimated by dividing the DE per day values in this table by the air-dry DE kg^{-1} content

of feed stuffs. Typical values are 7–8 MJ kg^{-1} for a grass and clover hay mixture, 11.5 MJ kg^{-1} for oat grain and 12.8 MJ kg^{-1} for barley grain.

Table 2. Recommended nutrient concentrations in diets with 90% dry matter and 9 MJ DE kg^{-1} for horses and ponies.

	Crude protein (g kg^{-1})	**Ca** (g kg^{-1})	**P**(g kg^{-1})
Mature horses and ponies at maintenance[a]	72	3.2	2.0
Mares, last 90 days of gestation	94	5.5	3.0
Lactating mare, first 3 months	120	5.5	3.0
Lactating mare, 3 months to weaning	100	4.0	2.5
Creep feed	160	8.0	5.5
Foal, 3 months old	160	8.0	5.5
Weanling, 6 months old	135	6.0	4.5
Yearling, 12 months old	115	5.0	3.5
Long yearling, 18 months old	105	4.0	3.0
Two-year-old, light training	95	4.0	3.0

	Crude protein (g kg^{-1})	**Ca** (g kg^{-1})	**P**(g kg^{-1})
Mature horse, light to intense work	95	3.2	2.0

[a] Also for non-breeding stallions. In the breeding season stallions should receive a diet providing 94 g crude protein kg^{-1} feed.

Table 3. Mineral and vitamin requirements of horses and ponies kg^{-1} diet (90% dry matter and 9 MJ DE kg^{-1}).

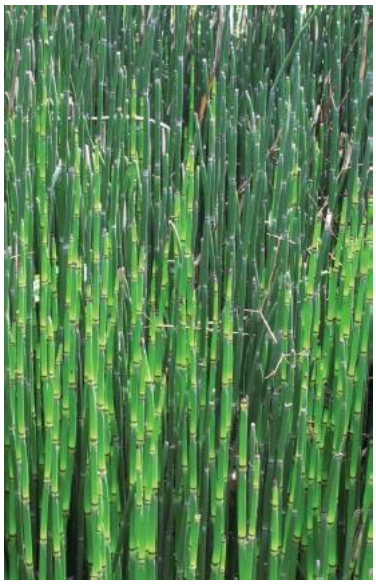
	Mature horse maintenance[a]	**Last 90 days gestation, lactation and growing horse**[b]
Sodium (g)	3.5	3.5
Potassium (g)	4.0	5.0
Magnesium (g)	0.9	1.0
Iron (mg)	40	50
Zinc (mg)	60	80
Manganese (mg)	40	40
Copper (mg)	15	30
Iodine (mg)	0.1	0.2
Selenium (mg)	0.2	0.2
Cholecalciferol, vitamin D_3 (mg)	10 (400 IU)	10 (400 IU)
Retinol, vitamin A (mg)	1.5 (500 IU)	2.0 (666 IU)
D-α-Tocopherol, vitamin E (mg)	30	30
Thiamine (mg)	3.0	3.0

	Mature horse maintenance[a]	Last 90 days gestation, lactation and growing horse[b]
Available biotin (mg)	0.2	0.2

[a]Also for the stallion out of the breeding season.
[b]Also for the stallion in the breeding season.

Horsetail (*Equisetum arvense*)

Plant with horizontal and angular rhizome and stems 50–60 cm tall , of two types: fertile and sterile. It grows in humid areas and the underground stems are up to 1 m deep in the soil. Fertile stems are red, without **chlorophyll**, and have spikes containing spores at the top, which can produce both male and female prothalli. Sterile stems, which have many leaves, possess chlorophyll, and therefore are of a green colour. Horsetail is a rich source of **silica**, at up to 25% of its **dry matter**. Its medicinal use has been little researched, but the historical origin of its use goes back several centuries, used for the treatment of tuberculosis. It has also been reported to be effective in increasing white **blood** cells (Zargari, 1997). The plants contain significant amounts of silicic, oxalic and malic acids, **potassium**, **calcium**, **aluminium**, **manganese**, **magnesium**, **phosphorus**, a **saponin** compound called equisetine, a series of **alkaloid**s, **phenolic compound**s, **tannin** and tri-flavonoids, terpenoids and types of phytosterols. The plant contains significant amounts of dimethyl sulphone, which is found in several plants and in animal tissues. In animals, dimethyl sulphone can be derived from dietary sources, as well as the **catabolism** of **methionine** via the **transamination** pathway in the **liver** and intestinal bacteria.



Horsetail, *Equisetum hyemale*. Photo courtesy of Juuyoh Tanaka. Licensed under CC BY 2.0.

Horsetail plants may be extracted to produce **mineral**-rich pharmaceuticals for the treatment of **kidney disease**, prostate pain, diuretic, wound healing and increasing the elasticity and resistance of the skin. The extracts also have **antioxidant** effects, with anti-cancer, antimicrobial, anti-diabetic, and anti-inflammatory benefits, helping to treat osteoporosis, and strengthening the immune system (Zargari, 1997; Albadri, 2016; Al-Snafi, 2017). Studies on the use of this plant in feeding domestic animals are limited, but there is some evidence that **silica** from the consumption of horsetail plants in **feed formulation** poultry diets leads to the improvement of the calcification process and deposition of bone and **eggshell**. The presence of other bioactive compounds can lead to increased thickness and strength of the eggshell (Tufarelli *et al*., 2021). (AS; BH-G; CJCP; GW)

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Human

Humans (*Homo sapiens*) are members of the primate order in the animal kingdom who are normally omnivorous and highly social. The global population of humans was 7.9 billion in 2021 and has been projected by the United Nations to reach 9.7 billion by 2050. Thus, there are increasing demands for both plant- and animal-sourced foods to feed the world. The qualitative requirements for most nutrients (including proteinogenic **amino acid**s, **fatty acid**s, **glucose**, **minerals**, **lipid**-soluble **vitamins** and a majority of **water-soluble vitamins**) are similar between humans and pigs, but the amounts per kg body weight at comparable developmental stages are much greater in pigs than those in humans. In contrast to piglets, human infants have a limited ability to synthesize **taurine** from cysteine and must be provided with taurine-containing foods (e.g. breast **milk** or **taurine-supplement**ed formulas) to prevent retinal and cardiac damage. Although adult humans can synthesize a nutritionally significant quantity of taurine when their diets contain sufficient **methionine** or **cysteine**, the rates of synthesis are much lower than those in livestock (e.g. pigs, cattle and sheep) and poultry. Children and possibly adults receiving taurine-free long-term parenteral nutrition have a nutritional requirement for **taurine**. Unlike pigs, humans do not form **vitamin C** from **glucose** and, therefore, must consume this vitamin to maintain health, particularly the integrity and function of the **connective tissue**. (GW)

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Human nutrition, digestion

Diets consumed by humans are a mixture of different ingredients (e.g. cereals, pulses, dairy, meat, vegetables and fruit). Each ingredient contains an array of nutrients (e.g. carbohydrates, proteins and lipids) occurring in different ratios, which together provide a specific nutrient matrix for the ingredients. These nutrients are embedded within complex physicochemical structures (the macro-structure). Furthermore, each nutrient within an ingredient has a specific chemical structure. For instance, proteins have different **amino acid** sequences (i.e. primary structures); carbohydrates have different monomeric **sugars** with different glycosidic bonds; and lipids have **fatty acid**s of different chain length and saturation. Moreover, the chemical structure of organic nutrients may be modified when the ingredient is processed (e.g. heated, milled). To determine the nutritional value of a food ingredient (or diet), it is common to analyse the nutrient composition. However, due to the effects of different physical and chemical structures and **antinutritional factor**s (e.g. protease-inhibitors and **saponin**s) that may be present, not all nutrients can be utilized by the body to the same extent.

Nutrients need to be digested and absorbed to be utilized for body functions (e.g. **growth**, **reproduction** and **maintenance**). These processes are well regulated and highly interdependent. In humans, the **digestion** of nutrients starts in the mouth and continues throughout the **gastrointestinal tract** (GIT) in specific locations. For instance, proteins need to be digested in the upper GIT (**stomach** and **small intestine**) to be able to be absorbed as amino acids or di- and tri-peptides in the small intestine; **starch**

polysaccharide digestion starts in the mouth with salivary α-**amylase**, while **non-starch polysaccharide**s appear to be mainly digested in the **ileum** and **large intestine** by microbial **enzymes**. Furthermore, the anatomical differences (mouth to **rectum**) affect the location and degree of nutrient digestion in the GIT. The digestion of nutrients in humans is summarized in the following paragraphs for the main food components (protein, starch, lipids and **dietary fibre**).

The digestion of nutrients starts in the mouth through **particle size** reduction of the meal by **mastication**, except when the meal is provided as a **mash**. The digestion of starch and lipids starts in the mouth with salivary α-amylase and lingual **lipase**, respectively, but this digestion is considered negligible due to the short **retention time**.

The bolus enters the stomach, stimulating the secretion of **hydrochloric acid**, pepsinogen and gastric lipase. The secretion of hydrochloric acid reduces gradually the pH of the **chyme** and it converts pepsinogen to **pepsin** to start the digestion of proteins (pepsinogen is also converted to pepsin by active pepsin). Pepsins are aspartic proteases able to cleave **peptide** bonds between hydrophobic aromatic and large aliphatic amino acids. In the stomach, salivary α-amylase continues to digest starch at least during early gastric digestion when the pH of the stomach chyme is within the range of the enzyme's activity. Lingual and gastric lipases digest lipids at position 3 of the triglycerides (predominantly at short- and **medium-chain fatty acid**s). The period of time that the chyme remains in the stomach is controlled by neuro-hormonal mechanisms, which are affected by several factors (such as meal size, particle size and **chemical composition** of the meal). For instance, it has been shown that dietary fibres and proteins can influence the stomach emptying rate. A negative association between the degree of **hydrolysis** of protein in the stomach and the stomach emptying rate has been shown (i.e. the chyme of meals with poorly digested proteins have a higher stomach retention time). Thus, the digestion of nutrients in the stomach is influenced by both the gradual reduction of the

chyme pH and the stomach emptying rate. As there is limited or no **absorption** of nutrients in the stomach, all of the digested (or enzymatically hydrolysed) nutrients are released into the small intestine.

Postprandially, the nutrients of the chyme entering the small intestine are digested to different degrees, and this plays an important role in affecting the rate of digestion and absorption and location in the small intestine where nutrients continue to be digested. In the duodenal lumen, the chyme mixes with **pancreatic juice** and **bile**. The pancreatic juice contains **bicarbonate**, which increases the pH of the chyme entering the small intestine, and an array of enzymes (e.g. proteases, α-amylase and lipase). The pancreatic proteases (**trypsin**, **chymotrypsin**, **carboxypeptidase**s and **elastase**) and **brush-border** peptidases (**aminopeptidase**s, dipeptidylcarboxypeptidase and dipeptidylaminopeptidase IV) continue to hydrolyse the digested protein entering the small intestine, releasing amino acids, di- and tri-peptides. In the small intestine, the partially digested starch continues to be digested by the pancreatic α-amylase into **dextrin** (**oligosaccharide**s), **maltotriose** (trisaccharide) and/or maltose (**disaccharide**) prior to being hydrolysed into **glucose** by the brush-border enzyme, **maltase**. Other brush-border disaccharidases (e.g. **lactase**, **sucrase**) are also involved in the digestion of other dietary carbohydrates (e.g. **lactose**, **sucrose**). The lipids entering the small intestine (e.g. di- and tri-glycerides) are emulsified with the bile creating smaller fat droplets. This complex helps to increase the surface area to improve the hydrolysis by pancreatic lipase facilitated by co-lipase, which is able to hydrolyse fatty acids at positions 1 and 3 of the triglyceride-releasing fatty acids and monoglycerides. Thus, the building blocks of proteins, starch and lipids released during digestion are absorbed mainly in the small intestine. However, nutrients that are not absorbed in the small intestine enter the large intestine, where digestion continues, but absorption of the digested material appears to be mainly through microbial end-products of **fermentation** (e.g. **short-chain fatty acid**s).

Another important component of the diet is dietary fibre, and there are many types of dietary fibre with different physico-chemical properties. Dietary fibre cannot be hydrolysed by host endogenous enzymes, but is hydrolysed to varying degrees by exogenous enzymes produced by the microbiota residing in the GIT lumen. It has been commonly believed that the fermentation of fibre occurs mainly in the large intestine. However, recent evidence has shown that microbial fermentation of fibre and other nutrients (e.g. proteins and starch) can occur throughout the whole GIT, and in particular in the lower small intestine. Thus, it could be expected that the digestion of nutrients (apart from dietary fibre) throughout the GIT is a result of both mammalian and microbial enzymes. For instance, **glutamine** endoprotease is secreted by salivary microbes. The role of microbial enzymes in assisting in the digestion of foods throughout the GIT has received little investigative attention.

The digestion of nutrients can be enhanced above and beyond normal digestion when exogenous enzymes are either present in an ingredient consumed (e.g. actinidin in green **kiwifruit**) or supplemented (e.g. lipase, **phytase**, protease and **cellulase**) in the diet. The **supplementation** of exogenous enzymes can affect both the rate and extent of digestion of nutrients throughout the GIT. (CAM; PJM)

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Human nutrition, essential nutrients

Humans have requirements for **amino acids**, α-**linolenic acid** and **linoleic acids**, **carbohydrates**, **minerals**, **vitamins** and water. Various amounts of these nutrients are provided from animal- and plant-sourced foods. The essential nutrients for humans are highlighted herein.

Amino acids

Dietary **protein** consists of about 20 amino acids, which are involved in every metabolic process in the body. The amount and proportions of amino acids in foods vary with their sources. The human body can normally synthesize *de novo* **alanine**, **arginine**, **asparagine**, aspartate, **glutamate**, **glutamine**, **glycine**, **proline**, **serine** and **taurine**, but not **cysteine**, **histidine**, **isoleucine**, **leucine**, **lysine**, **methionine**, **phenylalanine**, threonine, **tryptophan**, **tyrosine** and **valine**. In healthy individuals, methionine and phenylalanine are converted into cysteine and tyrosine, respectively. Except for cysteine and tyrosine when methionine and phenylalanine are consumed, the amino acids that are not formed *de novo* must be provided in human diets. In people who cannot convert phenylalanine into tyrosine due to **inborn errors of metabolism**, tyrosine must be included in their diets. Although the amino acids that are synthesized *de novo* may not be needed in the diet to maintain minimum **nitrogen balance**, some of them must be supplied exogenously to maintain normal physiological functions (for example, arginine for spermatogenesis and embryonic survival) and recover from illness (for example, proline for wound healing). In addition, infants, particularly pre-term infants, must ingest taurine to protect retinal cells and heart from damage. Compared with plant-sourced foodstuffs, animal-sourced foodstuffs generally contain higher contents of proteinogenic (protein-creating) amino acids (particularly glycine, lysine, methionine, proline, threonine and tryptophan) on a dry matter (DM) basis. Current evidence suggests that intakes of 1 to 1.2 g high-quality protein kg^{-1} body weight per day can help to reduce **muscle** loss in elderly people.

Since 1993, the **protein digestibility**–corrected amino acid score (PDCAAS), which measures dietary **protein quality**, has

been used in many countries, replacing the **biological value** score. In recent years, there have been proposals by the Food and Agriculture Organization (FAO) to replace the PDCAAS system with a new method of measuring protein quality called the digestible indispensable amino acid score (DIAAS) that is based on the content of truly digestible amino acids in protein. Although it is recommended that humans eat about 30 g of protein at each meal, there is considerable interest in high-protein, low-carbohydrate diets for reducing weight in obese individuals. Animal-sourced foods provide specialized **nitrogen**-containing **antioxidant**s as **taurine**, **creatine**, **carnosine** and anserine. Adequate amounts and proper ratios of all proteinogenic amino acids in diets are crucial for the optimum growth, development and health of humans.

Lipids

Dietary **lipids** primarily comprise saturated, monounsaturated and polyunsaturated **fats**, all of which are found in animal and plant foods, primarily in the form of triglycerides. However, **cholesterol** and many minor dietary lipids such as **phospholipid**s, **sphingolipid**s and gangliosides are also present in animal foods. In an average Western diet, **animal fat** provides about 35% of dietary **energy**. People often focus on **saturated fatty acid**s and cholesterol as the key lipids in human nutrition. However, saturated fatty acids are a family of **fatty acid**s and there is emerging evidence that some of them, such as **palmitic acid** (a 16-carbon fat, high in dairy), have effects on raising low-density **lipoprotein** (LDL)-cholesterol (one of the risk factors for cardiovascular disease), whereas **stearic acid** (an 18-carbon fat, high in pork and beef) does not. This debate will likely continue for a number of years as new science is emerging daily.

Cholesterol is found at very high concentration in **eggs** and some animal foods, but is absent from plants. This lipid can be synthesized from acetyl-CoA in humans. Cholesterol is a component of cell membranes, as well as a precursor for the production of key **hormone**s (e.g. testosterone and **oestrogen**) and **bile** acids (that are needed to digest and absorb fats and **fat-**

soluble vitamins). The amount of cholesterol is tightly regulated in the body of healthy individuals. However, there is a current debate regarding whether high intakes of cholesterol are associated with negative cardiovascular health outcomes. Current evidence suggests that reducing cholesterol intake may help some individuals with high blood cholesterol to reduce their LDL-cholesterol. To date, there is little evidence that dietary cholesterol will cause an increase in LDL-cholesterol in healthy humans.

α-Linolenic acid and linoleic acid are nutritionally **essential fatty acid**s in humans. Docosahexaenoic (DHA) and eicosapentaenoic (EPA) acid are found in **fish** fed **algae** or the diets containing both fatty acids, whereas **arachidonic acid** is abundant in peanut **oil**. These fatty acids form an important part of cell membranes and they are needed for brain development and immune health. DHA and EPA are generally present at low concentrations in plants, with the exception of genetically modified sources. Recently, EPA and DHA have been found in eggs, dairy and meats when animals were fed **fish product**s.

Carbohydrates

Humans have no specific dietary requirement for **glucose**, because it can be synthesized from glucogenic amino acids, **lactate**, **pyruvate** and **glycerol**. The adult brain needs 125 g glucose per day as the exclusive source of energy in fed and post-absorptive states when the concentrations of **ketone** bodies in plasma are low. Consumption of starch from food grains can substantially reduce the need for **gluconeogenesis** in the human body, therefore sparing the use of amino acids for this physiological process and minimizing the production of ammonia (a toxic substance at elevated concentrations in plasma). An adequate intake of **dietary fibre** (25 and 35 g per day for women and men, respectively), which is provided only from plant-sourced foods, is crucial for maintaining intestinal health and reducing risk for **colon** cancer.

Minerals

Humans require seven macro-minerals in their diets (**sodium** (Na), **potassium** (K), chlorine (Cl), **calcium** (Ca), **phosphorus**

(P), **sulphur** (S) and **magnesium** (Mg)), and nine micro-minerals (**iron** (Fe), **copper** (Cu), **cobalt** (Co), **manganese** (Mn), **zinc** (Zn), **iodine** (I), **selenium** (Se), **molybdenum** (Mo), and **fluorine** (F)). **Chromium** (Cr), tin (Sn), **vanadium** (V), **silicon** (Si), **nickel** (Ni), **boron** (B) and bromine (Br) may also be needed for physiological functions in humans but are generally of little practical significance, due to their widespread presence in animal- and plant-sourced foodstuffs. However, Cr deficiency may occur in humans during long periods of *stress*, such as pregnancy, infection, physical trauma and strenuous exercise. Like any other essential nutrients, too much of a nutritionally essential mineral is toxic. There are suggestions that trace amounts of traditionally classified toxic minerals (e.g. **arsenic**, **cadmium** and **lead**) may be essential for plants and rats, but experimental evidence for humans is lacking.

Minerals function as the major structural components of bones and **teeth**, contributors to the mechanical stability of the body, **electrolytes** in the body, osmolytes, modulators of amino acid and **glucose** transport, facilitators of the digestion of foods, regulators of food intake, co-factors or components of **enzymes**, and components of complex organic molecules (for example, iron in **haemoglobin**, cobalt in vitamin B_{12} and iodine in thyroid hormones). Animal-sourced foods generally provide more bioavailable minerals than plant-sourced foods. The major sources of calcium in Western societies are **milk** and dairy products, but most plants contain relatively low content of calcium. The haem form of iron that is found in **meat**, especially red meat, is better absorbed in the **small intestine**, compared with the non-haem iron found in plant foods. Iron deficiency is one of the most prevalent nutrient deficiencies worldwide. Zinc is mainly found in animal foods, particularly oysters.

Vitamins

Humans require **water-soluble vitamins** (thiamin (vitamin B_1), **riboflavin** (vitamin B_2), **niacin** (vitamin B_3), **pantothenic acid** (vitamin B_5), **pyridoxine** (vitamin B_6), **cobalamin** (vitamin B_{12}), **biotin**, **folate** and ascorbate (**vitamin C**)) and lipid-soluble

vitamins (retinol (**vitamin A**), **vitamin D**, **vitamin E** and **vitamin K**). Humans can synthesize vitamin D_3 from the subcutaneous 7-dehydrocholesterol (when exposed to sunlight), vitamin A from β-carotene and **niacin** from **tryptophan**, but cannot form other vitamins. Quasi-vitamins (i.e. vitamin-like compounds) include *p*-aminobenzoic acid, **carnitine**, **choline**, flavonoids, **myo-inositol**, lipoic acid, pyrroloquinoline **quinone** and ubiquinones, and most of them are soluble in water.

Vitamins function as **coenzyme**s for enzymes, co-factors for **blood** clotting and potent **antioxidant**s, as well as the regulators of gene expression and the **intestinal absorption** of **calcium** and phosphate. The amounts of vitamins in foodstuffs vary with their sources. For example, vitamin A is responsible for maintaining good vision, a strong immune system, healthy skin and the integrity of epithelial tissues. Vitamin A itself is only found in animal products, whereas plants contain β-carotene as the precursor of vitamin A. Vegetables, fruit, and milk are excellent sources of vitamin C (an antioxidant) and **folate**, but these two nutrients are limited in meat. Plants also provide β-carotene, carotene-like substances (e.g. **lycopene**, canthaxanthin, **lutein** and zeaxanthin), **tocopherol**s, **tocotrienol**s, lipoic acid, bioflavonoids and ubiquinones, which are all antioxidants.

Vitamin B_{12} is essential for cellular **metabolism**, including amino acid and one-carbon metabolism, and is particularly essential for the synthesis of red blood cells and **myelin** in the nervous system. Most people in Western countries who consume animal products obtain the majority of their vitamin B_{12} from meat, fish, poultry, dairy and eggs, but this vitamin is absent from nearly all plants (although it can be obtained from fermented plants and **algae**). The majority of vitamin D in the Western diet comes from fortified foods such as milk and a few other dairy products, but oily fish (e.g. salmon, sardines, herring, and mackerel), red meat, **liver**, egg yolks and sunlight-dried vegetables are also good sources of this vitamin. Vitamin K_2 **(menaquinone, synthesized by** bacteria**)** *is found* in fermented foods and in **beef**, **liver**, **pork** and **chicken** at high concentrations, whereas plants contain vitamin K_1

(**phylloquinone**). Vitamin K_2 has a greater efficacy in promoting blood clotting than vitamin K_1.

The **B-complex vitamins** are found in both animal- and plant-sourced foodstuffs. Thiamin (vitamin B_1) has an essential role in **energy metabolism** and therefore in the **growth**, development and functioning of humans. **Riboflavin** (vitamin B_2) and niacin (vitamin B_3) are essential for energy metabolism in every cell. Pyridoxine (vitamin B_6) is required for the **metabolism** of amino acids and **pentose phosphate pathway**, and the creation of red blood cells. As the precursor of 4′-phosphoapntetheine (a component of **coenzyme** A and the **prosthetic group** of acyl carrier protein), **pantothenic acid** (vitamin B_5) participates in nutrient oxidation and fatty acid synthesis. Biotin (vitamin B_7) is involved in a wide range of metabolic processes, primarily those related to the utilization of fats, carbohydrates and amino acids. *Choline in the form of* ***phosphatidylcholine*** *is found in the highest amounts in animal foods and is needed for the synthesis of cell membranes, neurotransmitters and bile.*

Water

Water is the most abundant nutrient in the body. The adult human contains up to 60% water. It is required for biochemical reactions, the maintenance of osmo-equilibrium and the production of **saliva**. In addition, as a component of synovial fluid, water plays an important role in lubricating the joints to facilitate muscle locomotion. Water is lost from the body through the urine, faeces, evaporation and the respired air. On average, men and women require about 3.7 and 2.7 l of water per day, respectively, unless the women are pregnant or lactating, in which case daily allowances are increased to 3.0 and 3.8 l. (DP; JE; CJF)

See also: History of nutritional sciences

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Hunger

A craving or urgent need of an animal for food or a specific nutrient. This condition is brought about by a prolonged lack or insufficiency of food. As the opposite of **satiety**, hunger motivates the consumption of food by animals. Changes in gastrointestinal (e.g. osmoreceptors, distension and pressure), hormonal (e.g. **insulin**, **ghrelin** and **cholecystokinin**), neurological (for example, the *vagus nerve* and **hypothalamus** peptides (neuropeptide Y and agouti-related **peptide**)), and metabolic factors (such as reduced **glucose** concentration in the plasma), as well as negative **energy balance** contribute to the sensation of hunger in animals. According to the World Health Organization, globally 821.6 million (or 1 in 9) people went hungry in 2018. (GW)

Hydrochloric acid

An inorganic acid, HCl, which is secreted into the **stomach** from the **parietal cell**s in the gastric glands. The secretion varies with the diet but the HCl concentration in gastric juice is normally about 0.1 M, sufficient to lower the pH of the digesta to less than 3.0. HCl is bactericidal, it denatures proteins and it is essential for the activation of pepsinogen, the secreted inactive precursor of

pepsin. (SB)

Hydrogen

Gaseous hydrogen, H_2, is formed during anaerobic **fermentation** in the **rumen** of ruminants and, to a lesser extent, in the **large intestine** of most animals. Some or most of the hydrogen released by fermentation may be converted to **methane** by methanogenic bacteria. (SB)

Hydrogen cyanide:

see Cyanide

Hydrogen sulphide

An extremely toxic gas (H_2S). It is produced by anaerobic **fermentation** in animal wastes and in intestinal contents from **sulphate**, SO_4^{2-}. It can be produced in the **metabolism** of methanethiol CH_3SH (methyl mercaptan), which is derived from the metabolism of the amino acids, **methionine** and *S*-methylcysteine. (NJB)

Hydrogenated fatsTriacylglycerols, mainly of vegetable origin and rich in **polyunsaturated fatty acid**s, that have undergone chemical hydrogenation to reduce their **iodine** value and increase their melting point. This process is used to produce margarines and can result in the production of *trans* **unsaturated fatty acid**s. Unsaturated **fats** are also hydrogenated by the microflora of the rumen. (JRS)

Hydrogenation:

see Hydrogenated fats

Hydrolases

Enzymes that catalyse hydrolytic cleavage by adding water across C–O, C–N, C–C and other bonds. An example of a C–O hydrolase is cholesteryl **ester** hydrolase, which produces free **cholesterol** and a **free fatty acid**. Another example is **lipase**, which produces free fatty acids and **glycerol** from **triacylglycerol**s. Peptidases

hydrolyse C–N bonds, separating the carboxyl carbon of one amino acid from the amino-nitrogen of another. A C–C cleavage occurs in L-**tyrosine catabolism** when fumarylactoacetate is converted to acetoacetate and fumarate. (NJB)

Hydrolysis

The process whereby water is added across C–O, C–N, C–C and other bonds to create two compounds with their original functional groups. Hydrolysis of the C–O linkage converts the functional group from an **ester** to an alcohol and an acid. Hydrolysis of the C–N linkage in a **peptide** functional group produces an acid and an **amine**. The converse process is called condensation. (NJB)

Hydroxybutyrate

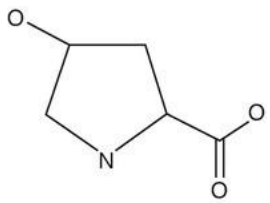
In **metabolism**, 3-**hydroxybutyrate** ($CH_3{\cdot}CHOH{\cdot}CH_2{\cdot}COO^-$) is one of the **ketone** bodies and is usually produced from acetoacetate ($CH_3{\cdot}CO{\cdot}CH_2{\cdot}COO^-$) followed by reduction of the keto group by NADH to form 3-hydroxybutyrate (*see* Ketones). (NJB)

Hydroxycholecalciferols:

see Calciferol

Hydroxylysine

An amino acid ($H_2N{\cdot}CH_2{\cdot}CHOH{\cdot}(CH_2)_2{\cdot}CHNH_2COOH$, molecular weight 163.2) found in protein (mainly **collagen**). It is synthesized in the body by hydroxylation of protein-bound **lysine**. (DHB)



Hydroxyproline

An amino acid ($C_4OH_8N{\cdot}COOH$, molecular weight 131.1) found in protein (mainly in **collagen**). It is synthesized in the body by hydroxylation of protein-bound **proline**. (DHB)

Hypercalcaemia

A condition of excessively high **blood calcium** concentration which, if prolonged, can lead to metastatic calcification of soft tissues. The major nutritional cause of hypercalcaemia is **vitamin D** intoxication. (JPG)

See also: Hyperparathyroidism

Hypercarotenosis

Excessive accumulation of **carotenoid**s in the plasma and tissues following ingestion of large amounts of β-carotene and other carotenoids. It can give a yellow-orange tint to skin and internal organs but does not result in **vitamin A** intoxication. (JPG)

Hyperglycaemia

An elevation of **blood glucose**. A brief hyperglycaemia is to be expected after a meal; a prolonged elevation of plasma glucose concentration can be detrimental to health. In non-ruminant animals the expected plasma glucose concentration is 4.4–5.5 mmol l^{-1} (80–100 mg dl^{-1}). Prolonged elevated plasma glucose concentrations of 16–28 mmol l^{-1} (300–500 mg dl^{-1}) such as those observed in **diabetes** are detrimental. An increased **glucose** loss in the **urine** (glycosuria), increased urine volume (polyuria) and a decreased body protein content (because of a decrease in **protein synthesis** and increased use of protein for **gluconeogenesis**) are all expected consequences of prolonged uncontrolled glucose concentrations. (NJB)

Hyperinsulinaemia

An elevation in the concentration of plasma **insulin**. A brief hyperinsulinaemia may be expected after a meal but a prolonged elevation of plasma insulin may be deleterious. Clinical reference values for serum insulin vary from 29 to 181 pmol l^{-1} (4–25 μU ml^{-1}). The consequences of excessive levels of insulin are low plasma **glucose** concentrations (< 3 mmol l^{-1}), resulting in a limitation of glucose to support the nervous system. This can lead to progressive deterioration of normal behaviour, i.e.

disorientation, lethargy, coma, **convulsion**s and death. (NJB)

Hyperkeratosis

Hypertrophy of the stratum corneum of the skin. This may be caused by **poisoning** with chlorinated naphthalenes (insecticides such as BHC and DDT, generally no longer used because organochlorine compounds enter the **food chain**) and is seen as thickening and roughness of the skin. (WRW)
See also: Parakeratosis; Skin diseases

Hyperlipidaemia

Elevated levels of **lipids** and **cholesterol** in the **blood**, also called hyperlipaemia. It is associated with decreased **feed intake** and mobilization of **adipose tissue** at times of high nutritional demand, particularly in obese animals. This can alter the lipid content of platelets and the endothelial cells that line blood vessels, and the risk of thrombosis (blockage of blood vessels) increases. Hyperlipidaemia is seen in cattle and horses with fatty **liver disease** and in dogs with pancreatitis. (EM)

Hypermagnesaemia

A condition of abnormally high blood **magnesium** concentration. Small (20–50%) increases in blood magnesium concentration are harmless and often occur secondary to disorders that elicit an increase in **parathyroid hormone** secretion, which increases renal conservation of magnesium. (JPG)

Hyperparathyroidism

Abnormally increased activity of the **parathyroid** glands which may be primary or secondary. The primary condition is associated with either a tumour or hyperplasia of the parathyroid cells. Secondary hyperparathyroidism is usually of nutritional origin, often as a result of an excessive intake of phosphate relative to **calcium**, leading to the formation of insoluble calcium **phosphate** in the more alkaline regions of the **small intestine**. This in turn leads to incipient **hypocalcaemia**. A deficiency of

vitamin D may also be responsible for a decrease in plasma calcium ion concentration, as may an excessive intake of **oxalate**. Chronic renal failure with consequent impaired excretion of phosphate also leads to secondary hyperparathyroidism. (ADC)

Hyperphagia

Overeating, when spontaneous food intake is more than required for meeting **nutrient requirement**s. Temporary hyperphagia can be induced by selective damage to the ventromedial **hypothalamus**, or provision of highly palatable food; but it is difficult to identify with certainty in birds (*see* Overfeeding). Compare with hypophagia (undereating) and aphagia (no eating). (JSav)

Hypertension

High arterial **blood** pressure. Measurement of arterial blood pressure is more difficult in animals than in humans but, even so, hypertension appears to be less common and most likely to be a result of disease in a variety of organs. Arteriosclerosis, which is similar to the vascular changes seen in humans, can be found in pigs with organomercurial **poisoning** and oedema disease, and in the vessels of the heart in **mulberry** heart disease and hepatosis dietetica. (EM)

Hyperthermia

A condition in which the core body **temperature** is elevated above the normal range for more than a brief period of time. It can result from **heat stress**, when the animal is unable to dissipate heat as fast as it is produced and gained from the environment. It can also be symptomatic of disease, especially certain infectious diseases. The susceptibility to hyperthermia is increased by the **heat increment of feeding**. (MFF)

Hypervitaminosis

Excessive intake of one or more vitamins, especially A and D which, being fat-soluble, accumulate in the **liver**. Adverse

symptoms, which occur at several hundred thousand IU **vitamin A** or **vitamin D** kg^{-1} ration, are typically **growth** depression and renal tubular mineralization for vitamin D and **lameness** for vitamin A. There is some **antagonism** between these two vitamins, and hypervitaminosis A may also be alleviated by large doses of **vitamin E**. (CJCP)

Hypocalcaemia

A condition of abnormally low **calcium** concentration in the blood which disrupts nerve and muscle function. The onset of **lactation** in ruminants can cause acute hypocalcaemia (*see* Milk fever), requiring intravenous calcium administration to prevent death. Prolonged inadequate dietary calcium can also cause a moderate chronic hypocalcaemia. Renal failure causes hypocalcaemia in many species. (JPG)

Hypoglycaemia

A deficiency of **glucose** in the blood. It can quickly affect the nervous system and result in disorientation and collapse, so glucose levels are maintained at normal levels by a range of homeostatic mechanisms, even in the early stages of **starvation**. When there is a high requirement for glucose, for example in the heavily pregnant ewe or lactating animal, low **energy intake** may lead to hypoglycaemia and then to acetonaemia (**ketosis**). Hypoglycaemia is common in newborn, weak lambs and piglets. (EM)

See also: Liver diseases

Hypomagnesaemia

A condition of abnormally low blood **magnesium** concentration which can interfere with cell function, especially nerve cell function, leading to **tetany** and **convulsion**s. It is caused by inadequate dietary magnesium or, as commonly occurs in ruminants, interference with magnesium absorption by **potassium** or **ammonia**. (JPG)

Hyponatraemia

Inadequate intake of **sodium**. It mainly affects grazing herbivores. **Salt** is an inexpensive ingredient of herbivore **feed supplement**s and so it is usually added in sufficient quantities to prevent hyponatraemia. It is mainly unsupplemented grazing animals that are susceptible. The **appetite** for sodium is acute in most herbivores but very high concentrations are unpalatable, and so salt can be added at comparatively high levels to **feed block**s to regulate the intake of energy-rich ingredients.

Sodium is readily taken up by plants and the concentration varies considerably with the soil type and the plant's translocation ability. Although sodium is an essential **trace element** for farm animals and its concentration in animal food is very variable, the homeostatic mechanisms for maintaining a constant sodium concentration in **blood** are extensive. It is therefore effectively conserved, principally by recovery in the kidney, but is not stored as effectively as other minerals. The losses of sodium in **milk** are not homeostatically controlled and high-yielding lactating dairy cows grazing pasture without supplements are particularly at risk of inadequate sodium intake. In addition, the use of **potassium** fertilizer restricts sodium uptake by the **grass** plant, with concentrations sometimes declining to below 1 g Na kg^{-1} dry matter (DM). Cattle grazing tropical grasses are especially at risk, as the sodium concentrations of such grasses are very low and sodium losses in **sweat** can be high.

The effects of hyponatraemia on herbivores are non-specific and relate principally to attempts by the animal to restore the sodium balance. Milk production is reduced in dairy cows and a pica develops that causes the cattle to lick objects. There is a general loss of appetite and the animal loses condition and acquires a haggard appearance, with lustreless eyes and a dry, harsh coat. The best diagnostic method is to assess the ratio of sodium to potassium in **saliva**, which is used to recycle surplus sodium. The ratio should be between 17:1 and 25:1; anything less than 15:1 indicates possible sodium deficiency. The correct diagnosis can often only be confirmed by observing the impact of **supplementation**, with a rapid increase in appetite and milk

production. (CJCP)

Hypophosphataemia

A condition of abnormally low **phosphorus** (inorganic phosphate) concentration in the blood. Dietary phosphorus inadequacy is the common cause and, if chronic, leads to rickets and osteomalacia. Severe acute hypophosphataemia can occur at the onset of **lactation** in dairy cows, contributing to the 'downer **cow**' syndrome. (JPG)

See also: Parathyroid; Rickets

Hypothalamus

An area of the brain beneath the thalamus at the base of the cerebrum. It controls many peripheral autonomic mechanisms, somatic functions and endocrine activity. In particular the hypothalamus regulates water balance, body **temperature**, sleep, **hunger** and thirst. It also influences the release and inhibition of **hormone**s from the anterior pituitary gland (hormones affecting **reproduction**) and the thyroid (hormones affecting **metabolism**). (EM)

Hypothermia

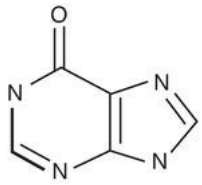
A condition in which the **temperature** of the body is below the normal range for more than a brief period of time. It can result from exposure to a **cold environment**, when the animal is unable to generate heat as fast as it is lost, and can also occur in certain disease conditions. The susceptibility to hypothermia is increased in animals that have a low rate of **heat production**, for example newborn mammals that have not suckled. (MFF)

Hypothyroidism

A syndrome involving inadequate secretion of thyroid hormones by the thyroid gland, causing retarded **growth**, impaired **reproduction**, reduced **milk** production and an inability to increase **metabolic rate** in response to cold weather. Nutritional causes include dietary **iodine** deficiency or the presence of

goitrogenic substances in the diet. (JPG)
See also: Goitre; Goitrogen

Hypoxanthine
An **organic compound** with the elemental composition $C_5H_4N_4O$, normally found in solution in cells. It is one of the intermediates in the **catabolism** of the **purine** adenosine to uric acid. Uric acid is the end-product of purine (adenosine and guanosine) catabolism and is excreted in the **urine**. (NJB)



Hypoxia
Inadequate **oxygen** supply. This can be caused by vasoconstriction during parturition. The resulting lethargy may result in mammals failing to **suckle** in the crucial hours after parturition. (JMF)
See also: Haemoglobin

I

Ideal protein
The current concept of 'ideal protein' in nutrition had traditionally referred to the optimum pattern of so-called nutritionally essential amino acids (EAAs) but ignored so-called nutritionally

non-essential amino acids (NEAAs). This concept was based solely on the EAA composition of the body, but results of recent research over the past 30 years have shown that the pattern of amino acids in the **diet** does not reflect that in the animal. This mismatch can be explained as follows: (i) individual amino acids in the diet undergo extensive **catabolism** and transformations at different rates in the **small intestine**; (ii) the concentrations of amino acids in the circulation differ markedly from the relative abundance of amino acids in the diet; (iii) individual amino acids in plasma have different metabolic fates in different animal tissues; and (iv) the content of amino acids in tissue proteins differs greatly from that in the diet. These major shortcomings limit the usefulness of the early versions of the ideal protein in formulating pig and poultry diets for maximal growth or production performance.

The 'ideal protein' concept greatly advanced the field of pig and poultry **protein** nutrition over the past four and six decades, respectively, and has also been highlighted in the literature concerning the nutrition of other animals (including humans, as well as fish and crustaceans). However, the concept of 'ideal protein' in animal nutrition has major conceptual limitations, because it has ignored: (i) the more abundant NEAAs due to the insufficient knowledge of amino acid biochemistry and nutrition, as well as inadequate research tools between the 1950s and the 1990s; and (ii) the nutritional and physiological needs of the small intestine for NEAAs, which are not only major **energy source**s for **enterocyte**s but also key regulators of gut integrity, **immunity**,

health, and function. Thus, the 'ideal protein' is not ideal for the optimum nutrition and health of animals. Continuing to formulate diets based on the 'ideal protein' concept is not an optimum practice in animal nutrition. Any ideal diet must provide all physiologically and nutritionally essential AAs (including EAAs, NEAAs and, in the case of carnivores, also **taurine**). Thus, the 'ideal protein' concept should be replaced with 'optimum ratios of all proteinogenic AAs' for animals. In the different stages of the life cycle, the requirements of humans and other animals for the amounts and ratios of all amino acids, particularly NEAAs whose synthesis depends on not only **enzymes** but also **substrates** and co-factors, are influenced by a plethora of factors, including genotypes, the environment and diseases. This means that dietary requirements for all proteinogenic amino acids are dynamic and are not constant under all practical conditions. Optimal ratios of amino acids in diets change with different physiological factors, such as exercise, gestation, **lactation** and **weaning** of mammals, diseases and other stressors (e.g. **heat stress**). This new concept can guide the formulation of the diets of all non-ruminants (including pigs, poultry, humans, fish and crustaceans), particularly low-protein diets for cost effectiveness and sustainability. Thus, nutritionists and producers must move beyond the half-a-century old 'ideal protein' concept. (GW)

Further reading

Wu, G. (2014) Dietary requirements of synthesizable amino acids by animals: a paradigm shift in protein nutrition. *Journal of Animal Science and Biotechnology* 5(34), 1–12.

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Ileal digestibility:
see Digestibility

Ileum
The distal section of the **small intestine** located between the **jejunum** and the **large intestine**. At the end of the ileum is the ileocaecal junction where **digesta** enter the **caecum** (as in the horse) or the ileocaecocolic junction where digesta enter both the caecum and the **colon** (as in pigs, ruminants and poultry).

The absorptive surface of the ileum is relatively smaller than in the upper intestine, because the **villi** are shorter and the crypts not as deep. Because the **absorption** of those degradation products that are absorbable in the small intestine is completed at the terminal ileum, digesta collected from this site are often used to determine the **digestibility** of nutrients in the upper digestive tract.

In birds, the proximal ileum is the most important site for absorption of the end-products of digested **lipids**, **carbohydrates** and proteins.

In the ileum there is nearly complete reabsorption of **bile** acids via a specific transport system, which operates by **sodium** co-transport, directly back to the liver (enterohepatic recirculation). There are also mechanisms for **electrolyte** absorption, including **chloride**-coupled sodium absorption, chloride–**bicarbonate** exchange, bicarbonate absorption and **potassium** absorption,

though generally these systems are more important in the colon.

In **newborn animal**s the ileum is the main site for the absorption of immunoglobulins by **pinocytosis**. The same mechanism is probably also involved in the absorption of the complex between B_{12} and intrinsic factor, a glycoprotein with a molecular weight of 60,000, from the gastric **mucosa**.

The ileum plays an important role in controlling the transit of digesta through the small intestine so as to ensure efficient absorption of nutrients. This control is achieved by isolated segmental contractions that are also more effective in mixing than propelling. (SB)

See also: Gastrointestinal tract

Imino acids

Amino acids that have an imine R·HC═NH group. Most of the α-amino acids released upon **hydrolysis** of protein can be described by the general formula $R{\cdot}HCNH_2{\cdot}COOH$, where the amino group $-NH_2$ is on the α carbon. Two amino acids that do not have this general structure are **proline** ($C_5H_9NO_2$) and **hydroxyproline** ($C_5H_9NO_3$), which are correctly designated as α-imino acids. (NJB)

Immune tolerance

A lack of response by the immune system to an **antigen** to which it has been previously exposed. Tolerance can be acquired during early gestation before the fetus becomes immunocompetent, for example to an early viral infection leading to persistent infection or to an antigen from a non-identical twin sharing placental

circulation. The blockade theory describes immune tolerance in the neonate caused by the continued presence of an antigen in the thymus 'deleting' the immune response. It is believed that immune tolerance in old age is caused by either a lack of immune cells, the action of T suppressor cells or possibly the absence of interleukin-2, a **cytokine** released by T cells that stimulates the immune response. (EM)

Immunity

The ability of animals to resist disease, usually resistance to an infection or infectious disease. There are two major types: innate and acquired (Fig. 1). Innate immunity acts as a first line of defence by presenting chemical and physical barriers to infectious organisms and other noxious substances gaining entry to the body. Antimicrobial proteins and enzymes are present in mucous secretions, which cover many of the non-keratinized surfaces of the body, for example respiratory and **gastrointestinal tract**s. Acids and **lipids** present on the skin deter bacterial establishment. The presence of body **hair** acts as a physical barrier to damage or infection. The presence of cilia on epithelial cells prevents pathogens reaching the cells. Natural immunity is influenced by genetic and age factors and some pathogens are completely or partially host-species specific. The presence of certain genes may confer resistance or susceptibility to a particular pathogen. Irrespective of previous exposure, animals may be resistant to specific pathogens at a certain age; for example, rotavirus only causes disease in the very young animal.

Internal innate mechanisms involve body cells and fluids. These

can act independently to protect the animal from invasion but also act in combination with specific immune defences. Phagocytosis is the recognition, adherence and engulfing of foreign material by granulocytic leukocytes (neutrophils), monocytes and macrophages. Once within a phagosome inside the phagocytic cell, the foreign invader (e.g. bacterium) is killed by a variety of chemicals, including acids, proteolytic enzymes and lysosyme peroxidase. However, some bacteria can survive phagocytosis, for example some staphylococci, listeria and mycobacteria.

Interferons are cellular proteins produced early in response to microbial infection, particularly by viruses. They spread by the **blood** (and **saliva**) and diffuse through extracellular fluids to cells that have an interferon receptor. Interferon prevents viral replication by inhibiting the production of viral proteins by ribosomes. Interferons are specific to host species but are non-specific in their activity.

Inflammation is the defensive reaction of tissues to injury. It can be stimulated by many noxious agents: heat, excessive cold, chemical burns, physical injury and invasion by **microorganism**s. The cardinal signs of inflammation are redness, swelling, heat, pain and sometimes loss of function. Inflammation can occur in any tissue and is generally designated by the suffix '-itis'; for example, enteritis is inflammation of the intestine. In the inflammatory reaction, increased vascular permeability and a cascade release of messenger proteins increase the availability of phagocytic cells and non-specific and specific defence chemicals at the site of injury. Chemotaxis specifically draws white blood cells to the site and

acute-phase protein production is stimulated. These proteins include fibronectin, which coats bacteria and promotes phagocytosis, and the complement system, which is a cascade release of proteins that act on cell or microbe surfaces to enhance clumping of bacteria and cell lysis. C-reactive proteins facilitate phagocytosis. **Lysozyme** and **iron-binding protein**s remove the iron available for and necessary to bacteria for multiplication. Later in the inflammatory reaction, chemicals involved in repair and the healing process are found. Some of the features of inflammation, though it is a major defence mechanism, are undesirable in certain disease conditions, such as pneumonia, meningitis and arthritis. Anti-inflammatory drugs may be used to suppress some or all of the inflammatory responses.

Specific or acquired immunity is associated with either the humoral response or cell-mediated immunity. Lymphocytes are involved in both types. The B cells involved in the humoral response originate from bone marrow stem cells, develop in tonsils and intestinal lymphoid tissue (especially the bursa of Fabricius, or cloacal bursa, in birds) and then may migrate to other lymphoid tissues. Macrophages process phagocytosed **antigen**s and present them to lymphocytes of both the humoral and cell-mediated immune systems. These specific antigens in contact with B cells stimulate the cells to divide and develop into antibody-secreting plasma cells. Plasma cells are found in lymph nodes, the spleen and at sites of infection. The antibody produced is specific to the protein shape of the presenting antigen and will bind with it. As pathogenic organisms have a range of antigenic sites (epitopes), a

single pathogen will stimulate the production of a range of different **antibodies**. Frequent stimulation of the immune system by the same antigen leads to a build-up of antibody production and establishment of a memory cell population. This enables a rapid antibody response to be mounted if the animal encounters the same antigen in the future. The antibody response is not immediate; it takes several days from initial stimulation for significant levels to be found but antibody levels may remain high for months or years.

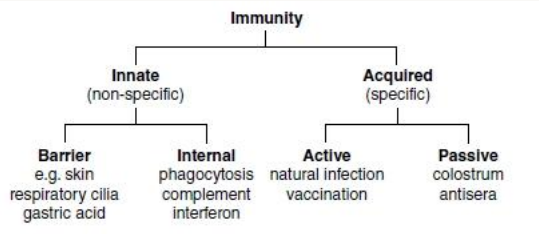


Fig. 1. Different types of immunity.

Lymphocytes originating from the thymus (T cells) are found in many body tissues and are responsible for cell-mediated immunity. These cells act directly on invading pathogens and infected cells. They are particularly important in some viral infections and are also responsible for tissue graft rejection. T cells sensitized to a particular antigen may kill infected cells by binding to them and secreting toxic chemicals (cytotoxic T cells). Other lymphocytes moderate the action of cytotoxic cells by releasing **cytokines** (T helper or suppressor cells). Exposure to antigens also leads to a build-up in memory cells in the cell-mediated immune system.

A fetus develops immunocompetence during gestation. However, infection in early gestation may not stimulate an immune

response as the fetus may be too immature to recognize foreign proteins. Lack of immunocompetence in the post-natal period may be due to a primary deficiency of a component of the immune system or a secondary immunodeficiency. Some viral infections, for example the immunodeficiency viruses (HIV, FIV) and others (e.g. BVD), affect immunocompetence, as do severe **malnutrition**, radiation and use of corticosteroids. Stress is thought to play a role in reduced immune function through corticosteroid release, and some **mineral deficiencies** may also be involved.

Stimulation of the humoral or cell-mediated immune systems, either by natural infection or by vaccination, produces active immunity, which may provide protection to the specific antigen for months or years. This property is used in vaccination, where antigen, from inactivated pathogens or toxins, attenuated organisms, related mild strains, or genetically engineered forms, is used to stimulate an immune response with the intention of providing long-term specific protection. Vaccines may contain an adjuvant to improve the immune response. More than one dose of vaccine may be required in an initial course to provide satisfactory protection, particularly where the antigen is not a live replicating organism. The initial dose will produce a small primary antibody response, and the second a secondary or amnestic response (Fig. 2). Satisfactory establishment of a memory cell population may also need an initial course of vaccination. Booster doses of vaccine may be used to prolong the protection or to raise circulating antibody levels.

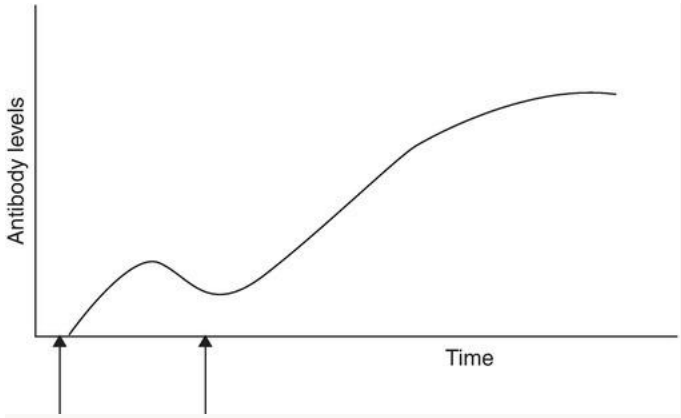


Fig. 2. Antibody response to two doses of vaccine (indicated by ↑).

Passive immunity does not require exposure to an antigen: the antibody is given to the animal either in colostrum or in antiserum. Protection is limited to a few weeks, as the protein immunoglobulin is broken down over time. Passive immunity does not aid the production of protective antibodies in the animal, as exposure to the antigen is needed. The presence of passive immunity may interfere with the immune response to a vaccine and this should be taken into consideration when a vaccine programme is drawn up. (EM)

See also: Colostral immunity

Immunity and nutrition

Animals (particularly aquatic animals) are constantly exposed to various pathogens in the environment, and their health critically depends on dietary intakes of energy and nutrients. Mammals, birds and fish are protected from various pathogens by both innate (natural, non-specific) and acquired (adaptive, specific) immune systems. By contrast, crustaceans, like other invertebrates, lack the adaptive immune system and depend solely on the innate immune system to defend against infectious pathogens.

The skin and **mucosa**l barriers (major components of the innate system) consist of **collagen** that is rich in **glycine**, **proline** and 4-**hydroxyproline**. **Nitric oxide** (NO), a product of **arginine** catabolism in macrophages (a component of the innate system), is the major killer of pathogens, including bacteria, parasites, fungi and viruses. Through antioxidative effects and the regulation of mucosal gene expression, **vitamins** A, C and E and **zinc** are important for an effective skin barrier.

The adaptive system mainly depends on proteins that are synthesized from amino acids. The innate and immune systems are highly interrelated through various kinds of T and B lymphocytes (also called T cells and B cells), as well as **cytokines** (proteins) and signalling molecules. **Glutamine** and **glucose** are major metabolic fuels for lymphocytes, macrophages and other cells of the immune system to support their integrity and function. Adequate intakes of amino acids (particularly **arginine**, **cysteine**, **glutamine**, glycine, **taurine** and **tryptophan**), **fatty acid**s (particularly ω3 and ω6 **polyunsaturated fatty acid**s), minerals (particularly **copper**, **iron**, **manganese**, **molybdenum**, **selenium** and **zinc**) and vitamins (particularly vitamins A, B_6, B_{12}, C, D and E) are essential for the development and function of the immune systems. Many of the **micronutrient**s are also important for antibody production. **Vitamin D_3** is associated with downregulating the production of proinflammatory cytokines. Supplements of vitamin D can reduce mastitis in dairy cows, reducing the need for antibiotics, and **supplementation** with the other nutrients to deficient animals can increase circulating

antibodies, eosinophils, granulocytes, lymphocytes and cytokines (Bertoni *et al*., 2016). Mastitis is associated with an increase in **sodium** in **milk**, which reduces the growth of *Staphylococcus aureus* (Arney and Phillips, 2005), but the implications of sodium deficiency, which is common in cattle, are not known. The competitors for **absorption** of micronutrients must be considered; for example, **potassium** inhibits sodium uptake and **sulphur** can reduce the uptake of both selenium and copper. Dietary energy is apparently less important than an adequate protein, mineral and vitamin supply (Bertoni *et al*., 2016). **Protein supplementation** and amino acid composition optimization both have the potential to improve immunity to parasites. During the Covid pandemic, there was increased interest in purchasing vitamin supplements to boost the immune system. However, although there are benefits of high intakes of **vitamin C**, and possibly zinc, on reducing the impact of the common cold, there is no evidence yet that these are beneficial in controlling Covid infections. Generally, it is believed to be more effective to have a healthy diet containing adequate intakes of minerals and vitamins, than to take supplements. Many fruits and vegetables are high in **antioxidant**s, including carotene, flavonoids and **polyphenol**s, whereas watermelon is a highly rich source of **citrulline** (the major precursor of **arginine**).

Some plant secondary **metabolite**s, such as **caffeine** and digoxin, have the potential to suppress the generation of tissue necrosis factors, but others, such as condensed **tannins**, can increase mast cell and leukocyte production in sheep, perhaps

through their protection of proteins from degradation in the rumen and possibly the modulation of the intestinal immune system.

The pathology of any injury, infection or irritation is associated with a cascade of events, all centring on an inflammatory response. This may be triggered by poor nutrition – a protein, vitamin and **mineral deficiency**, pro-oxidative conditions, giving rise to reactive oxygen species (e.g. **superoxide** anion and peroxynitrite), **endotoxin**s, and toxins in feeds or even nutritional excesses that give rise to **obesity** (Bertoni *et al*., 2016). The inflammatory response aims to confer protection to the affected tissue through the initiation of an acquired immune response, mediated by pro-inflammatory **cytokines** and **eicosanoid**s to recruit phagocytic cells to the area (Bertoni *et al*., 2016). In any inflammatory response, immune system cells, in particular macrophages, produce cytokines, nitric oxide, reactive oxygen species and eicosanoids. If the inflammatory response occurs in the absence of foreign organisms, the animal's health may be damaged if it continues for long. Health effects include **anorexia**, fever and depression. However, there are anti-inflammatory effects of the stress hormone, **glucocorticoid**, which will be elevated during stresses such as those arising during transport, concomitantly with abstinence from food. Stressed animals reduce their food and drink consumption, as in postpartum animals that demonstrate depression and a reduced **appetite**. Thus, nutritional deficiencies in pre-natal and early post-natal life of both humans and farm animals can hinder the development of the immune system. Conversely, in humans there is good evidence that enhanced intake

of **polyunsaturated fatty acid**s, in particular conjugated **linoleic acid**, and antioxidants, including vitamins C and E, carotene, zinc and selenium, can reduce the inflammatory response (Bertoni *et al*., 2016).

This is also demonstrated in the bimodal pathways regulating the relationship between disease and nutrition. Inadequate nutrition predisposes to disease and an animal being in a diseased state leads to **inappetence** and inadequate nutrient supply. In the future, the analysis of gene expression is likely to lead to a better understanding of immunonutrition. (GW; CJCP)

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Immunoglobulin:

see Immunity

In sacco

Literally 'in a bag'. Methods of measuring the **digestion** or microbial degradation of feeds in a bag within the **gastrointestinal tract** are called *in sacco* techniques. To measure the degradation of feeds within the **rumen**, samples of feed are sealed in bags of woven plastic (e.g. nylon or Dacron) that has pores small enough to retain the feed particles but large enough to allow microbes to enter and the end-products of digestion to leave. The bags are suspended in the rumen via a fistula in the rumen wall; they are retrieved at intervals and analysed to determine how much of the original material has been lost. The same approach can be used to measure digestion in the **stomach** and a 'mobile nylon bag' technique is also used to measure digestion in the intestine. The bags are usually introduced via a **cannula** and recovered either through another cannula further down the intestine, or from faeces, according to which part of the digestive process is being studied. (MFF)

***In vitro* digestibility**

Digestibility determined in the laboratory by simulating the *in vivo* digestion. Commercial enzyme preparations or appropriate inocula (e.g. **digesta** or rumen liquor) are used in controlled **incubation**s. To derive reliable predictions of *in vivo* digestibility from *in vitro* assays requires equations describing the relationship between *in vivo* and *in vitro* digestibility **values** obtained with identical feed samples. (SB)

See also: Digestibility

Further reading

Boisen, S. (2000) *In vitro* digestibility methods. History and specific approaches. In: Moughan, P.J., Verstegen, M.W.A. and Visser-Reyneveld, M.I. (eds) *Feed Evaluation. Principles and Practice*. Wageningen Pers, Dordrecht, The Netherlands, pp. 57–76.

Inappetence

Loss or reduction of **appetite**. It may be accompanied by some interest in feed, e.g. sniffing at it, but is characterized by a failure to eat normally. It is widely recognized in **zoo animals**, companion animals and livestock. A distinction may be drawn between inappetence (also known as inanition), which involves suppression of appetite, and **anorexia**, which involves complete cessation of food or feed consumption. The underlying cause (given that food consumption is essential for survival) may be disease related, such as **liver** or kidney disorders, nausea or inflammatory bowel disease, or it may relate to stress and difficulties in obtaining food or feed. It has been associated with mortality in sheep exported from Australia to the Middle East, a journey of 1–2 weeks, with a range of stresses being experienced by the sheep, including novel surroundings, high stocking densities, motion, difficulty accessing feed and **heat stress**. Some genetic lines of sheep are more susceptible than others and sheep that are too timid to approach the **feed trough** under conditions of high stocking density may be most susceptible. Unpalatable, spoiled or novel feed may also be implicated in this disorder. In sheep on ships, the expectation that sheep from pasture will eat pelleted concentrate feed is partly responsible. The lack of **feed intake** reduces rumen pH and **volatile fatty acid** content, which predisposes sheep to

salmonellosis and subsequent mortality. A period of acclimatization of approximately 1 week before embarkation will help sheep to get use to **pelleted feed** and reduce the instance of inappetence. Once on board, offering **straw** or **hay** to affected animals in hospital pens can encourage them to begin eating. It is also recognized in intensive feeding facilities, or **feedlot**s, where typically 2–5% of animals fail to eat, at least for the first 2 weeks, which is the approximate time required for the rumen to adapt to a new diet. (CJCP)
See also: Restricted feeding

Inborn errors of metabolism
Congenital abnormalities of metabolic pathways. Most inborn errors of metabolism (IEMs) are due to **enzyme** deficiencies or defects in metabolic transport. In the human population there are over 300 identified IEMs but far fewer are known in farm animals. Because farm animals are bred from a smaller gene pool than humans, there are probably fewer IEMs but they may individually be more prevalent because of the high level of inbreeding. Most are inherited through the monogenic recessive mode and may go undetected in farm livestock because farmers accept a high level of neonatal mortality. Examples in cattle include carbonic anhydrase deficiency syndrome, citrullinaemia, an inborn error of **urea**-cycle metabolism characterized by deficiency of argininosuccinate synthetase and consequent life-threatening hyperammonaemia, and deficiency of uridine monophosphate synthase. In sheep there is an inherited lysosomal storage disease that involves deficiencies of β-**galactosidase** and α-neuraminidase. There are also **copper**

storage diseases and depressed biliary transport of conjugated sulphobromophthalein (SBP) compounds. **Glycogen** storage diseases have been recognized in cattle, quail and **laboratory animal**s and are among the most widespread of IEMs. (CJCP)

Incubation

The time taken for the embryo to develop *in ovo* and then hatch varies from species to species, but there is a trend for the time required for incubation to increase as the size of the hatchling increases (see table).

Incubation times

Species	Incubation time (days)
Chicken (standard)	21
Chicken (bantam)	20
Duck (except Muscovy)	28
Muscovy duck	33–35
Goose, small (e.g. Chinese, Canada)	30
Goose, large (e.g. Emden, Toulouse)	33–35
Guinea fowl	28
Japanese quail	17
Ostrich	42
Partridge	23
Pheasant	24

Pigeon	17
Turkey	28

The times shown in the table are intended as a guide only. For example, when incubating chickens under commercial conditions, the incubation period may be extended by 12 or more hours to allow time for the hatching process to be completed and the hatchlings to dry off. Similarly, extra time will be required if the eggs have been stored for more than 1 week, for example, or come from older parent stock or are incubated at a suboptimal **temperature**. (NS)
See also: Sex ratio.

Indicator
A substance that shows a change in chemical conditions (e.g. pH), often by a change in colour. In nutrition, indicators are simple measures that change with more complex or deep-seated alterations in **metabolism**. Examples are the use of blood **urea** concentration as an indicator of **protein utilization** and the activity in plasma of the enzyme, **glutathione** reductase, as an indicator of **riboflavin** status. A method of estimating the requirement for an **amino acid** also uses the **oxidation** of a non-limiting ('indicator') amino acid: with increasing intake of the limiting amino acid, the oxidation of the excess indicator amino acid decreases up to the point at which the requirement of the test amino acid is met. (MFF)

Indirect calorimetry

Indirect calorimetry is used to measure an animal's rate of metabolic **heat production**. Heat represents a high proportion of the total **energy intake** and it is generated in a complex chain of chemical reactions. Despite this, it can be estimated with remarkable accuracy from the rates of exchange of **oxygen consumption** and **carbon dioxide** production in respired air as the animal metabolizes the **energy source**s in its feed. This is possible because of a natural law first discovered by Germain Hess in 1838. Hess's law states that the heat produced in a chemical reaction is always the same regardless of whether it proceeds directly or via a number of intermediate steps. It means effectively that the heat generated by metabolizing a nutrient through the complex web of metabolic reactions may be duplicated by measuring the heat produced by burning the same nutrient in a **bomb calorimeter**.

Food energy is supplied by **proteins**, **carbohydrates**, **fats** and indigestible matter. The last is excreted in the faeces and takes no part in the consideration of the heat produced. Carbohydrates, as their name implies, are composed of the elements of carbon and water. Their **oxidation** may be represented chemically as:

$$Cn(H2O)m+nO2 \rightarrow nCO2+mH2O+\text{Heat of combustion (mol}-1).$$

Although the heat of combustion varies between one carbohydrate and another, the heat produced per litre of oxygen consumed is found to be nearly the same for all carbohydrates (21.2 kJ l^{-1}); also, as seen from the formula of the chemical reaction, the **respiratory quotient** (RQ), i.e. the volume ratio of carbon dioxide produced to oxygen consumed, is equal to 1. Similarly for

fats, which are triglycerides; the heat per litre of oxygen is remarkably consistent at 19.8 kJ l^{-1} and the RQ is 0.711.

Proteins include **nitrogen** in their composition, in addition to **oxygen**, **hydrogen** and carbon. Unlike carbohydrates and fats, they cannot be completely oxidized to carbon dioxide and water; additional compounds of nitrogen are formed, such as **urea**, **ammonia** and uric acid. Again, it is found that the heat per litre of oxygen consumed in the conversion of proteins to carbon dioxide, water and urea is consistent at 19.2 kJ l^{-1} and the RQ is 0.809.

These **calorific factors** relevant to oxidation of carbohydrate, fat and protein are summarized in the table.

Calorific factors relevant to oxidation

	Approx. heat of combustion (kJ g^{-1})	Heat/oxygen ratio (kJ l^{-1})	Respiratory quotient
Carbohydrate	17.6	21.2	1.000
Fat	39.8	19.8	0.711
Protein (to urea)	18.4	19.2	0.809

Indirect calorimetry thus requires measurement of the amounts of oxygen consumed, of carbon dioxide produced and of nitrogen excreted in the **urine**. From the values in the table, it is then possible to take the following steps.

1. Calculate the quantities of oxygen produced and carbon dioxide

consumed by protein metabolism in forming the observed quantity of nitrogen excreted.

2. Calculate the remaining volumes of oxygen consumed and carbon dioxide produced (which are attributable to carbohydrate plus fat metabolism).
3. From their ratio (the non-protein RQ), calculate the proportions of the 'non-protein' oxygen that are attributable to metabolism of carbohydrate and of fat.
4. Calculate the heat produced by carbohydrate and fat metabolism.
5. Add together the heats of metabolizing all three food constituents to arrive at the total heat production.

In practice these tedious calculation steps may be replaced by a simple formula. Also, the calculation may be extended for herbivorous animals by incorporating a term to allow for the energy expelled as **methane**. The final equation (known as the **Brouwer formula**) for the heat produced (M, kJ) is:

$$M=16.18\times O2+5.02\times CO2-5.99\times N-2.17\times CH4$$

where O_2 is the volume (l) of oxygen consumed, CO_2 and CH_4 are volumes of carbon dioxide and methane produced and N is the mass (g) of urinary nitrogen. This equation was first proposed by Brouwer in 1958 and later endorsed by an international committee as applicable to all farm animals. The oxygen term contributes almost 75% and the carbon dioxide 25% to the total estimate of heat production; the nitrogen and methane terms each usually contribute less than 1%. For poultry, which excrete waste nitrogen

as uric acid, the formula is:

$$M=16.20\times O_2+5.00\times CO_2-1.20\times N$$

and for **fish**, whose waste product is ammonia, it is:

$$M=15.94\times O_2+5.15\times CO_2-9.14\times NH_3$$

where NH_3 is weight (g) of ammonia.

Indirect calorimetry is performed by confining an animal inside a **respiration chamber** or making it wear a face mask. Either technique may be adapted to closed- or open-circuit operation. In closed-circuit systems air is circulated, either by the respiratory effort of the animal or by a fan, around a circuit that contains absorbers for carbon dioxide and water vapour, and into which a measured amount of oxygen is added to replace that used up. Carbon dioxide consumption is obtained from the weight gain of its absorber. The system must be leak-proof, which is difficult to ensure with animals wearing masks. Closed-circuit systems using chambers are called respiration chambers.

In open-circuit indirect calorimetry, fresh air is continuously drawn through the face mask or chamber, usually by a fan, and its volume measured as it is exhausted again. Sampling and analysis of outlet air are usually continuous, using electronic gas analysers. Leakage is not important as long as it can be ensured that all leaks are inward (i.e. of fresh air). For open-circuit calorimetry, calculations are of the rate of heat production, rather than the total heat produced over a lengthy period of measurement. The Brouwer equation is modified to:

$$M(W)=VE\times(-20.47\times dFO_2+0.73\times dFCO_2-6.46\ dFCH_4)-5.99\times N$$

where V_E is exhaust air ventilation rate (l s^{-1}), N is nitrogen

excretion rate (g s^{-1}) and dFO_2, $dFCO_2$ and $dFCH_4$ are differences between concentrations (fractions) of the gases in exhaust air and fresh air (note that, because oxygen is consumed rather than produced, dFO_2 has a negative value). In this equation the term involving carbon dioxide has a multiplying factor that is small compared with that for oxygen; consequently it, like the terms involving methane and urinary nitrogen, has very little influence on the final result. Little accuracy is sacrificed in open-circuit **calorimetry** by measuring only oxygen concentration and using the equation:

$$M=-20.5\times VF\times dFO2$$

This type of approximation is *not* permissible with the Brouwer equation in closed-circuit calorimetry. It is important to note that ($V_E \times dFO_2$) is not synonymous with oxygen consumption, because inlet and outlet ventilation rates are only equal when RQ = 1.

The above description has centred on the **metabolism** of protein, carbohydrate and fat from food, without reference to energy retention as **growth**, i.e. the formation of **animal protein** and fat. The quantities of protein, carbohydrate and fat are in reality net quantities (i.e. digested minus retained protein, carbohydrate and fat) and the arguments are still valid when applied to growing, productive or even starving animals.

It has been shown that indirect calorimetry is based on assuming fixed values for the RQs and heats per litre of oxygen consumed in the metabolism of protein, carbohydrate and fat in both food and animal tissue. These are certainly gross approximations, though averaging throughout the body over all the

wide range of compounds involved helps to reduce variation. It is nevertheless hard to prove accuracy for the method on theoretical grounds. Perhaps the best proof of its accuracy and consistency lies in the fact that repeated observations over the past 100 years have failed to show any unexplainable difference between the results of indirect calorimetry, where heat is inferred from measurement of chemical quantities, and **direct calorimetry**, where the measurement is of the heat given up by the animal to its environment. (JAMcL; GMcLD)

See also: Calorific factors; Energy balance

Further reading

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McLean, J.A. and Tobin, G. (1987) *Animal and Human Calorimetry*. Cambridge University Press, Cambridge, UK, 338 pp.

Indispensable amino acids:

see Essential amino acids

Individual feeding

Provision of food to individual animals, usually housed separately, for specified feeding treatments or measurement of food consumption. Animals may also be fed individually using equipment that identifies the individual electronically by a coded tag and either dispenses a set amount of feed or records the animal's voluntary consumption. (JSav)

Indoles

Indoles (C_8H_7N) and **skatole**s (methyl-indol) are produced by

fermentation of **tryptophan** ($C_{11}H_{12}N_2O_2$) in the intestinal tract. Both give rise to the powerful odour of faeces. Some can be absorbed from the intestine and excreted in the urine. (NJB)

Infertility:
see Fertility

Inositol
A compound with the empirical formula $C_6H_{12}O_6$. It may exist in one of seven optically inactive forms and in two optically active forms. Of these, only **myo-inositol** is biologically active. Inositol is widely distributed in plant and animal cells. In the rat, myoinositol is not required under normal dietary conditions. However, rats treated with antibacterials have been shown to benefit from supplemental myo-inositol. The positive effect of added myo-inositol is presumably due to suppressed intestinal microfloral synthesis of it. No information is currently available for chicken, pig or horse.

In the animal, inositol is found in the inner leaflet of cell membranes as **phosphatidylinositol** and phosphatidylinositol 4,5-bisphosphate. Phosphatidylinositol 4,5-bisphosphate is the chemical connection between certain cell membrane **hormone** receptors and rapid changes in cellular concentrations of **calcium**. The hormone receptor in the plasma membrane activates **phospholipase** C, which cleaves phosphatidylinositol 4,5-bisphosphate to inositol 1,4,5-triphosphate (IP3) and diacylglycerol. IP3, a soluble compound, diffuses through the cytosol and binds to specific IP3 receptors on the endoplasmic

reticulum to cause the release of stored calcium. The increased calcium binds to and activates any of several different classes of regulatory proteins to initiate a physiological effect. The diacylglycerol remains in the cell membrane and together with the elevated calcium is a potent activator of protein kinase C, another important signalling protein. (NJB)

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Insecticide residues:

see Pesticides

Insectivore

Mammalian species whose diet is principally insects. Many bird species also have an insectivorous diet, but they are not usually known as insectivores. (CJCP)

Insects as animal feed

Insects have recently been proposed as a suitable **protein source** for animal **feed**, specifically for poultry, pigs and **aquaculture** production systems (Sogari *et al*., 2019). However, the regulatory systems on the use of insects in animal feed differ between countries. The nutritional profile of insects places them as a potential replacement for **soybean** meal or fish meal, due to their

high protein content, **amino acid** profile and good **digestibility** (Hall *et al*., 2018). Whole insect meal is rich in protein, energy and minerals. However, processing to separate into a high-protein meal, high-energy **oil** and a **chitin by-product** would be preferable, to facilitate the replacement of specific feed ingredients. Insects contain several bioactive components, such as **lauric acid** (Jackman *et al*., 2020), antimicrobial peptides (Wu *et al*., 2018) and chitin (Park and Kim, 2010), suggesting potential value if used as **feed additives**.

Nutritional composition of insects is driven by both the feed **substrate** and the insect growth or developmental stage. There is often a reflection of the nutritional composition of the feed within the insect itself. **Fat** (as total oil and **fatty acid**s) content has the greatest variation, generally reflecting the diet suitability, while there is little evidence of amino acid variation in **true protein** within an insect species (Fitches *et al*., 2019). The second factor is the growth or developmental stage of the insect, which is also influenced by the type of insect and whether it is holometabolous (larval followed by a pupal stage and then the adult form; three distinct stages) or hemimetabolous (larvae hatch into a form similar to the adult; non-distinct stages) (Finke and Oonincx, 2017). Chitin content of insects will vary throughout the life cycle and generally increases as they go through the various **moulting** cycles.

Protein is the main component of insects on a dry matter (DM) basis, followed by fat (Rumpold and Schlüter, 2013). Average **crude protein** content ranges from 40% to 62% of DM for the

species in Table 1, which is similar to the average for 'Hipro' soybean meal (54% of DM) and fish meal (73% of DM) as traditional protein sources. The crude protein content may overestimate true protein content (Jonas-Levi and Martinez, 2017), due to the presence of *N*-acetyl glucosamine monomers within the insect cuticle (exoskeleton) (Rathore and Gupta, 2015). Crude protein is typically calculated by multiplying the total **nitrogen** content of a feed material by a conversion factor (6.25), but 4.76 and 5.60 have been suggested as alternative conversion factors for whole insects and protein extracts, respectively, as these take the extra **non-protein nitrogen** (NPN) in the exoskeleton into consideration (Janssen *et al*., 2017).

Insects contain ten essential amino acids: **lysine**, **tryptophan**, **histidine**, **phenylalanine**, **leucine**, **isoleucine**, threonine, **methionine**, **valine** and **arginine**. Thus, they have a well-balanced amino acid profile which is comparable to soybean meal and fish meal (Table 2). Animals have a dietary requirement for essential amino acids (EAA) and those that are below the animal's requirement are considered limiting. Lysine, tryptophan, methionine and **cysteine** are often limiting in raw materials used in livestock feeds and have to be supplemented with synthetic amino acids. Housefly larvae have very similar methionine and a higher cysteine content compared with fish meal. All species in Table 2, apart from the superworm and lesser mealworm, have a higher methionine content than soybean meal, which may make these more desirable to include in **feed formulation**s.

Protein quality is directly correlated to the digestibility or

bioavailability of the sum of the amino acids. **Protein digestibility** of insect meal has been suggested to be between 77% and 98% (Ramos-Elorduy *et al*., 1997) and similar to that of fish meal (Hall *et al*., 2018), although there can be variation in protein digestibility between species and processing methodologies.
The fat content of insect meal is predominantly made up of **triacylglycerol** (Kourimska and Adámková, 2016). Of the species in Table 1, the superworm has the highest average total fat content (38.8% of DM) and housefly the lowest (19.0% of DM). The fat content is much higher than traditional **protein source**s, but it is important to highlight that soybean meal has already been processed to remove some of the fat. The main **fatty acid**s in insect meals are palmitic (C16:0), oleic (C18:1) and linoleic (n-6 C18:2) acids, as shown in Table 2. Uniquely, black soldier fly larvae have 43.6% of total fatty acids as the medium-chain **saturated fatty acid** (MCFA), **lauric acid** (C12:0), which is comparable to **coconut** oil (Dayrit, 2015).

The **carbohydrate** content of the insect body is very low (Finke and Oonincx, 2017). There is little published data reporting the acid detergent fibre (ADF) or neutral detergent fibre (NDF) content of insects. Black soldier fly larvae have been reported to have an ADF content ranging from 13% (Campbell *et al*., 2020) to 29% (Shumo *et al*., 2019) and NDF content from 7.9% (Campbell *et al*., 2020) to 15% (Shumo *et al*., 2019), on a DM basis. When **labelling** commercial livestock feed products, **crude fibre** is one of the nutrients required for regulatory purposes. The averages for these are reported in Table 1 but investigation is still needed for a

better understanding of the composition of this fibre in insects.

Chitin is a component of the insect exoskeleton and has a structure similar to that of **cellulose**, therefore it is relatively resistant to degradation. However, many mammals and avian species can express **chitinase** in their digestive tracts. Although there may be concerns as to the insolubility of chitin within the gut, it has also been reported to have beneficial **antioxidant** and anti-inflammatory properties (Park and Kim, 2010).
Both the macro-minerals (**calcium**, **phosphorus**, **magnesium**, **sodium**, **potassium** and **chloride**) and trace minerals (**iron**, **zinc**, **copper**, **manganese**, **iodine** and **selenium**) in insects are likely to be sufficient to meet the requirements of most animals (Barker, 1998; Finke and Oonincx, 2017). Average insect **ash** content varies from 2.7% (superworm) to 15.1% (black soldier fly) of DM. Due to a lack of a calcified skeleton, insects have less calcium than other protein sources. Black soldier fly larvae have a mineralized exoskeleton, therefore they have an increased calcium content when compared with the other insect species; however, mineral bioavailability may be limited as it is usually bound to chitin, which has limited digestibility in **monogastric**s (Rathore and Gupta, 2015). There may be increased bioavailability of phosphorus from insects due to the lack of the **antinutritional factor**, **phytate**, which is common in plants.

Data on vitamin content of insects is varied. Commercially farmed insects tend to have low levels of **vitamin D** (< 400 IU kg^{-1} DM) (Finke and Oonincx, 2017). **Vitamin E** content of various

insect species has been reported to vary from 15 to 509 IU kg^{-1} and **vitamin A** from 150 to 2400 IU kg^{-1} (Barker *et al.*, 1998). Insects are a good source of **B-complex vitamins**, but there are concerns that processing and storage reduces this content. Unprocessed, whole insect meal is a good source of **riboflavin** (B_2), **niacin**, **pantothenic acid**, **pyridoxine** (B_6), **biotin**, folic acid and cyanocobalamin (B_{12}) (Finke and Oonincx, 2017).

Legislation regarding the use of insects in animal feed varies between countries, with no global consensus. Previously the use of terrestrial **animal protein** in poultry and pig diets was prohibited owing to regulations concerning bovine spongiform encephalitis and other transmissible spongiform encephalopathies. In the European Union, terrestrial invertebrates (insects) have historically been permitted for use either live or dead as an unprocessed 'whole insect' feed material. The use of insect-derived processed animal proteins (PAPs) was also permissible in pet food, feed for fur animals and other non-food producing animals under Regulation (EC) No 1069/2009. In 2017, the use of insect PAPs originating from seven insect species (black soldier fly (*Hermetia illucens*), common housefly (*Musca domestica*), yellow mealworm (*Tenebrio molitor*), lesser mealworm (*Alphitobius diaperinus*), banded cricket (*Gryllodes sigillatus*) and field cricket (*Gryllus assimilis*)) was permitted in **aquaculture** (Regulation (EU) No 2017/893) and in August 2021 the Official Journal of the European Union of Commission Regulation (EU) 2021/1372 was published, an act that authorized the use of farmed-insect PAPs in poultry and pig feed within the EU.

There is an opportunity to utilize insects and insect products on a greater level as a potentially sustainable source of **macro**- and **micronutrients**. Although the insect production market is still in its infancy and so is more likely to have a variable composition, depending on species grown, life stage and feed materials used, there is a capability for it to be a replacement of traditional feed ingredients or to be used alongside them. (KH; HH)

Table 1. Average proximate composition of six commonly used insect species for animal feed (sources presented below)

Common name	**Latin name**	**Crude protein** (% DM)	**Total fat** (% DM)	**Crude fibre** (% DM)	**Ash** (% DM)	**Gross energy** (MJ kg^{-1} DM)
Black soldier fly larvae	*Hermetia illucens*	40.2 (30–56.1)	25.9 (1.7–57.8)	7.0	15.1 (3.9–31.1)	23.1 (19.9–26.7)
Black soldier fly prepupae		42.5 (30.8–60.7)	26.0 (8.0–41.0)	2.6 (2.1–3.4)	11.8 (2.7–19.7)	21.3 (18.3–24.3)

Common name	**Latin name**	**Crude protein** (% DM)	**Total fat** (% DM)	**Crude fibre** (% DM)	**Ash** (% DM)	**Gross energy** (MJ kg^{-1} DM)
Mealworm	*Tenebrio molitor*	49.0 (37.9–63.0)	29.7 (2.1–47.5)	6.8 (2.0–9.5)	3.8 (2.6–6.1)	24.7 (21.4–27.8)
Superworm	*Zophobas morio*	44.4 (38.7–49.3)	38.8 (21.0–46.3)	9.1 (5.1–11.3)	2.7 (0.6–4.9)	23.8 (22.2–24.8)
Lesser mealworm	*Alphitobius diaperinus*	59.2 (48.3–64.8)	28.9 (22.2–34.0)	N/D	4.2 (4.1–4.3)	20.2
Housefly	*Musca domestica*	54.9 (42.3–64.0)	19.0 (6.8–29.7)	6.8 (1.4–16.8)	8.8 (1.3–19.1)	22.8 (20.1–29.7)
Cricket	*Acheta domesticus*	62.4 (52.8–71.7)	21.3 (10.4–32.0)	15.6 (4.6–19.2)	5.4 (4.8–6.2)	18.2 (17.4–18.8)

Common name	**Latin name**	**Crude protein** (% DM)	**Total fat** (% DM)	**Crude fibre** (% DM)	**Ash** (% DM)	**Gross energy** (MJ kg^{-1} DM)
For comparison:						
Hipro Soybean Meal		55.2	1.7	4.4	7.3	19.7
Fish meal, protein 70%		74.8	9.8	0	15.2	21.3

DM, dry matter; N/D, no data

Sources:

BSF larvae: Bosch *et al.*, 2014; De Marco *et al.*, 2015; Oonincx *et al.*, 2015; Liland *et al.*, 2017; Shumo *et al.*, 2019; Campbell *et al.*, 2020; Ewald *et al.*, 2020; Melenchon *et al.*, 2020; Oddon *et al.*, 2021

BSF prepupae: (St-Hilaire *et al.*, 2007; Spranghers *et al.*, 2017; Julita *et al.*, 2018; Meneguz *et al.*, 2018)

MW: (Jones, Cooper and Harding, 1972; Ravzanaadii *et al.*, 2012; Bosch *et al.*, 2014; Belforti *et al.*, 2015; De Marco *et al.*, 2015; Oonincx *et al.*, 2015; Adámková *et al.*, 2016; Ghosh *et al.*, 2017; Benzertiha *et al.*, 2020; Melenchon *et a*l. 2020; Harsanyi *et al.*, 2020; Oddon *et al.*, 2021)

SW: (Barker, Fitzpatrick and Dierenfeld, 1998; Jabir, Razak and Vikineswary, 2012b, 2012a; Adámková *et al.*, 2016; Benzertiha *et al.*, 2020; Harsanyi *et al.*, 2020; Kulma *et al.*, 2020)
LM: (Bosch *et al.*, 2014; Adámková *et al.*, 2016; Oonincx *et al.*, 2020; Kurecka *et al.*, 2021)
HF: (Akpodiete, Ologhobo and Oluyemi, 1997; Téguia, Mpoame and Okourou Mba, 2002; Sogbesan *et al.*, 2006; Hwangbo *et al.*, 2009; Aniebo and Owen, 2010; Pretorius, 2011; Pieterse and Pretorius, 2014; Obeng, Atuna and Aihoon, 2015; Hall *et al.*, 2018; Fitches *et al.*, 2019; Ganda *et al.*, 2021)
HC: (Finke, 2002; Bosch *et al.*, 2014; Oonincx *et al.*, 2015, 2020; Udomsil *et al.*, 2019; Harsanyi *et al.*, 2020)
HPSBM: available at https://www.feedtables.com/content/soybean-meal-**oil**-5-50-protein-oil (accessed 2 September, 2021)
Fish meal: available at https://www.feedtables.com/content/fish-meal-protein-70 (accessed 2 September, 2021)

Table 2. Average essential amino acid (mg g^{-1} crude protein) and common fatty acid (% fatty acid) content of six commonly used insect species for animal feed (sources presented below).

	Essential amino acids[b]										Fatty acids[c]					
Species[a]	**His**	**Ile**	**Leu**	**Lys**	**Val**	**Met**	**Cys**	**Phe**	**Thr**	**Trp**	**C16:0**	**C16:1**	**C18:0**	**C18:1**	**C18:2**	**C18:3**
BSFl	30.6	46.6	65.0	60.4	59.6	24.5	37.4	39.0	41.2	N/D	13.4 (11.6–17.0)	3.2 (1.5–6.6)	2.3 (1.7–2.8)	13.1 (10.2–18.1)	9.0 (3.6–17.1)	2.2 (0.2-9.7)

	Essential amino acids[b]										Fatty acids[c]					
Species[a]	**His**	**Ile**	**Leu**	**Lys**	**Val**	**Met**	**Cys**	**Phe**	**Thr**	**Trp**	**C16:0**	**C16:1**	**C18:0**	**C18:1**	**C18:2**	**C18:3**
BSFp	31.0 (27.1–33.0)	43.0 (41.7–46.0)	70.3 (63.9–71.1)	57.6 (53.4–60.9)	61.8 (55.8–65.4)	18.3 (16.6–20.0)	5.8 (5.1–6.1)	48.7 (41.3–55.8)	39.3 (37.6–40.8)	14.5 (12.6–16.8)	16.6 (11.3–20.4)	4.0 (2.1–6.1)	2.0 (1.7–2.8)	9.0 (8.5–12.5)	13.1 (4.1–23.5)	1.3 (0.4–2.5)

	Essential amino acids[b]										Fatty acids[c]					
Species[a]	**His**	**Ile**	**Leu**	**Lys**	**Val**	**Met**	**Cys**	**Phe**	**Thr**	**Trp**	**C16:0**	**C16:1**	**C18:0**	**C18:1**	**C18:2**	**C18:3**
MW	27.8 (17.2–32.1)	38.8 (26 (6–44.3))	64.6 (57.8–80.4)	58.8 (38 (4–68.5))	56.0 (47.0–70.9)	17.5 (11 (5–19.3))	17.8 (11.5–23.9)	34.3 (23 (0–41.1))	40.2 (35 (3–53.4))	10.0 (0)	17.1 (15.3–20.2)	12.10 (11.54–12.29)	34.08 (23.6–45.0)	42.52 (36.5–51.7)	20.25 (12.30–22.68)	0.7 (0.1–1.6)

	Essential amino acids[b]										Fatty acids[c]					
Species[a]	**His**	**Ile**	**Leu**	**Lys**	**Val**	**Met**	**Cys**	**Phe**	**Thr**	**Trp**	**C16:0**	**C16:1**	**C18:0**	**C18:1**	**C18:2**	**C18:3**
SW	21.2 (13.8–28.6)	32.8 (20–44.2)	51.2 (30.4–72)	44.6 (34.5–55.0)	44.8 (29.0–60.2)	95.7 (45.8–96)	5.4 (0.8–9.9)	23.9 (21.1–36.9)	30.6 (22.2–36.9)	11.6	20.3 (17.3–30.0)	0.6 (0.5–0.7)	7.2 (5.8)	32.6 (31.1–34.1)	2.3 (1.2–3.4)	0.9

	Essential amino acids[b]										Fatty acids[c]					
Species[a]	**His**	**Ile**	**Leu**	**Lys**	**Val**	**Met**	**Cys**	**Phe**	**Thr**	**Trp**	**C16:0**	**C16:1**	**C18:0**	**C18:1**	**C18:2**	**C18:3**
LMW	41.3 (37.7–45.2)	55.3 (37.5–64.3)	88.7 (79.7–96.9)	46.0 (40.4–89.0)	81.1 (56.5–93.9)	12.1 (5.1–20.1)	4.2 (3.8–8.6)	54.3 (43.9–59.6)	49.1 (37.1–57.1)	N/D	22.7 (20.8–26.4)	0.5 (0.3–1.0)	9.1 (8.0–14.2)	4.4 (4.3–35.9)	4.8 (0.4–27.1)	4.0 (1.0–9.9)

	Essential amino acids[b]										Fatty acids[c]					
Species[a]	**His**	**Ile**	**Leu**	**Lys**	**Val**	**Met**	**Cys**	**Phe**	**Thr**	**Trp**	**C16:0**	**C16:1**	**C18:0**	**C18:1**	**C18:2**	**C18:3**
HF	29.1 (24.0–34.1)	37.2 (23.2–34.1)	63.2 (54.0–71.9)	72.7 (61.0–84.3)	45.4 (34.0–50.6)	25.9 (20.0–29.6)	19.6 (3.2–71.0)	58.5 (45.6–72.3)	48.7 (35.5–73.3)	46.0 (12.5–77.0)	30.0 (25.5–38.0)	20.0 (8.0–33.3)	3.0 (2.2–4.0)	2.7 (1.8–4.2)	1.63 (0.5–2.3)	1.5 (0.5–2.0)

	Essential amino acids[b]										Fatty acids[c]					
Species[a]	**His**	**Ile**	**Leu**	**Lys**	**Val**	**Met**	**Cys**	**Phe**	**Thr**	**Trp**	**C16:0**	**C16:1**	**C18:0**	**C18:1**	**C18:2**	**C18:3**
C	23.0	42.00	75.00	59.00	65.00	18.00	8.9	39.00	40.00	8.4	25.8 (23.1–27.8)	0.8 (0.6–1.0)	8.0 (6.3–8.2)	27.7 (23.6–29.8)	28.4 (25.5–34.9)	5.2 (0.8–12.7)

	Essential amino acids[b]										Fatty acids[c]					
Species[a]	His	Ile	Leu	Lys	Val	Met	Cys	Phe	Thr	Trp	C16:0	C16:1	C18:0	C18:1	C18:2	C18:3
Insectmeal																
SBM	27.0	6.0	7.0	6.0	4.8	1.4	1.6	5.1.0	3.8.0	1.4.0	11.2	.1	3.8	23.1	54.0	7.2

	Essential amino acids[b]										Fatty acids[c]					
Species[a]	**His**	**Ile**	**Leu**	**Lys**	**Val**	**Met**	**Cys**	**Phe**	**Thr**	**Trp**	**C16:0**	**C16:1**	**C18:0**	**C18:1**	**C18:2**	**C18:3**
FM	23.8	42.1	71.8	75.4	49.7	25.7	8.4	38.9	41.4	10.3	17.8	7.2	3.6	12.3	2.1	1.9

Gianotten and Bastiaens (2020)
Common fatty acids: (Hwangbo *et al.* (2009); Ravzanaadii *et al.* (2012); Jabir, Razak and Vikineswary (2012a); Makkar *et al.* (2014); Pieterse and Pretorius (2014); Zielinska *et al.* (2015); Oonincx *et al.* (2015, 2020); Adámková *et al.* (2016); Hussein *et al.* (2017); Meneguz *et al.* (2018); Cullere *et al.* (2019)

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Insects as human food

Entomophagy, or eating insects, is a traditional common practice for more than two billion people from 130 countries worldwide, currently consuming 2100 insect species. Edible insects could provide an alternative **meat** source, while improving human global food security. The most popular species include grasshoppers, crickets, locusts (orthopterans), beetles (Coleoptera), fly larvae (dipterans), caterpillars (lepidopteran larvae) butterflies (Rhopalocera), moths (Lepidoptera), ants (Hymenoptera), bees (Anthophila), wasps (Vespidae), cockroaches (Blattodea), termites (Isoptera), dragonflies (Anisoptera), mealworms (coleopteran larvae), silkworm (Bombyx mori), scorpions (Scorpiones), cicadas (Cicadoidea). Species consumed, preferences and availabilities vary by region, due to differences in environment, ecosystems and climate. Amongst the many cultures worldwide, consumption of edible insects is least common in the Western countries.



Insects being sold for human consumption at a Mexican market. Photo courtesy of Kate Sheets. Licensed under CC BY 2.0.

Edible insects are rich in **protein**, **fat** and **energy** and can also be a significant source of **vitamins** and **minerals**. Compared with conventional livestock, they have minimal space requirements for rearing and they have a high **reproduction** level. Some insect species are multivoltine, having several broods in a season, undergoing more than one life cycle per year. Insects have low environmental impact, as they emit less greenhouse gases and **ammonia** than pigs and cattle and have a relatively high **feed conversion** efficiency for terrestrial animals. For example, crickets require only 2 kg of feed to gain 1 kg body weight. The energy levels of insects are comparable with other proteinaceous food sources such as fresh meat (per unit of fresh weight), i.e. approximately 400–500 kcal per 100 g of dry matter (DM). Despite the diverse practical advantages of edible insects, many barriers persist in accepting insects as food, because the concept is still foreign to the conventional Western eating habit.

Insects identified as appropriate for industrial production use

are black soldier flies, larvae, yellow mealworms, silkworms, grasshoppers and termites. Insect-based food or, less importantly, feed, could provide further advantages in improving the **taste** of final meat or **fish products**. In Asia and Africa insects are commonly used as fish feed. Locusts (*Schistocerca gregaria*) are used as human food in Africa, provided that they are not killed by **arsenic**. After sun-drying to remove the offensive smell, the ground locust meal is palatable. Locust meal has a DM content of 890–895 g kg^{-1} and its nutrient composition (g kg^{-1} DM) is **crude protein** (CP) 510–520, **crude fibre** 140 and **ether extract** (EE) 105–110. Lakefly from Lake Victoria have a DM of 910 g kg^{-1} and contain CP 620, minerals 180 and EE 39 g kg^{-1}. Silkworm pupae have traditionally been consumed in north-eastern China. Pupae contain **chitin** and only about 75% of their high crude protein content is **true protein**. Pupae are best utilized separated from their cocoons, thus reducing the fibre content. They are high in unsaturated fats and this can affect the taste. (JKM; DB)

Nutrition composition of edible insects (based on dry matter)

Type of insect	**Scientific name**	**Protein content** (%)	**Fat content** (%)
Larvae	*Allomyrina dichotoma*	54.18	20.24
	Gonimbrasia belina	56.95	10.00

Beetle	*Heteroligus meles*	38.10	32.01
Rhynchophorus phoenicis	50.01	21.12	
Grasshopper	*Ruspolia differens*	44.59	49.00
Zonocerus variegatus	26.80	3.80	
Crickets	*Gryllus bimaculatus*	58.32	11.88
	Teleogryllus emma	55.65	25.14
Termites	*Macrotermes bellicosus*	20.10	28.20
Macrotermes falciger	43.26	43.00	
Bee	*Apis mellifera*	21.00	12.30

The composition of various insects used as animal food.

	Nutrient composition (g kg^{-1} DM)

	Dry matter (g kg^{-1})	Crude protein	Crude fibre	Ash	Ether extract	NFE	Ca	P
Whole locusts								
Raw, Kenya	294	635	135	87	141	2	–	–
Dried, Tanzania	895	516	140	–	109	–	–	–
Silkworm (*B. mori*)								

Solvent extracted	925	776	43	73	10	98	1	15
Raw	200	542	39	52	303	64	1	11
Silkworm (*A. mylitta paphia*)								
Solvent extracted	928	742	102	69	11	76	2	8
Raw	200	563	77	53	300	7	2	7

Source: FAO (2002), available at http://www.fao.org/ag/AGA/AGAP/FRG/AFRIS/Data/239.HTM

NFE, nitrogen-free extract.

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Insulin

A **peptide hormone** with a molecular weight of 5808, containing two chains. The A chain has 21 **amino acid**s and the B chain 30 amino acids. The chains are linked by two disulphide bridges. Insulin is synthesized in the β-cells of the islets of Langerhans in the **pancreas**. It is synthesized in the rough endoplasmic **reticulum**, transported to the Golgi and packaged in membrane-bound granules. Its half-life in plasma is about 5 min. Its action is initiated by binding to insulin receptors on the cell surface. Insulin is anabolic, increasing the cellular storage of **glucose**, **fatty acid**s and amino acids. An excess of insulin results in **hypoglycaemia**, coma and death. Continuous low concentrations of insulin result in **diabetes** mellitus, leading to high circulating levels of glucose which, if left unchecked, results in a debilitating disease that ultimately becomes fatal. (NJB)

Insulin-like growth factor (IGF)

Designated as IGF-I and IGF-II. IGF-I is a polypeptide of 70

amino acids whereas IGF-II has 67 amino acids. A significant degree of amino acid sequence homology exists between **insulin** and IGF-I and IGF-II. IGF-I is regulated by **growth hormone** and nutritional status. It is synthesized in the **liver** and other tissues and is involved in skeletal and **cartilage** growth. In plasma it is found bound to IGF-**binding protein**s (five or more), which inhibit its action. IGF-II is synthesized in many tissues and factors involved in its regulation are not known. As with IGF-I in plasma, IGF-II is bound to binding proteins. It is thought to be involved in embryonic development. (NJB)

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Intake:

see Feed intake

Interactions:

see Environment–nutrition interaction; Genotype–nutrition interaction

International units

The International System of units is abbreviated as SI (Système Internationale d'Unités), a coherent system based on seven basic

units and two subsidiary units, the radian and steradian. These are listed in Table 1 along with a number of derived SI units. SI units replace the British FPS (foot, pound, second) system and the metric CGS (centimetre, gram, second) system. SI units are based on the MKS (metre, kilogram, second) system; they are decimal and coherent. Coherent means that all derived units are formed by multiplication or division of the basic SI units without the introduction of any numerical factor, or even a power of ten. This has the advantage that when measurements expressed in basic SI units are substituted into an equation, the result is automatically in the appropriate basic unit of the SI. SI units are given unit symbols that follow all the usual rules of algebra. They do not need a full stop as in abbreviations, nor do they need an 's' to form a plural (i.e. two centimetres is 2 cm, not 2 cms). Multiplying prefixes listed below can be used to indicate decimal subunits or multiples of units to allow convenient and manageable numbers in the range 0.1–999.9.

Table 1. The International System of units.

Property	**SI unit**	**Symbol**
length	metre	m
mass	kilogram	kg
time	second	s

electric current	ampere		A	
temperature	kelvin		K	
amount of substance	mole		mol	
luminous intensity	candela		cd	
angle	radian		rad	
solid angle	steradian		sr	
Derived SI units				
frequency	hertz	Hz	=	s^{-1}
force	newton	N	=	kg m s^{-2}
energy	joule	J	=	kg m^2 s^{-2}

power	watt	W	=	$kg\ m^2\ s^{-3}$
luminous flux	lumen	lm	=	cd sr
illumination	lux	lx	=	$cd\ sr\ m^{-2}$
pressure	pascal	Pa	=	$kg\ m^{-1}\ s^{-2}$
electric charge	coulomb	C	=	A s
e.m.f.; p.d.	volt	V	=	$kg\ m^2\ s^{-3}\ A^{-1}$
resistance	ohm	Ω	=	$kg\ m^2\ s^{-3}\ A^{-2}$
capacitance	farad	F	=	$A^2\ s^4\ kg^{-1}\ m^{-2}$
magnetic flux	weber	Wb	=	$kg\ m^2\ s^{-2}\ A^{-1}$
flux density	tesla	T	=	$kg\ s^{-2}\ A^{-1}$
inductance	henry	H	=	$kg\ m^2\ s^{-2}\ A^{-2}$

conductance	siemens	S	=	Ω^{-1}	

Decimal multiple and sub-multiple prefixes

10^{18}	exa	E	10^{-1}	deci	d
10^{15}	peta	P	10^{-2}	centi	c
10^{12}	tera	T	10^{-3}	milli	m
10^{9}	giga	G	10^{-6}	micro	μ
10^{6}	mega	M	10^{-9}	nano	n
10^{3}	kilo	K	10^{-12}	pico	p
10^{2}	hecto	H	10^{-15}	femto	f
10	deca	D	10^{-18}	atto	a

Dimensionless numbers

Since SI unit symbols follow algebraic rules, dimensionless numbers can be created by dividing a quantity symbol by an appropriate unit symbol. If h = 5 m, where h denotes height, we

may write $h/\mathrm{m} = 5$, so that the right-hand side has no unit and is dimensionless. This is useful for heading columns of figures or **labelling** axes of graphs, making the numbers on the axes more manageable; for example, an axis labelled wavelength/nm can be labelled wavelength/10^2 nm, thus removing two zeros from every number along the axis.

Note the following:

The mole is based on the gram, not the kilogram.
SI thermodynamic temperature is the kelvin symbol K (not °K).
The Celsius scale is more often used in practical measurements: 273 K is approximately 0°C. The Celsius scale has intervals of 1 kelvin.
In the USA, metre is spelt 'meter' and litre is 'liter'.
A number of non-SI units persist in usage: litre, **calorie**, per cent, parts per million. A number of these are listed in Table 2.

Table 2. Non-SI units.

Non-SI unit	Abbreviation	Definition
atmosphere	atm	101,325 Pa (definition)
Torr	torr	133.322 Pa = 1/760 atm
atomic mass unit	amu	1.66054×10^{-27} kg
bar	bar	1×10^5 Pa
electron volt	eV	1.602178×10^{-19}J

Non-SI unit	Abbreviation	Definition
poise	P	0.1 kg m^{-1} s^{-1}
litre	l	1×10^{-3} m^3 = 1 dm^3
ångström	Å	1×10^{-10} m
debye	D	3.335641×10^{-30} C m
calorie	cal	4.184 J (definition)
Calorie (kilocalorie)	Cal	4.184 kJ
inch	in / "	0.0254 m (definition)
pound	lb	0.4536 kg
per cent	%	0.01 kg kg^{-1}; 0.01 kg l^{-1}
part per million	ppm	mg kg^{-1}; mg l^{-1}
part per billion	ppb	µg kg^{-1}, µg1^{-1}

International units (IU or i.u.) are used to express the quantities of **vitamins** A, D and E in terms of their biological activity. They are older units, devised before these vitamins could be separated by HPLC and their **isomer**s measured accurately. However, their use persists and they can be converted by the following factors:

0.3 micrograms (µg) retinol equivalent = 1 IU vitamin A

0.6 µg beta carotene = 1 IU beta carotene

1.0 µg vitamin D = 40 IU vitamin D

1.0 mg natural vitamin E (D-alpha tocopherol) = 1.49 IU vitamin

E

1.0 mg synthetic vitamin E (DL-alpha tocopherol acetate) = 1.0 IU vitamin E(IM)

Intersuckling

The taking of **milk** direct from the teat of another cow. Also known (incorrectly) as intersucking. It may stem partly from the **cross-sucking** behaviour of calves whose **suckling** behaviour is thwarted by being provided milk from a bucket. (CJCP)

Intestinal absorption

The process by which **nutrients**, including **vitamins**, **minerals** and water, enter the body from the lumen of the **gastrointestinal tract**.

As outlined by Mace and Marshall (2013), after the consumption of food the epithelial cells in the **small intestine** are primed to selectively absorb substances from the **digesta**. Among the epithelial cells are absorptive cells and enteroendocrine cells (EEC). The primary purpose of absorptive epithelial cells, which account for approximately 90% of the epithelial **mucosa**, is to selectively take up nutrients from the intestinal lumen across the **brush border** membrane (BBM) to the extracellular fluid (ECF), from where they pass to the lymph and **blood**. Nutrient-sensitive chemosensors are positioned strategically within the gastrointestinal tract to control the process of nutrient **absorption** and gut **hormone** secretion. The composition of the diet modulates the absorptive capacity of the intestine and the secretion of gut peptides, including glucoinsulinotropic polypeptide,

glucagon-like **peptide**-1 and peptide YY. Through these mechanisms, chemosensors including nutrient transporters and G **protein**-coupled receptors are able to regulate cellular **energy** uptake, expenditure and **homeostasis** in the intestine. This is achieved by modulating the expression of key nutrient-transporting proteins at the BBM to upregulate nutrient absorption. Nutrients may also be absorbed by para-cellular absorption, by which the nutrients move directly to the ECF through the tight junctions between the epithelial cells or by **pinocytosis** (amoeba-like engulfing of macromolecules and ions).

Complex **carbohydrates**, proteins and **lipids** are generally not absorbed intact: they must first be broken down (digested) to absorbable units. The membranes of the epithelial cells contain glycoprotein **enzymes** that hydrolyse **oligosaccharide**s and disaccharides into **monosaccharide**s, and **oligopeptide**s into di- and tripeptides and **amino acid**s, before absorption.

Absorption of sugars

Glucose is transported across the intestinal epithelium by a Na^+-dependent facilitative transporter protein (GLUT2) to enter the systemic circulation. **Galactose** is transported by the same carrier protein. **Fructose** is transported by a different facilitative transporter protein (GLUT5), which is independent of Na^+. Some fructose is converted to glucose in **mucosa**l cells.

Absorption of amino acids

The final products of **protein digestion** are a mixture of amino acids and small peptides. Amino acids are transported in a similar

manner to glucose with co-transport of Na^+ or H^+, whereas di- and tri-peptides are transported across the BBM by an H^+-coupled peptide transporter (PepT1). Several transporters are involved in the process of amino acid absorption. A separate system transports di- and tripeptides into the mucosal cells, where they are hydrolysed to amino acids. The transported amino acids, as well as those produced by intracellular **hydrolysis** of di- and tripeptides, accumulate in the mucosal cells and then enter the ECF by simple **diffusion** and facilitated diffusion. Some small peptides may also enter portal blood. Only about half of absorbed amino acids come from ingested food. The other half come from endogenous sources, mainly proteins in digestive juices and desquamated mucosal cells. Several specific factors in the food may influence the reabsorption of endogenous protein in the **ileum**. **Nucleotides**, produced from the hydrolysis of **nucleic acid**s (DNA and RNA) by pancreatic nucleases, are hydrolysed to nucleosides and phosphoric acid and further to their constituent **pentoses**, **purine** and **pyrimidine** bases by enzymes located on the luminal surfaces of the epithelial cells. The liberated bases are absorbed by active transport.

Absorption of lipids

Dietary lipids enter the small intestine as lipid droplets, which are emulsified by **bile** acids and pancreatic secretions. Triacylglycerides are hydrolysed by pancreatic **lipase** to **fatty acid**s and monoglycerides and associate with bile acids to form micelles. Distinct from carbohydrate, peptide and amino acid absorption, micelles enter the lymphatic circulation as **chylomicron**s (**lipoprotein**s). Fatty acids with fewer than 10–12

carbon atoms pass directly from the epithelial cells into the portal blood, where they are transported as free (unesterified) fatty acids, whereas fatty acids with more than 10–12 carbon atoms are re-esterified to triglycerides. They are then coated with a layer of protein, **cholesterol** and **phospholipid** to form chylomicrons. These leave the cell by pinocytosis, enter the lymphatics and are transported by the lymph system to the systemic blood circulation They are then coated with a layer of protein, cholesterol and phospholipid to form chylomicrons. These leave the cell by pinocytosis, enter the lymphatics and are transported by the lymphatic system to the systemic blood circulation through the thoracic lymph duct. Mucosal-associated lymphoid tissue and other lymphatic tissue also defend against entry of pathogens.

Absorption of minerals

Minerals can be absorbed from any portion of the gastrointestinal tract but this takes place mainly in the small intestine via two pathways (Goff, 2018). In high concentrations, many minerals utilize paracellular absorption, where the mineral diffuses across the tight junction between epithelial cells or moves with the bulk flow of water between intestinal epithelial cells to enter the systemic blood. At lower dietary concentrations, the body relies on transcellular absorption that requires special transporters to meet its mineral needs. The form in which the mineral source is present in the diet can influence mineral availability. For instance, some organic and **chelate**d minerals supply the mineral in a more bio-available form than in traditional inorganic forms of these minerals.

Sodium is actively absorbed in the small intestine either with glucose, galactose or amino acids or alternatively by a sodium/**potassium** pump. Furthermore, sodium can diffuse into and out of the small intestine, depending on the concentration gradient throughout the small and **large intestine**s. The sodium concentration in the intestinal lumen is maintained by a high sodium concentration in the digestive secretions. Potassium is absorbed primarily by passive diffusion. **Chloride** is absorbed in a coupled transport with sodium or by exchange with **bicarbonate**.

Calcium is absorbed primarily in the proximal small intestine by active transport, but there is also some passive transport. Active transport is facilitated by 1,25-dihydroxycholecalciferol, a **metabolite** of **vitamin D**, which induces the synthesis of a Ca^{2+}-**binding protein** in the epithelial cells. The synthesis of the metabolite from vitamin D is controlled hormonally and related to the concentration of calcium in the blood. Thus, calcium absorption is adjusted to the body's needs. The absorption of calcium, as well as of **magnesium**, is affected by certain dietary factors. For instance, dietary **lactose** has been shown to enhance calcium absorption while the presence of **phytate** acid in **dietary fibre** binds strongly to calcium and interferes with its absorption.

Iron is absorbed primarily in the proximal small intestine and primarily in the ferrous state (Fe^{2+}). However, if dietary iron is in the ferric form (Fe^{3+}) it can be reduced by **ascorbic acid** and other reducing agents once dissolved at the low pH in the **stomach**. Haem is also absorbed and the Fe^{2+} it contains is

released in the epithelial cells. The mucosal cells contain an intracellular iron carrier, but the polypeptide **transferrin** is also important for iron transport in the plasma. Apoferritin is a protein in the epithelial cells that binds iron. The resulting **ferritin** is lost when the epithelial cells are shed into the intestinal lumen at the end of their life cycle. Absorption of iron is inhibited by phytic acid, phosphates and **oxalates** that form insoluble complexes with iron in the intestine.

Phosphorus in feeds is either organically bound or as inorganic phosphates. Phosphorus in the form of **phytate** (inositolphosphate) is not bio-available to non-ruminants, which do not possess an effective endogenous **phytase** secretion. **Supplementation** of the diet with phytase is necessary to obtain release of the phosphorus. Absorption occurs via two distinct mechanisms: passive para-cellular absorption when the diet contains a high level of P; and by a saturable, active transcellular transport system when the diet is low or marginal in P.

Absorption of vitamins

Most of the vitamins are absorbed in the proximal small intestine. **Fat-soluble vitamins** are absorbed together with other lipids after the formation of micelles. Each of the **water-soluble vitamins** appears to require its own membrane transport process for absorption across the **enterocyte**. The absorption of vitamin B_{12} (**cobalamin**) is unique in requiring multiple factors from the stomach to the **ileum** that involve at least four different binding proteins. All water-soluble vitamins are absorbed from the small

intestine, but **folate**, **biotin** and **riboflavin** can also be transported across colonic epithelial cells, with uncertain nutritional significance.

Water moves freely into and out of the intestines and maintains an osmotic pressure that equals that of the plasma. Almost all the water entering the digestive tract, whether from intake or secretions, is absorbed in the intestine. (RB; SB)

See also: Absorption; Digestion; Lipid absorption

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Intestinal diseases:

see Digestive disorders

Intestinal fluid:

see Chyme; Digesta

Intestinal microorganisms:

see Gastrointestinal microflora

Intestinal motility:

see Motility

Intestinal mucosa
The tissue between the muscularis mucosae and the intestinal lumen. The **mucosa** is made up of the muscularis mucosae, the lamina propria, vascular bed, lymphatic system and the **enterocyte**s that cover the intestinal **villi**. In the **small intestine** the epithelial cells are of at least three types: columnar, **goblet cell**s and argentaffine cells. Goblet cells secrete **mucin**, a glycoprotein that provides protection to the intestinal surface. The columnar cells have microvilli that face the intestinal lumen; these microvilli are where the **disaccharidase** enzymes and peptidases are found. Argentaffine cells are found in the crypts of Lieberkühn. (NJB)

Intestinal mucosal proteins and peptides
The **mucosa** of the **small intestine** accounts for approximately 0.6–0.8% of the body weight in livestock and poultry, depending on animal species and age. Major proteins (including digestive and antioxidative **enzymes**) and peptides present in the intestinal mucosa are summarized in Table 1. These high- and low-molecular-weight substances have important physiological roles, including the growth of mucosal epithelial cells, the maintenance of intestinal integrity, the restitution of the mucosal epithelium, antioxidative responses and intestinal **immunity** against pathogen invasion. After hogs are slaughtered at certain **pork** processing facilities, luminal content in the small intestine is carefully removed, and its mucosal tissues are collected and subjected to

extraction for heparin and other molecules. The protein-rich mixture post extraction undergoes various drying processes for the manufacturing of intestinal mucosal products as ingredients for animal diets. Use of the spray-drying method usually is more effective in preserving bioactive proteins and peptides in the intestinal mucosa, while other drying methods with carriers such as **soybean** meal and soy protein are also applied by certain manufacturers. This category of intestinal mucosal protein products includes numerous commercial brands, such as MucoPro 80P (Sonac, a subsidiary of Darling Ingredients, USA), Dried Protein Solubles (Nutro-Flo, USA), and Pro-Pep (International Nutrition, USA). These palatable feedstuffs contain about 60% **crude protein** (on an as-fed basis) and provide farm, companion, and **zoo animals** with a large amount of highly digestible protein and peptides (Myers *et al*., 2014; Li and Wu, 2020; Tang *et al*., 2021), while the composition of bioactive compounds in this category of intestinal mucosa protein products and their influences on animal performance are yet to be fully elucidated.

Table 1. Proteins and peptides in the small-intestinal mucosa of animals[a]

Molecules	Classification	Major functions
Antibodies (e.g. IgA)	Proteins	Cell-mediated immunity
Azurocidin	Protein	Antimicrobial and innate immunity

Molecules	Classification	Major functions
Catalase	Protein	Kill pathogenic organisms and support innate immunity
Cathelicidins	Small peptides	Antimicrobials and innate immunity
Cathepsin G	Protease	Antimicrobial and innate immunity
Cathepsin K	Protease	Antimicrobial and innate immunity
Cholecystokinin (CCK)	Polypeptide	Stimulate pancreatic secretions
Chymase	Protease	Antimicrobial and regulation of intestinal mucosal homeostasis
Collagen	Protein	Structure and function of the extracellular matrix
Dopuin (pigs)	62-AA peptide	Antimicrobial
Epidermal growth factor	Protein	Promote the grown of epithelial cells and restitution of the epithelium

Molecules	Classification	Major functions
Fibroblast growth factors	Proteins	Stimulate the growth of epithelial cells
Gastrin	Small peptide	Stimulate gastric acid secretion to enhance digestion and kill bacteria; promote gut maturation
Ghrelin	Polypeptide	Stimulate food intake by animals
Glucagon-like peptide-1	Polypeptide	Regulate glucose metabolism
Glucagon-like peptide 2	Polypeptide	Promote intestinal mucosal integrity
α-Defensins (cryptdins)	Small peptides	Antimicrobials and innate immunity
β-Defensins	Small peptides	Antimicrobials and innate immunity
Diamine oxidases	Proteins	Antimicrobials and innate immunity
Digestive enzymes[b]	Proteins	Enhance the digestion of protein, carbohydrate and fat in diets

Molecules	Classification	Major functions
Glutathione	Small peptide	A major antioxidant
Glutathione reductase	Protein	An antioxidant enzyme
Histidins	His-rich large peptides	Antimicrobials and innate immunity
Insulin-like growth factor 1	Large peptide	Stimulate the growth of epithelial cells
Interferon-γ	Protein	Regulates epithelial homeostasis
Interleukin-2	Protein	Protect the intestinal epithelium
Interleukin-4	Protein	Protect the intestinal epithelium
Interleukin-10	Protein	Increase the survival of mucosal T cells
Lysozymes	Proteins	Antimicrobials, innate immunity and maintain extracellular matrix
Mucins	Thr-rich glycoproteins	Maintain intestinal mucosal integrity

Molecules	Classification	Major functions
Myeloperoxidase	Protein	Kill pathogenic organisms and support innate immunity
Phospholidase A2	Protein	Antimicrobial and innate immunity
Superoxide dismutase	Protein	Kill pathogenic organisms and support innate immunity
Peptide YY	Small peptide	Regulate gut development and motility
PR-39 peptide	Pro-Arg-rich peptide	Antibacterial and innate immunity
Transforming growth factor-α	Protein	Enhance the growth of epithelial cells and the restitution of the epithelium
Transforming growth factor-β	Protein	Enhance the growth of epithelial cells and the restitution of the epithelium

Molecules	Classification	Major functions
Vascular endothelial growth factor	Protein	Maintain microvasculature structure

[a] Adapted from Li *et al.* (2021).

[b] Including disaccharidases, proteases, and peptidases.

When mucosal proteins and peptides are fed to an animal, they are hydrolysed to free **amino acid**s as well as dipeptides and tripeptides for **absorption** into the **enterocyte**s of the small intestine, thereby contributing to **nutritive value**s. The content of amino acids in intestinal mucosa protein products is summarized in Table 2. Compared with **feather meal** (on an as-fed basis), intestinal mucosal product contains lower amounts of the following amino acids: **alanine** (–12%), **arginine** (–35%), **cysteine** (–78%), **glycine** (–52%), 4-**hydroxyproline** (–79%), **isoleucine** (–33%), **leucine** (–38%), **phenylalanine** (–41%), **proline** (–73%), **serine** (–66%), threonine (–29%), **tryptophan** (–14%) and **valine** (–42%); greater amounts of the following amino acids: aspartate (+27%), **glutamate** (+24%), **histidine** (+47%), **lysine** (+90%) and **methionine** (+57%); and similar amounts of the following amino acids: **asparagine**, **glutamine** and **tyrosine**. Compared with **meat and bone meal** (on an as-fed basis), mucosal protein contains lower amounts of the following amino acids: alanine (–23%), asparagine (–29%), glycine (–50%), 4-hydroxyproline (–64%), proline (–46%), and **taurine** (–58%); greater amounts of the following amino acids: aspartate (+20%),

cysteine (+84%), glutamate (+47%), isoleucine (+33%), leucine (+18%), lysine (+31%), phenylalanine (+25%), serine (+46%), threonine (+17%), tryptophan (+74%), tyrosine (+46%) and valine (+51%); and similar amounts of the following amino acids: glutamine, histidine and methionine.

Table 2. Composition of amino acids in the intestinal-mucosa protein product[a]

Amino acid	Content (%)	Amino acid	Content (%)
Alanine	3.69	Leucine	4.21
Arginine	3.76	Lysine	4.10
Asparagine	1.57	Methionine	1.18
Aspartate	3.70	Phenylalanine	2.32
Cysteine	0.90	Proline	3.15
Glutamine	2.96	Serine	3.04
Glutamate	5.97	Tryptophan	0.68
Glycine	4.32	Threonine	2.83
Histidine	1.29	Tyrosine	2.12
4-Hydroxyproline	1.03	Valine	3.36
Isoleucine	2.56	Taurine	0.165

[a] Values are % of the feedstuff (as-fed basis). Dry matter content of the feedstuff was 89.0%.
Adapted from Li *et al.* (2021).

When used alone as a **protein supplement**, the inclusion level of intestinal mucosa products in plant-based diets for fish, poultry and weanling pigs is usually 5% to improve the balance of dietary amino acids and confer physiological effects of the supplement's bioactive proteins and peptides on the small intestine (Li *et al*., 2021). Intestinal mucosal products (1.5%) can be used in a combination with both feather meal (1.5%) and meat and bone meal (1.5%) to bring about a desired complementary effect on improving amino acid nutrition and gut health (such as supporting intestinal ATP production, improving intestinal immunity and alleviating or preventing intestinal oxidative stress) in animals. These ingredients can help to sustain global animal agriculture (including **aquaculture**) and also provide **carnivore**s (such as cats, dogs, mink, ferrets, tigers, hybrid striped bass and largemouth bass) with taurine and proteinogenic amino acids to reduce competition with the growing human population for edible foods. (PL; WH; GW)

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Intolerance:
see Food intolerance

Inulin
A **fructose** polymer found in tubers of the **Jerusalem artichoke**. It is soluble in warm water. Inulin is the preferred substance to test the kidney glomerular filtration rate, because it is not reabsorbed by the kidney and can be quantified in the collected urine. After infusing inulin IV to obtain a steady state in **body fluid**s, a **sample** of urine is taken and the inulin concentration determined. By comparing the plasma concentration of inulin with the amount recovered in the urine over a specific time, the volume of **blood** cleared of inulin can be calculated. In an average human the glomerular filtration rate determined by use of inulin is 125 ml min^{-1}. (NJB)

Iodine (I)

A non-metallic element with a molecular mass of 126.9045 that exists in the elemental state as I_2. Iodine is an essential nutrient for all species of farm animals. The I content of plants can vary widely: forages contain from 0.5 to 2.5 mg kg^{-1} while seeds, such as **soybean** and **groundnut**, contain only 0.1–0.2 mg kg^{-1}. In feeds, I occurs mostly as the inorganic iodide, which is readily absorbed in all parts of the **gastrointestinal tract**. Both organic and iodate **salt** forms of I are degraded to the iodide form before **absorption** can occur.

Upon absorption, I is distributed to all parts of the body but most of it is concentrated in the thyroid gland as mono- and triiodotyrosine and thyroxine, with a small amount of 3,5,3′-**triiodothyronine**. The latter is the active form of the thyroid **hormone**.

Iodine deficiency in farm animals is demonstrated most vividly by reproductive impairment. Development of the fetus can be slowed and death *in utero* can occur, or the newborn can be weak and hairless. In adult animals, enlarged thyroid glands can develop. Iodine deficiency also can affect male **fertility**, primarily as a result of deterioration in the quality of the semen. The US National Research Council (NRC) recommends approximately 0.6 mg I kg^{-1} dry diet for cattle and horses, approximately 0.14 mg kg^{-1} diet for pigs and 0.35 mg kg^{-1} diet for poultry.

Tolerance to I in the diet varies among species of farm animals. As little as 50 mg I kg^{-1} diet for young calves reduced growth rate;

older animals tolerated as much as 200 mg I kg^{-1} diet. As a safety measure, the US NRC set the upper tolerance level for dietary I for cattle and sheep at 50 mg kg^{-1} diet. Pigs and poultry can tolerate higher amounts of I, up to an estimated 300 mg kg^{-1} diet. Horses, on the other hand, seem to be sensitive to the concentration of dietary I and the upper tolerance limit is estimated at 5 mg kg^{-1}. (PGR)

See also: Selenium; Thyroid

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Ion balance

The regulation of the amount of inorganic ions (or **electrolytes**) in the body, including Na^+, K^+, Cl^-, HCO_3^-, H^+, Ca^{2+} and PO_4^{3-}, in such a way that excretion matches daily intake. Some excretion of NaCl occurs through perspiration but the majority is highly regulated by the kidney. (GG)

Ion transport

The movement of inorganic ions across a cell membrane by the action of a specific carrier **protein**. Movement may occur by primary active transport, which requires direct energy input from **metabolism** in the form of ATP, or by secondary active transport, using the gradient of another ion such as Na^+ to power the process. (GG)

Ionophores

Ion-bearing compounds that surround cations so that the hydrophilic ion can be shuttled across hydrophobic cellular membranes to defeat the normal concentration gradient essential in living cells. Ionophores display diverse structures and profiles of cation selectivity. For example, valinomycin is a cyclic **peptide** which binds **potassium**, while monensin is a carboxylic ionophore which displays a binding preference for **sodium**. Both can act as antibiotics. Ionophores are produced by strains of *Streptomyces* bacteria. They are used in **beef cattle** to improve feed efficiency by shifting rumen **fermentation** towards the production of more **propionic acid**, which can be used by the animal, and less **methane**, which is lost. Ionophores such as monensin, lasalocid, narasin and salinomycin can be used to prevent rumen acidosis by selectively targeting *Streptococcus bovis* and *Lactobacillus* spp. which produce **lactic acid**. (JDR; GMcLD)

Iron (Fe)

A transition element with atomic number 56. The most abundant isotope of iron has an atomic weight of 55.85. Iron is one of the most abundant elements in the earth's crust. It is chemically versatile, which results in advantages and disadvantages concerning its use in biology. Iron is an essential nutrient for nearly all organisms, because it is a co-factor for proteins that perform life-sustaining processes such as the production of ATP. In vertebrates and other higher organisms, iron is required for cell division. Biological forms of iron include haem iron, in which the iron atom is inserted in the porphyrin ring of protoporphyrin IX, as

in **haemoglobin**. A variety of non-haem iron proteins also exist, the iron–**sulphur** (Fe–S) proteins being particularly important, with critical roles in ATP production by mitochondria. Other types of non-haem iron proteins include diferric **transferrin**, the serum iron transport protein, or the cytosolic iron storage protein, **ferritin**. In vertebrates, some of the major processes supported by iron-containing proteins include DNA synthesis, respiration (ATP production) and **oxygen** transport (haemoglobin). Diseases of iron **metabolism** include iron overload and iron deficiency, which can be important for some farm animals, particularly pigs. Iron deficiency can result in reduced capacity to transport oxygen (**anaemia**). It can also impair the ability of **skeletal muscle** to generate ATP and can impair the function of the immune system. Problems with the use of iron by organisms relate to its very low **solubility** and its propensity to participate in chemical reactions that lead to the formation of **free radical**s such as hydroxyl radical. Body iron content is primarily regulated through changes in the capacity of the **small intestine** to absorb iron. Once iron is absorbed it is very tightly retained, as there is no regulated way to excrete it. Approximately two-thirds of the iron in the body is present as haemoglobin. Non-haem iron is transported between organs by transferrin. (RSE)

Iron deficiency anaemia

In **metabolism**, iron is required for the production of the **blood** pigment **haemoglobin**. In iron-deficient **anaemia**, erythrocyte numbers are reduced, as is the haemoglobin content of each red

blood cell (microcytic hypochromic anaemia). Iron stores in the neonate are not high and, although the iron content of colostrum may be up to 15 times that of **milk**, this may not be sufficient to meet the requirements of a rapidly growing neonate until **weaning**. Sows' milk only provides approximately 1 mg iron per day per piglet, compared with an average requirement of 7 mg. Iron deficiency anaemia is most commonly seen in fast-growing housed piglets without access to dirt, and in young ruminants fed an unsupplemented milk-based diet with little or no **roughage**.

Piglets can be given iron by injection or orally. There have been deaths associated with these treatments. A turf can be supplied as a source of iron, or the sow can be supplemented with 2000 mg iron per day; she will pass sufficient iron in her faeces to supplement her piglets' diet.

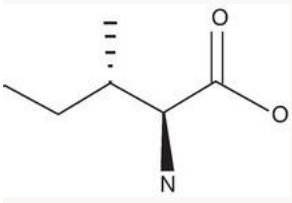
In calves, iron deficiency may be deliberately induced to give the meat a pale colour, preferred by some consumers as the meat is expected to be tender. Milk-fed calves develop iron deficiency anaemia within about 10 weeks unless a source of supplementary iron is given. Veal calf producers may attempt to provide sufficient iron for adequate growth but not enough for high levels of muscle myoglobin. Typically, this requires provision of about 25–50 mg Fe kg^{-1} DM intake, whereas milk only contains 5 mg kg^{-1}. The calf's stores of iron at birth, in the **liver**, are crucial in avoiding iron deficiency anaemia. Iron and **copper** are absorbed in **competition** and iron **supplementation** should be given judiciously to adult cattle that may be at risk of hypocupraemia. Allowing calves access to solid feed, and in particular pasture, will

allow adequate iron intake as the iron content of leaves is greater than that in seeds or milk. In the European Union it has been determined that calves must have sufficient iron in their body to have adequate haemoglobin in **blood**, considered to be 4.5 mmol l^{-1}. If blood haemoglobin is less than this, a supplement of between 25 and 50 mg Fe kg^{-1} should be provided in their diet. (EM; CJCP)

Isoenzymes:
see Isozymes

Isoflavones:
see Flavonoids

Isoleucine
An essential amino acid ($CH_3{\cdot}CH_2{\cdot}CH(\cdot CH_3){\cdot}CHNH_2{\cdot}COOH$, molecular weight 131.2) found in protein. It is one of the **branched-chain amino acid**s. Isoleucine is rarely deficient in common diets for pigs and poultry, but **blood meal** (and red blood cells per se) are quite deficient in this amino acid. The first two reactions in isoleucine **catabolism**, **transamination** followed by **oxidative decarboxylation**, are catalysed by enzymes that also act on **leucine** and **valine**. (DHB)



See also: Essential amino acids

Isomaltase
An enzyme found in the **brush border** membranes of epithelial cells in the **duodenum** and **jejunum**. Also known as α-dextrinase, it functions to 'debranch' the α-limit dextrins by cleaving α(1→6) linkages located at these branch points in **starch**. (GG)

Isomaltose
A **disaccharide**, $C_{12}H_{22}O_{11}$, molecular weight 342, of two D-**glucose** residues joined by glycosidic α(1→6) linkage; produced from branch points of **amylopectin** and **glycogen** during enzymatic **digestion**. Isomaltose is the repeating unit in dextran, an extracellular **polysaccharide** synthesized by some bacteria. Isomaltose is rarely found free in nature, except in honey and **fermentation product**s. Depending on the enzymatic system, variable amounts of isomaltose are present in partially hydrolysed amylopectin, glycogen and **maltodextrin**s. During digestion in animals, it is enzymatically hydrolysed to glucose. (JAM)
See also: Carbohydrates; Oligosaccharides; Starch

Isomers
Molecules that have the same number and kind of atoms but have them in a different arrangement, making them act as a different molecule. For example, **leucine** and **isoleucine** have the same empirical formula ($C_6H_{13}NO_2$) but act like entirely different **amino acid**s. The same is true for the **monosaccharide**s **glucose** and **galactose** ($C_6H_{12}O_6$). (NJB)

Isozymes
Different proteins that catalyse the same chemical reaction. Isozymes are found in such different organisms as human vs. bacterium. A second definition for isozymes exists in which tissues within an animal may have different subunit combinations of a multi-subunit **enzyme** such as lactic **dehydrogenase**. Lactic dehydrogenase has four subunits. There are two subunit types: H (heart) and M (muscle). The two extremes are HHHH vs. MMMM but can vary from HHHM to MMMH. This type of subunit variation has been seen for multi-subunit enzymes that are identified as dehydrogenasesoxidases, transaminases, phosphatases, etc. (NJB)

J

Jackbean (*Canavalia ensiformis* (L.) DC)
A **drought**-resistant annual **legume**, also known as sword **bean**, grown mainly in South and Central America. It is commonly used as green manure or cover crop in erosion control. Seeds are sources of **lectins**, canavanine, **urease** and other enzymes used in chemistry, biochemistry and medicine. Young pods and immature

seeds are used as vegetables after prolonged boiling or **fermentation** to detoxify. Raw seed is high in **protein** (*c.* 30% in **dry matter**) and **nitrogen-free extract** (*c.* 50%), half of which is **starch**. Raw seeds cannot be used as a feed for pigs and poultry because of **antinutritional factor**s (toxic **amino acid**s, **alkaloid**s, **polyphenol**ics, lectins, **saponin**s, **trypsin inhibitor**s and immuno-proteins) which severely reduce intake and **growth**. Boiled jackbeans included at 10% of chick diets did not impair growth, intake or feed conversion. Pigs fed boiled beans at 30% of diet showed a large reduction in initial **feed intake**. Raw seed meal in cattle diets should be < 30%. Raw beans contain urease and therefore should not be included in diets containing **urea**. Some jackbean is grown, under irrigation, for **forage** but the forage is unpalatable unless dried. (EO)



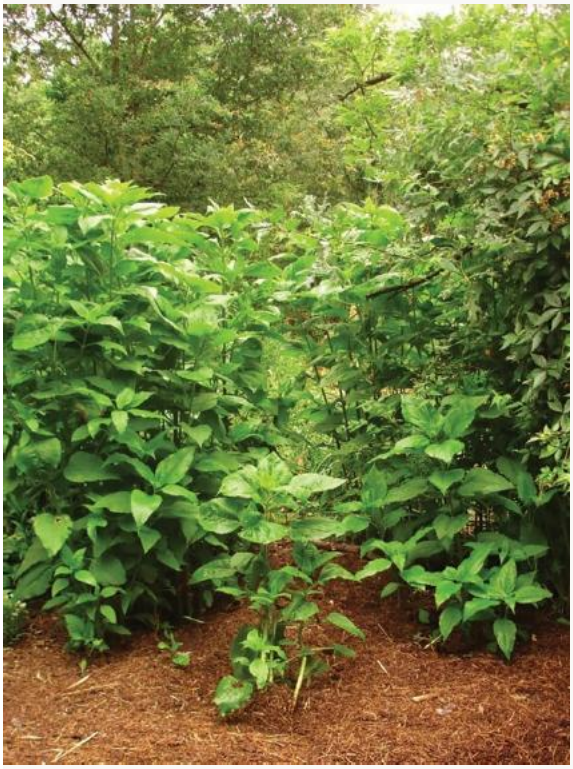
Jackbean. Jackbean seed pod and flower. Photo courtesy of Shimbe Avare. Licensed under CC by SA-2.0.

Jejunum

The central section of the **small intestine**, between the **duodenum** and the **ileum**. It is the main site for the **absorption** of the degradation products of organic nutrients, i.e. **glucose**, **amino acid**s, small **peptide**s, **fatty acid**s, monoglycerides and

glycerol. (SB)

Jerusalem artichoke (*Helianthus tuberosus*)
A perennial herb cultivated in tropical and subtropical countries for both human and animal use. The fresh tops are used as **fodder** and its white-, red- or purple-skinned tubers are used to fatten cattle, sheep and pigs. The storage **carbohydrate** in the tubers is not **starch** but **inulin**. For pigs, up to 33% can be used in place of **maize** but larger amounts reduce **digestibility** and productivity. Older pigs adapt to larger quantities of Jerusalem artichokes. (JKM)



Jerusalem artichoke plant. Photo courtesy of La Ferme de Sourrou. Licensed under CC BY-SA 2.0.

Nutrient composition of Jerusalem artichokes.

		Nutrient composition (g kg^{-1} DM)						
	Dry matter (g kg^{-1})	**Crude protein**	**Crude fibre**	**Ash**	**Ether extract**	**NFE**	**Ca**	**P**
Fresh leaves, Malaysia	217	207	124	161	23	485	20.4	3.6
Fresh aerial part	323	105	167	155	34	539	–	–
Fresh tubers, Malaysia	168	83	48	60	6	803	2.1	3.5

	Nutrient composition (g kg^{-1} DM)						
	Dry matter (g kg^{-1})	**Crude protein**	**Crude fibre**	**Ash**	**Ether extract**	**NFE**	**Ca**	**P**
Fresh tubers, Israel	196	77	66	61	5	791	–	–
Fresh tubers[a]	200	150	40	50	–	750	0.23	0.90

Sources: FAO (2002), adapted from Göhl (1981).
NFE, nitrogen-free extract.

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Jojoba (*Simmondoia chinensis*)

A small woody tree or shrub 0.5–2.5 m tall that is native to arid areas of northern Mexico and the south-west states of the USA. It is also cultivated in these areas, as well as in Argentina, Israel, Australia, Chile and India. The seed contains about 50 g **oil** kg^{-1} in the form of a wax consisting mainly of long-chain monoesters of indigestible C20 and C22 **fatty acid**s and with few triglycerides. Jojoba oil also contains a high level (121 g kg^{-1}) of **erucic acid**, a fatty acid that is toxic to animals and humans. Interest in cultivation of the plant was stimulated by the banning of commercial whaling by the International Whaling Commission in 1986, to protect depletion of world sperm-whale stocks. Jojoba oil is a good substitute for whale oil, with industrial uses as a lubricant in mechanical systems that involve high pressures and temperatures, as well as in pharmaceutical and cosmetic products.



Jojoba (*Simmondsia chinensis*) shrub, Pinto Basin, USA. Photo courtesy of Joshua Tree National Park. Licensed by Public Domain Mark 1.0.

Cattle, sheep and goats on range utilize the leaves of this shrub as browse but the nutritional value does not appear to have been established. The fact that the plant is recommended as deer-resistant for landscape plantings suggests that it is not an important source of nutrients for grazing animals.

Research has been conducted on the potential of the meal remaining after extraction of the oil as a feedstuff for livestock and poultry, particularly since it contains around 260 g **crude protein** kg^{-1} (on a DM basis). Results (Wisniak, 1994) indicate that the presence of **antinutritional factors** in the meal (mainly simmondsins, **trypsin inhibitor**s and condensed **tannins**) results in reduced **feed intake** and **growth** rate, and toxicity causing death in some cases. One application with breeding pigs and poultry is to include the meal in the diet as a way of controlling feed intake and prevent them becoming too fat. (RB)

Reference

Wisniak, J. (1994) Potential uses of jojoba oil and meal – a review. *Industrial Crops and Products* 3, 43–68.

Joule

The SI unit of **energy**. The joule (J) is defined as the work done when the point of application of a force of 1 newton is displaced through a distance of 1 m in the direction of the force (the newton being the force required to accelerate a mass of 1 kg by 1 m s^{-1}). Energy can take many forms (e.g. mechanical, electrical, chemical and heat), all of which may be quantified in joules. (JAMcL)

Jute

A fast-growing prickly woody herbaceous annual (*Hibiscus cannabinus* L.), growing up to 4 m tall. Jute is cultivated mainly for its fibre but also yields 6–30 kg seed ha^{-1}. The seeds contain about 20% **oil**, used for salad, cooking and lubricant oils. The seed cake produced after oil extraction can be fed to cattle and sheep. The stem is largely **cellulose** but contains relatively high levels of **ether extract**, which can serve as a source of **energy**. The leafy parts of some varieties contain as much as 30% **protein**, and young plants ensile easily. (JKM)



A jute field. Jute is retted – harvested, defoliated, and soaked in water to allow bacteria to rot away everything but the cellulose fibers, which are then made into twine, rope, and burlap. The plant likes very wet soils and is grown as an alternate crop in rice paddy areas. Photo courtesy of Malcolm Manners. Licensed under CC BY 2.0.

Nutrient composition of jute products (g kg^{-1} dry matter).

	Dry matter (g kg^{-1})	**Crude protein**	**Crude fibre**	**Ash**	**Ether extract**	**NFE**	**Ca**	**P**
Fresh stem, India	–	150	199	82	58	511	20.8	5.0

	Dry matter (g kg^{-1})	Crude protein	Crude fibre	Ash	Ether extract	NFE	Ca	P
Leaves dried, India	–	131	116	118	21	614	33.1	3.5
Seeds, South Africa	915	272	251	61	154	262	6.0	6.3
Dry press cake	–	330	174	60	–	376	–	–

NFE, nitrogen-free extracts.

Sources: FAO 2002 adapted from Göhl, B. (1981). http://www.feeds/html [26.01.02] Tropical Feeds. www.FAO. Rome

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[26.01.02]

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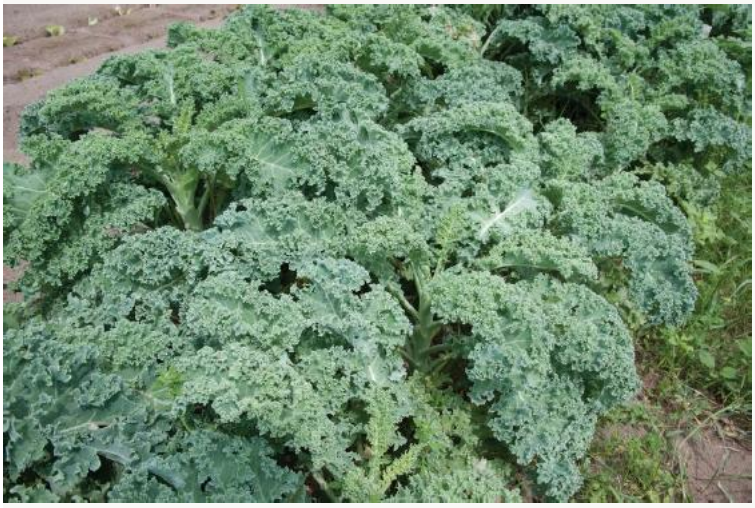
Göhl, B. (1981) *Tropical Feeds*. FAO Animal Production and Health Series No. 12. FAO, Rome.

K

Kale (*Brassica oleracea*)

An annual grown extensively in temperate areas as a feed for ruminants, to extend the **grazing** season in autumn. It is highly palatable for cattle and sheep and is usually fed by either strip or zero grazing, or as **silage**. The variety most commonly grown is marrowstem, which produces heavy crops but is not winter hardy. Thousand-headed and dwarf thousand-head are hardier and produce a large number of new shoots late in the winter. The feeding value of kale is proportional to the leaf content: the woody

stems are less palatable and less digestible. Kale has 86% water; the dry matter (DM) contains 16–17% **protein** and 20–25% soluble **carbohydrates** with a **metabolizable energy** (ME) of 11 MJ kg^{-1} (see table). Adequate **supplementation** with minerals is important, particularly **iodine** and **selenium**. Kale contains *S*-methyl **cysteine** sulphoxide, which may cause haemolytic **anaemia** after conversion in the rumen to dimethyl disulphide. Glucocinolates in kale can cause lesions of the **liver**, kidneys and thyroid, leading to thyroid dysfunction in cattle if kale is fed in excess of 20 kg per day per head over long periods. The **milk** from dairy cows may be tainted if they are fed kale at high levels. Dietary inclusion rates for fresh kale are 25% for cattle and ewes, 10% for calves and 10–33% of total **feed intake** for lambs. Kale silage can be consumed at greater levels (< 60% of the total feed intake of lambs). (JKM)



Kale ready for consumption. Photo courtesy of Photofarmer. Licensed under CC BY 2.0.

Nutrient composition of kale (g kg^{-1} DM) and metabolizable energy

(MJ kg^{-1} DM).

	Dry matter (g kg^{-1})	**Crude protein**	**Crude fibre**	**NDF**	**EE**	**Ash**	**Sugar**	**Starch**	**ME**
Fresh	130–145	157–200	175–185	243–440	21–36	125–150	170–233	5–9	11.4–12
Silage	176	201	–	232	–	–	65	–	12.3

EE, ether extract; ME, metabolizable energy; NDF, neutral detergent fibre.

Kaolin

Kaolin and kaolinitic clays are used as **binding agent**s to increase the durability of pellets. They are naturally occurring mixtures of minerals containing at least 65% complex hydrated **aluminium** silicates whose main constituents are kaolinite, bentonite and other montmorillonite clays. (MG)

Kapok seed meal

The kapok is a tropical tree of the Bombacaceae (Bombax) family; the main variety is *Ceiba pentandra*. Kapok seeds are **by-product**s of lint production. They are ground and the **oil** is used in edible products and cosmetics.



Kapok tree. Photo courtesy of city of St Pete. Licensed under CC BY-ND 2.0.

The residual oil cake is used as fertilizer and animal feed. Kapok oil cake has a high fibre content and low **digestibility**. It can be used up to a maximum of 70% in cattle diets, above which it is unpalatable. Kapok oil cake with 2% oil is toxic to chicks at > 20% of total diet and reduces growth rate at < 10%. It may also be toxic to pigs. The dry matter (DM) content of kapok seed oil cake is 865–890 g kg^{-1} and its nutrient composition (g kg^{-1} DM) is **crude protein** 290–340, **crude fibre** 220–320, **ash** 78–80, **ether extract** 64–88 and NFE 64–88. (JKM)

Kava (*Piper methysticum*)

A shrub that grows naturally in Oceania and the Hawaiian Islands. Consumption of the rhizome and its root as a non-alcoholic drink was common among natives of this region centuries ago.



Fijian kava ceremony. Photo courtesy of Jaejay77. Licensed under CC BY-SA 4.0.

The active compounds extracted from this plant include kawaine, methysticine and yangonine (Zargari, 1997). It is believed that the root of this plant has antiseptic and diuretic effects and is effective for treating genital diseases and intestinal parasites (Gutierrez *et al*., 2013). Despite numerous studies on the use of kava in the field of food and medicine for humans and various **laboratory animal** models, studies of its use in domestic animals are limited, mainly due to the existence of antinutritional and alkaloid compounds and the possibility of **liver** toxicity. In quail, consumption of kava root extracts had no negative effects on performance and may reduce stress, as measured by the tonic immobility time (TIT) (Da Silva *et al*., 2010). (AS; BH-G; CJCP)

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Gutierrez, R.M.P., Gonzalez, A.M.N. and Hoyo-Vadillo, C. (2013) Alkaloids from piper: a review of its phytochemistry and pharmacology. *Mini-Reviews in Medicinal Chemistry* 13(2), 163–193.

Zargari, A. (1997) *Medicinal Plants*. Tehran University of Medical Sciences. Vol. 4, pp. 313.

Keratins

A superfamily of proteins found in cells and their derivatives such as **hair** and nails. Apart from 'hard' keratins, which make up hair, nails and lens proteins, there are five major types of keratins based on genomic structure and **amino acid** sequence homology. Types I and II are termed 'soft' keratins and consist of at least 20 members that are specifically expressed in epithelial cells. Types III and IV are found in mesenchymal, **muscle** and neural tissues. Type V keratins make up the nuclear laminas. Obligate heterodimer pairs of keratins act as building blocks of intermediate filament proteins, which function in providing cell shape and protection from mechanical stress. (GG)

Keto acids

Acids that are the critical intermediates in the **metabolism** and interconversion of **amino acid**s. They have a structure in which a carbonyl carbon R·CO·COOH is α to a carboxyl carbon, i.e. they are α-keto acids. The majority of these compounds are produced from related amino acids by **transamination**. For example, upon transamination, **alanine** ($CH_3 \cdot HCNH_3^+ \cdot COO^-$) yields the keto acid **pyruvate** ($CH_3 \cdot C{=}O \cdot COO^-$). Keto acids of indispensable amino acids, with the exception of **lysine** and threonine, can be

transaminated to yield the corresponding L-amino acid. Keto acids are intermediates in the utilization of D-amino acids. Many D-amino acids can be deaminated to form a keto acid by the enzyme D-amino acid oxidase. The resulting keto acid can be transaminated with the amino group from glutamic acid or another amino (-NH_3^+) donor to become the L-amino acid. This is how D-**methionine** is converted to L-methionine. The majority of transaminations are dependent on glutamic acid as the **nitrogen** source. Alanine is another source but it does not participate in as many reactions as does **glutamate**. The amino acids alanine, glutamate and aspartate are dispensable amino acids; their biosynthesis is dependent on a final transamination step involving the keto acids pryuvate, α-ketoglutarate and **oxaloacetate**, respectively. Transamination and keto acid formation are critical to the movement of nitrogen from amino acids to aspartate, which is one of the nitrogen donors in the formation of **urea**, the major form in which mammals excrete nitrogen. (NJB)

Ketones

Substances with the general chemical structure R·C═O·R. Three ketones produced in animal **metabolism** are **acetone** (CH_3·C═O·CH_3), acetoacetate (CH_3·C═O·CH_2·COO^-) and β-**hydroxybutyrate** (CH_3·CHOH·CH_2·COO^-). They occur in high concentrations in **blood** of animals suffering from **ketosis**. Acetone is volatile and smells sweet and can be detected in the expired air of ketotic animals. Ketones are produced when the rate of production of acetyl-CoA from **fatty acid**s exceeds the capacity

of the tricarboxylic cycle to convert the carbon to CO_2. (NJB)

Ketosis
A metabolic disease, also called acetonaemia, caused by excessive amounts of toxic **ketone** bodies in the **blood**. It is common in dairy cattle, particularly those with fatty **liver** syndrome, in early **lactation** when the energy demands of **milk** production exceed **energy intake**, leading to a negative **energy balance**. Use of **adipose tissue** to provide energy is inefficient when blood **glucose** concentrations are low, leading to build-up of ketones. Some diets low in precursors of **propionic acid** are described as ketogenic. (EM)

Kid
A young **goat**.

Kidney beans:
see Bean

Kidney disease
There are eight major diseases of the kidney. Renal ischaemia, or reduced renal **blood flow**, is usually the result of a general circulatory failure; it may be acute, e.g. following serious haemorrhage, or chronic, as in congestive heart failure, and is one of the results of severe **water deprivation**. Glomerulonephritis affects primarily the glomeruli; it is rare in animals, being primarily a disease of humans, but it does occur in dogs. Nephrosis involves degenerative and inflammatory lesions of the renal tubules, usually associated with the ingestion of one of a wide range

of toxic substances. These range from **heavy metals**, such as **cadmium**, to overdosage with a variety of drugs that are safe in the usual prescribed dose. The **urine** is of high **specific gravity** and contains **protein**. Interstitial nephritis was common in the dog but is now seldom seen, because of vaccination against the causal organism. The condition has been observed in cows fed **roughage** treated with caustic soda. Embolic nephritis is usually associated with bacteraemia, when clumps of bacteria block the vessels supplying portions of the kidney; it is not usually a fatal condition. Pyelonephritis develops from an infection that ascends from the lower urinary tract; it is characterized by pus in the urine and inflammation of both the ureters and bladder.

Hydronephrosis is a cystic enlargement of the kidney resulting from obstruction of the ureter, often caused by a calculus. Renal tumours are uncommon in animals. (ADC)

Kilocalorie

1 kilocalorie (kcal) = 1000 **calorie**s. Formerly known as Calorie or large calorie or CALORIE. These forms, though still used, are confusing and should be avoided. (JAMcL)

See also: Energy

Kilojoule

1 kilojoule (kJ) = 1000 **joule**s. (JAMcL)

See also: Energy

Kitchen waste

Kitchen waste, swill or garbage waste may consist of food leftovers,

spoiled food, food past its expiry date, or mislabelled food. In some countries, kitchen waste cannot legally be used in pig diets, due the possible spread of swine fever and foot-and-mouth disease, while in others it can be fed after heat processing. Food that has not been in contact with **meat** or meat **by-product**s can safely be fed to pigs without processing. The **nutritive value** of kitchen waste for pigs is adequate with respect to **protein** and **energy** but it often has a low **dry matter** content which tends to reduce dry matter intake and **growth**, principally in younger animals fed *ad libitum* (see table). The **digestibility** of kitchen waste is variable and related to the source. If used as part of a balanced diet, the feeding of garbage residues to pigs has no detrimental effects on **carcass** quality. (JKM)

Typical composition of kitchen waste

	Dry matter (DM) ($g\ kg^{-1}$)	**Crude protein**	**Crude fibre**	**Ether extract**	**Gross energy** (MJ)
Composition ($g\ kg^{-1}$ DM)	132–310	175–195	36–53	201–341	–
Digestibility (%)	80.5–87.3	61–83	56.6–72.5	77–94	23.1

Kiwifruit

Actinidia chinensis; also called Chinese gooseberry. It grows on a vigorous, woody, twining vine or climbing shrub reaching 9 m in height. It originated in South China and was introduced commercially into New Zealand in 1934.



Kiwifruit bushes. Photo courtesy of Graeme Churchard. Licensed under CC BY 2.0.

The oval fruit is up to 6 cm long, with russet-brown skin densely covered with short, stiff brown hairs. The flesh, firm until fully ripe, is glistening, juicy and luscious, bright green, or sometimes yellow. It is grown mainly for human consumption and extraction of the enzyme, actinidin, for industrial food use, but can also be used fresh for animal feed or made into tropical **silage**. The fruit is low in **dry matter** (DM) and **protein** but rich in **carbohydrate**, **potassium** (332 mg 100 g^{-1}) and **vitamin E**, and extremely high in **vitamin C** with up to 100 mg per fruit. Overripe or poorly shaped fruits are used for livestock feed. They can be dried or fed

fresh. The hairs on the skin of the fruit cause irritation when eaten and may limit intakes. The DM content in kiwifruit is 198 g kg^{-1} and the nutrient composition (g kg^{-1} DM) is protein 39.9, **fat** 3.5, carbohydrates 883.8, **ash** 22.7, **calcium** 1.6, **iron** 0.51, **magnesium** 3, **phosphorus** 6.4, **thiamine** 0.02, **niacin** 0.5, **riboflavin** 0.05 and **ascorbic acid** 1.05. (JKM)

Kjeldahl
A procedure used to measure total **nitrogen** (N) in biological materials. N in a sample of the material is converted to ammonium **sulphate** by boiling in concentrated **sulphuric acid** in the presence of catalysts (**mercury** or **selenium**) and **potassium** sulphate (which raises the **temperature** of the **digestion**). The **ammonia** formed is then determined. Originally this involved steam-distillation of the ammonia, after making the digest alkaline by addition of **sodium** hydroxide, into a known volume of standard acid, the ammonia then being determined by titration. More convenient methods of determining the ammonia have since been developed. (CBC)

Klason lignin
An analytically defined fraction of plant material, measured gravimetrically as insoluble material remaining after treatment of a sample with 72% **sulphuric acid**, usually heated. The **lignin** content of plant tissue increases as it ages, making wood one of the more lignified tissues. (JAM)
See also: Dietary fibre

Kohlrabi (*Brassica oleracea* var. *caulorapa*)
A low biennial plant with green or purple skin and white flesh. Its swollen stem is a **carbohydrate** storage organ; it grows at ground level and is harvested for human consumption. It is a good source of **vitamin C** and **potassium**. As a stock feed, kohlrabi is similar to **turnip** and can be grazed by ruminants. Young kohlrabi are tender and the greens are palatable but the adult greens can become tough. The dry matter (DM) content of kohlrabi is 900 g kg^{-1} and the nutrient composition (g kg^{-1} DM) is **crude protein** 122, **crude fibre** 111, **ether extract** 22 and **ash** 78, with ME 11.2 and FME 10.4 MJ kg^{-1} DM. (JKM)

Kosher foods
The Jewish Torah prescribes the types and combinations of food and preparation methods that are available to Jews. Jews should only eat food certified as kosher by a rabbinic agency. Only **meats** from domesticated ruminant animals and poultry and finfish with scales are allowed. However, camels are non-kosher, as are other meats, including **pork**, horses, kangaroo, **rabbit**, predatory or scavenging birds, monkfish, **catfish**, **sturgeon**, **shellfish**, reptiles and many insect species. Only **eggs** and **milk** from kosher animals may be consumed. Dairy products such as cheese need certification that calves' rennet has not been used in the manufacturing process. Meat and dairy products may not be manufactured or eaten together. Meat must be obtained by shechita slaughter, which involves a single knife cut to the throat, without prior stunning of the animal, by a qualified slaughterer or shochet. **Blood**, some **fat**

deposits, tendons, blood vessels and the sciatic nerve must be removed before the meat is considered kosher. (CJCP)

Krebs cycle:
see Tricarboxylic acid (TCA) cycle

Krebs–Henseleit cycle
An older term for the **urea cycle**. It was named the Krebs–Henseleit cycle because Professor H.A. Krebs proposed (in 1932) a series of reactions to account for the catalytic effect of added **ornithine** or **citrulline** on urea production by **liver** slices. It was shown that the sum of the concentrations of ornithine + **arginine** did not change appreciably during an **incubation**, while the amount of **ammonia** which disappeared roughly equalled the amount of urea produced. (NJB)

Krill (*Norvegica pelagic*)
A collection of small **shrimp**-like crustaceans ranging from 8 mm to 70 mm, according to species. The main uses are as high-protein feed for farmed **fish** and marine tropical fish, and, in Japan, for human consumption. Krill is generally sold as a dried meal or hydrolysate. Krill should be frozen immediately after catching, since storage at room temperature results in the production of toxins. The fat is rich in **highly unsaturated fatty acid**s, of which the omega-3 series contribute 40%. The composition varies according to season, with increased proportions of **palmitoleic** and **omega-3 acids** in spring. The unsaturated fat content can adversely affect **cellulose digestion** in the **rumen**. The high

concentration of **carotenoid**s (150–200 ppm) gives fish such as salmon their pink colour. The dry matter (DM) content of krill is 900 g kg^{-1} and the nutrient composition (g kg^{-1} DM) is **crude protein** 580, **ether extract** 180, **starch** and **sugars** 20–40, **ash** 130; essential **amino acid**s: **valine** 53, **isoleucine** 50, **phenylalanine** 52, **lysine** 82, threonine 47, **methionine** 40, **tyrosine** 45, **histidine** 25, **arginine** 67; and **fatty acid**s C14:0 117 and C18:3 n-38. (JKM)



Antarctic krill (*Euphausia superba*). Photo courtesy of Dr Uwe Kils. Licensed under CC BY-SA 3.0.

Kwashiokor:
see History of nutritional sciences; Marasmus

L

Labelling

A means of marking a substance so that it can be distinguished from the unlabelled substance. The labels most commonly used in nutrition research are isotopes, either radioactive or stable, of one or more of the atoms in the substance. Because the major metabolic **substrates** are compounds of carbon, the stable (^{13}C) and radioactive (^{14}C) isotopes of carbon are very common labels, but isotopes of **hydrogen** (the stable isotope **deuterium**, ^{2}H, or the radioisotope tritium, ^{3}H) are also frequently used and, in work on **nitrogen metabolism**, its stable isotope ^{15}N. Isotopes of most minerals and **trace element**s are also available and are used to study the metabolism of those nutrients. Radioactive labels are measured by counting their disintegrations in a beta or gamma counter; stable isotopes are measured by **mass spectrometry**. Labels need not be isotopic: a molecule can be labelled by tagging it with an entity that can be measured by other means, such as fluorescence.

The dilution of a labelled substance in a pool of that same substance (unlabelled) in the body can provide various kinds of information. Most simply, it can give an estimate of the size of the pool (for example, the dilution of a known amount of $^{2}H_2O$ in **body water** is used to estimate **total body water**). If the labelled compound or 'tracer' is infused at a constant known rate, its dilution can be used to estimate the rate at which the substance is passing through the pool (the 'entry rate' or 'flux'). For example, if L-[1-^{13}C]**leucine** is infused at a constant rate into the **blood** (I),

the ^{13}C **enrichment** of leucine in the blood rises and approaches a plateau or equilibrium isotopic enrichment (E). The labelled leucine is then leaving the blood at the same rate as it is being infused and its ^{13}C enrichment is used to calculate the rate at which leucine as a whole (Q) is entering the plasma pool, from **absorption** (A) and from protein breakdown (B), and leaving the plasma pool for **protein synthesis** (S) and **oxidation** (O). Then, assuming a constant plasma pool size:

$$Q=I/E=A+B=S+O$$

Similar methods are used to estimate the pool sizes and entry rates of a wide range of **metabolite**s.

Isotopic labels are intrinsic, meaning that they do not alter the chemical structure, but substances can also be made distinguishable by tagging them with an extrinsic label, for example by the addition of radioactive **iodine**. Proteins such as **albumin** can be iodinated (by which radioactive iodine, ^{128}I or ^{131}I, is bound to **tyrosine** residues in the protein) and infused at a known rate. The equilibrium dilution of the label in the blood provides a measure of the rate at which albumin is being released into the blood and being taken up from the blood.

There is a danger that nutrients or metabolites with extrinsic labels may behave somewhat differently from the unlabelled substance. For example, the addition of the label may interfere with their interaction with enzymes or receptors. Isotopic labelling is not entirely free of this danger; especially with hydrogen, the large proportionate difference in mass (twofold for deuterium, threefold for tritium) means that the labelled and unlabelled substrates may

behave differently in their biochemical interactions. (MFF)

Lablab purpureus

A major leguminous pulse crop grown in tropical parts of the world, being frost tender. Lablab, or hyacinth **bean**, is widely cultivated, which started over 4000 years ago, probably in Africa, where the only wild plants are found. It has a deep tap root and is perennial, but may be grown as an annual.



Lablab or hyacinth bean. Photo courtesy of SBT4Now. Licensed under CC BY-SA 2.0.

It grows rapidly as a 6 m vine, though it may be grown as a trailing plant in fields for livestock, who consume both fresh and shed leaves. Humans mainly eat the seed, though the leaves, roots and flowers are also edible. Raw seeds and leaves contain **cyanogenic glycosides**, which is toxic for humans but denatured by cooking. This is reduced in domesticated cultivars, though **tannins** and **trypsin inhibitor**s are present. Cattle may graze the plant *in situ*, and the shed leaves make a locally important contribution in the dry season in some African countries. Under colonial rule, cultivation was discouraged, to enable farmers to grow the common bean (*Phaseolus vulgarus* L.) for export. (CJCP)

Laboratory animals

Most animals used for biological research are small species such as rats, mice, quail and zebrafish. Laboratory animals are often used as models for studying nutritional processes, the prenatal and postnatal development of organs, and metabolic diseases in humans and farm animals, being easier to handle and cheaper to keep than the latter. The validity of such studies relies on the assumption that the relevant metabolic processes are the same in different species, which may not always be the case. For example, there are substantial differences in the **metabolism** of, and dietary requirements for, some nutrients, particularly **arginine**, **methionine**, **phenylalanine** plus **tyrosine**, **taurine**, **arachidonic acid**, **α-linolenic acid**, **linoleic acid**, **niacin**, **vitamin C**, **vitamin A**, **vitamin D** and fibre among mammals, birds and fish. In addition, these animals also differ in digestive, reproductive and urinary systems; **feeding behaviour**; **taste** receptors and food selection; molecular species of **bile** acids and their conjugation with amino acid (**glycine**, **taurine**, or both); the sites of **lipogenesis** from acetyl-CoA (the liver or white **adipose tissue**) and of **gluconeogenesis** from amino acids (the liver, kidneys, or both); the major end-products of **nitrogen metabolism** (**urea**, uric acid, or **ammonia**); and sensitivity to imbalances and **antagonism**s of dietary nutrients (e.g. amino acids and micro-minerals). (MFF; GW)

Further reading

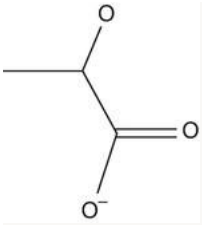
NRC (National Research Council) (1995) *Nutrient Requirements of Laboratory Animals,* 4th rev. edn. National Academies Press,

Washington, DC.
Wu, G. (2018) *Principles of Animal Nutrition*. CRC Press, Boca Raton, Florida, 772 pp.

Lactalbumin:
see Dairy products

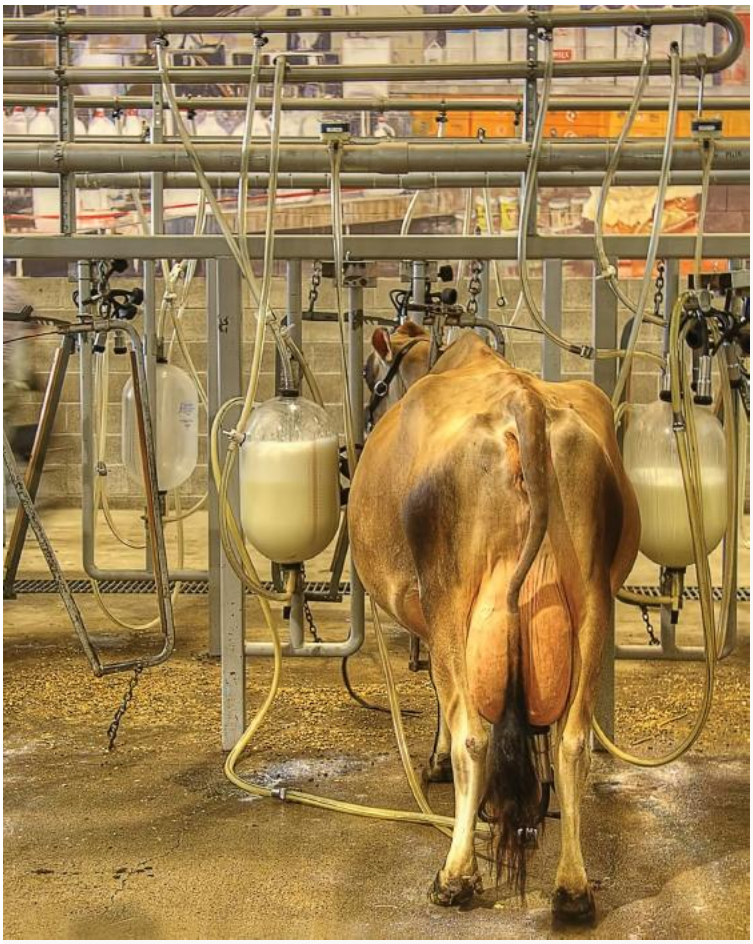
Lactase
An enzyme found in the **brush border** membranes of epithelial cells in the **duodenum** and **jejunum**. It splits the **disaccharide**, **lactose**, into **glucose** and **galactose**. The enzyme is present in most newborn mammals to assimilate the high concentrations of lactose present in **milk** and then may down-regulate or disappear following **weaning**. (GG)

Lactate
A three-carbon acid. L-Lactate, $CH_3{\cdot}HCOH{\cdot}COO^-$, is derived from **pyruvate** in **glucose catabolism**. Under anaerobic conditions the NADH + H^+ produced in the catabolism of glucose is used to reduce pyruvate to lactate with the regeneration of NAD, which can again participate in reactions leading to the production of ATP in **glycolysis**. Under anaerobic conditions or at levels of exercise intensity that exceed the aerobic metabolic capacity, lactate concentration increases. This may decrease **blood** and tissue pH and decrease **enzyme activity**, leading to metabolic complications. (NJB)



Lactation

The secretion of **milk** by the **mammary gland**s of mammals. Most animals provide sufficient milk to meet the requirements of their **suckling** offspring. Dairy cows, goats and some breeds of sheep have been selected for improved milk production. Annual milk yields are 4000–12,000 l in dairy cows, 600–1100 l in goats and 200–700 l in sheep. Lactation in dairy breeds typically lasts for 10 months in cows and goats and 7 months in sheep. Beef cattle lactate for 4–6 months. Milk yield in cattle is low following parturition and rises to a peak 8–16 weeks into lactation; it then declines steadily until milking ceases and the animal is dried off. The rate of decline is typically 2.5% per week in dairy cows, but higher-yielding animals are characterized by greater persistency.



Jersey cow being milked by teat cups, transferring milk to glass inspection jars. Photo courtesy of Glen Bledsoe. Licensed under CC BY 2.0.

Most lactating animals exhibit a period of negative **energy balance** in early lactation, because their voluntary **feed intake** is insufficient to meet the demands for increasing milk yield. Over this period the animal will mobilize body reserves, particularly **body fat**, in support of milk production. In later lactation, when **appetite** is more than sufficient for milk production, body fat reserves are replenished. The rate of mobilization of body fat is affected by **energy intake** in relation to **energy requirement**s for milk production. It is important that animals are not overfat at parturition, since excessive body fat reduces feed intake still further, leading to **ketosis**, fatty liver syndrome and reproductive

failure. On the other hand, animals that are too thin at parturition may have insufficient body energy reserves to compensate for reduced feed intake. This is not a problem if diets of high energy concentration are offered, since the rate of energy mobilization has a greater impact on health and **reproduction** than absolute levels of reserves (Garnsworthy and Webb, 1999). The recommended range of **body condition scores** at calving in dairy cows, for example, is 3–4 (on a 1–5 scale, where 1 is thinnest and 5 is fattest). Labile **protein** reserves are proportionately small, compared with fat reserves, since most body protein is found in **muscles**. Protein nutrition in early lactation can therefore be critical in determining the ability of the animal to support milk production from mobilized body fat.

The nutrient concentration of diets for animals in early lactation needs to be high, because of the imbalance between requirements and feed intake. However, for ruminants, the proportion of the ration dry matter (DM) derived from **forage** should not be allowed to drop below 30% or rumen **fermentation** will be impaired, leading to digestive upsets and reduced **butterfat** production (*see* Concentrate).

The energy and protein requirements for lactation are determined by milk yield, milk composition and **metabolizability** of the diet (which affects the efficiency of utilization of **metabolizable energy**). For cattle and goats, the **energy value** of milk is given by the equation

$$EV\ (MJ\ kg^{-1}) = 0.0376\ F + 0.0209\ P + 0.948$$

where F and P are the butterfat and protein contents,

respectively, of the milk (g kg^{-1}). For sheep, the equation is

0.0328 F + 0.0025d+ 2.2033

where *d* is the number of days of lactation. The efficiency of utilization of metabolizable energy (ME) for lactation (k_l) can be calculated as suggested by AFRC (1993) and CSIRO (2007), respectively:

kl=0.35q+ 0.420kl=0.02 × ME + 0.4

where *q* is the metabolizability of the diet (decimal), and ME is the metabolizable energy content of the diet (MJ kg^{-1} DM).

An average dairy cow will therefore require approximately 5.2 MJ ME l^{-1} milk produced. The requirement for **metabolizable protein** for lactation is equal to the **true protein** content of milk divided by the efficiency of utilization of absorbed **amino acid**s for milk production (0.68) (AFRC, 1993). An average dairy cow will require approximately 47 g metabolizable protein per litre of milk produced.

In sheep rearing lambs (in contrast to milking sheep), lactation lasts for 12–20 weeks. Milk yield reaches a peak in the third week of lactation and then steadily declines. Potential milk yield is impossible to measure in suckling animals, since the quantity of milk produced is determined by the ability of the lamb(s) to **suckle**. Estimates based on weighing lambs before and after suckling suggest that ewes with single lambs produce between 75 l and 130 l in a 12-week lactation and ewes with twin lambs produce between 80 l and 210 l. There is a large variation between breeds in milk yield. The energy requirement of a ewe for milk production is approximately 5.2 MJ ME kg^{-1} and the protein requirement is

approximately 74 g kg^{-1} milk.

In pigs, lactation lasts for 3–6 weeks, depending on the management system of the breeding herd. Milk yield rises after parturition to peak at about 4 weeks and then declines at a rate of 9% per week. Milk yield is related to the number of piglets in the litter, averaging approximately 0.8 l per day per piglet. The energy requirement of a sow for milk production is approximately 8.3 MJ of **digestible energy** kg^{-1} and the protein requirement is approximately 100 g kg^{-1} milk. (PCG; GMcLD)

References

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Garnsworthy, P.C. and Webb, R. (1999) Nutrition and fertility in dairy cows. In: Garnsworthy, P.C. and Wiseman, J. (eds) *Recent Advances in Animal Nutrition – 1999*. Nottingham University Press, Nottingham, pp. 39–57.

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Lactation disorders

The **metabolite**s for the synthesis of **milk** constituents come from dietary nutrients and from mobilization of body reserves, principally **adipose tissue**, muscle and bone (for **calcium**). In high-yielding mammals such as the dairy cow, early-lactation milk production is supported mainly by mobilization of body reserves,

but food rapidly takes over as the main source of **substrates** for milk synthesis. The extent of the mobilization depends on reserves: for **fat** it can last for half of the lactation but for calcium it is unlikely to last for more than a few days. If the diet continues to provide insufficient nutrients, the animal's potential milk yield will not be achieved. If such **malnutrition** occurs in early lactation, when new secretory tissue is still being developed in the **mammary gland**, subsequent increases in food intake are not likely to return milk yield to its potential level.

Specific nutrient deficiencies or imbalances reduce food intake and thereby depress milk yield. Especially important are adequate dietary supplies of nutrients required to support the synthesis of milk constituents; and of these, calcium is of special importance.

Milk fever, a disease common in high-yielding dairy cows, is caused by insufficient **absorption** of calcium. It usually occurs within the first few days of lactation, when an affected cow collapses. Treatment is by intravenous infusion of a solution of calcium **lactate** or calcium borogluconate. It can generally be prevented by feeding a diet low in calcium for several weeks before calving. This increases the efficiency of absorption of calcium so that if, at calving, the dietary content of calcium is increased, an adequate amount is absorbed to support the greatly increased requirements of lactation.

In dairy cows given rapidly fermentable diets a condition known as low-milk-fat syndrome is often evident. Such a diet produces a low **acetate**:**propionate** ratio in the rumen **fermentation** and the relative lack of acetate limits milk fat synthesis. The condition can

be alleviated by reducing the concentrate:forage ratio or by using concentrates with slower rates of fermentation.

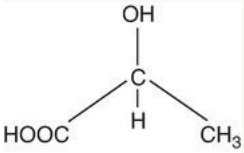
A common lactational disorder is bacterial infection of the mammary gland, or mastitis. The gland has various defences against infection but mastitis is common in situations where the invasion of bacteria into the teat canal is facilitated by dirty conditions or sharing of milking clusters, as often occurs with the dairy cow. Mastitis occurs less frequently in sheep and goats. The prevalence of mastitis, in dairy cows at least, is influenced by the adequacy of the **vitamin E** and **selenium** status, and possibly **magnesium**.

A less common disorder is the failure of milk letdown in cattle. This can often be rectified by an injection of **oxytocin**, which stimulates the mammary epithelial cells to contract and milk to be expelled from the alveoli into the gland cistern.

Other lactation disorders include agalactia in sows. (JMF)

Lactic acid

2-Hydroxypropanoic acid, $CH_3{\cdot}HCOH{\cdot}COOH$.



Because carbon 2 has four different substituents, lactic acid can have L and D forms. Commercially available lactic acid is usually a racemic mixture of the two. The pKa is 3.86, so at a normal body pH of ~7.4, the carboxyl carbon of lactic acid is not protonated and the molecule carries a negative charge. Under normal aerobic

conditions, all cells except erythrocytes oxidize **glucose** to CO_2 and H_2O, generating 38 ATPs per mole of glucose. Glucose is first catabolized to **pyruvate** via glycolytic **enzymes** found in the cytosol; pyruvate then enters the mitochondria to be completely oxidized to CO_2 and H_2O. However, under a workload with limited oxygen, mitochondria are not able to oxidize NADH at a rate that matches its production, and NADH is diverted to **lactate** production. Production of lactate is the result of pyruvate reduction to L-lactate by L-lactate **dehydrogenase**, i.e. $CH_3{\cdot}CO{\cdot}COO^- + NADH + H^+ \rightarrow CH_3{\cdot}HCOH{\cdot}COO^- + NAD$. All cells in the body can produce lactate, which is subsequently extracted from the circulatory system for **catabolism** by the liver and cardiac muscle. The net yield of ATP under anaerobic conditions (when the NADH produced during **glycolysis** cannot be oxidized by the mitochondria) is only 2 ATPs mol^{-1} glucose converted to 2 mol lactate. Under this condition, the rate of glucose catabolism must increase 19-fold (38/2) to meet the ATP flux demands. A notable source of lactate is fast twitch **skeletal muscle** (i.e. white muscle) under conditions of a high workload due to, for example, sprinting, pulling or lifting. As a result of this intense exercise, lactate is produced in muscle and accumulates in the **blood** and tissues. Blood lactate is extracted by the liver and converted to glucose via the pathways used in **gluconeogenesis**. Glucose is then released to the blood and may be taken up by skeletal muscle. In the older literature, this inter-organ coordination was referred to as the **Cori cycle**. A relevant **metabolic disorder** in ruminants is acidosis.

Following an abrupt increase in the ingestion of readily fermentable **carbohydrates**, the **rumen** and intestinal microflora respond with profuse production of **volatile fatty acid**s and DL-lactate. Clinical rumen acidosis is declared at pH 5.2. Acid absorption from the digestive tract causes an acidification of blood, and clinical systemic acidosis is declared when blood pH falls below 7.35. L-Lactate can be metabolized readily by ruminants, while D-lactate is metabolized very slowly. Until recently, D-**lactic acid** was considered to be the principal culprit in ruminant acidosis, but it now appears that the total acid load resulting from production and **absorption** of **fermentation** acids is responsible for the disorder.

Like several other **organic acid**s, lactic acid has antimicrobial properties, can lower gut pH and makes an energy contribution to animals' diets. It is recognized as a preservative in EU feeding stuffs legislation and is listed as 'E270, lactic acid, $C_3H_6O_3$, suitable for use in all feeding stuffs'.

It is a colourless, viscous liquid, miscible with water or **ethanol** and, although stronger than most short-chained carboxylic acids, is non-fuming so is relatively easy to handle. It has a mild, fruity, acid **taste** that does not reduce the **palatability** of feeding stuffs. It is, however, liable to corrode equipment.

In common with other organic acids, its antimicrobial properties stem from its ability to enter microbial cells in its undissociated state. When inside the cell, it dissociates to give **hydrogen** ions (H^+), which lower pH and result in wasteful **energy expenditure** in the effort to restore balance, and acid

radicals ($CH_3 \cdot CHOH \cdot COO^-$), which disrupt DNA synthesis, in turn interfering with **protein synthesis** and cell replication.

In the **small intestine**, lactic acid helps to maintain a balanced microflora and healthy gut development. It has also been shown to stimulate pancreatic activity in newly weaned piglets and there is some evidence that it may, in part at least, replace prophylactic antibiotics by stimulating non-specific **immunity** in the small intestine. In poultry, lactic acid acidifies the crop and to a lesser extent the caecal contents, reducing the potential for the growth of pathogens such as salmonella.

Lactic acid is important on-farm in the ensiling process. Typically, it is produced *in situ* from plant **sugars** by lactic acid-producing bacteria. Often, in practice, inoculants of selected, particularly efficient strains of homofermentative lactobacilli are introduced into **forage crop**s during harvesting for **silage**. (DMS; CRL)

Key reference

Adams, C.A. (2002) *Total Nutrition – Feeding Animals for Health and Growth*. Nottingham University Press, Nottingham, UK, 248 pp.

Lactic acid bacteria:

see Gastrointestinal microflora

Lactic acidosis

The transfer of large amounts of **lactic acid** from the **rumen** to the blood, resulting in a life-threatening decrease in blood pH (metabolic acidosis). This condition is often referred to as '**grain** overload', as it is generally caused by excessive ingestion of readily

fermentable **carbohydrates** and under-supply of forages that promote **chewing** activity and **saliva** production. Rumen flora not adapted to the **availability** of highly fermentable carbohydrates convert a large portion of this carbohydrate to lactic acid, rather than to the other **volatile fatty acid**s typical of rumen **fermentation**. As lactic acid accumulates in the rumen the pH of the rumen declines, which can kill many rumen microbes. If the lactic acid and the other **organic acid**s produced by carbohydrate fermentation are absorbed into the blood and exceed the ability of the liver to metabolize these acids, it can create an acidic condition within the blood and **body fluid**s. A severe decline in blood pH disturbs the **protein** structure of cells and causes a general failure of all systems of the body. In non-ruminants, lactic acidosis is usually secondary to anaerobic **glycolysis** within **muscle** tissue during prolonged anaerobic exercise. (JPG)

Lactitol

A **disaccharide** of **galactose** and sorbitol, 4-*O*-β-D-galactopyranosyl-D-glucitol ($C_{12}H_{24}O_{11}$), produced by the reduction of the **glucose** component of **lactose**. It is not hydrolysed by mammalian digestive **enzymes** but is readily fermented by the intestinal microflora. (NJB)

Lactoferrin

A protein in **milk**, structurally similar to **transferrin**. The molecular weight of lactoferrin is 78–80 kDa and, like transferrin, it binds 2 mol of **iron**. Lactoferrin binds iron with an affinity 300 times that of transferrin. Lactoferrin has antibacterial properties in

the gut, perhaps by decreasing iron availability to intestinal microbes. Although lactoferrin receptors have been identified on cells, its role in iron transport and delivery is not known. (NJB)

Key reference

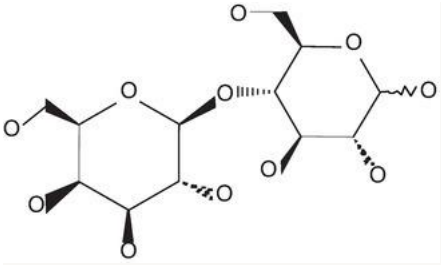
Hutchens, T.W. and Lönnerdal, B. (eds) (1997) *Lactoferrin Interactions and Biological Functions*. Humana Press, Totowa, New Jersey.

Lactoglobulin

A major **milk** protein accounting for more than two-thirds of the total protein found in the **whey** of cows' milk. It has a molecular weight of 38,000 and has 370 **amino acid**s arranged into four separate **peptide** chains. On electrophoresis, lactoglobulin separates into two components: A and B. Both A and B are dimers (i.e. AA or BB) of 19,000 each so that both A and B lactoglobulins have a molecular weight of 38,000. A or B or both may be found in samples from individual cows. (NJB)

Lactose

Milk **sugar**, 4-(β-D-galactopyranosyl)-D-glucopyranose, $C_{12}H_{24}O_{12}$, made up of **glucose** and **galactose**. In **milk** of the major dairy cattle breeds, the concentration of lactose varies from 4.67% to 5.04% of liquid milk and accounts for 35.9% of milk solids. In commercial preparations, lactose is a white powder and is stable, sweet and odourless. It is used in a variety of foods and as a diluent in the pharmaceutical industry.



Lactose is synthesized in the **mammary gland** from two molecules of glucose. One of the glucose molecules is activated to glucose-6-phosphate and in three subsequent steps is converted to uridine diphosphogalactose which, under the action of the **enzyme** lactose synthase, is combined with free glucose to form lactose.

The **digestion** and **absorption** of lactose occur in the **small intestine**. **Lactase** (the enzyme that hydrolyses lactose) is not uniformly distributed: its specific activity is highest in the upper **jejunum** and falls throughout the remainder of the small intestine. Lactase is found on the **brush border** (microvilli) of the **enterocyte**. The glucose and galactose that are released on the brush border are taken up by specific transporters into the enterocyte, then released into the bloodstream. The galactose can be converted into glucose in the liver and metabolized in the body as glucose, with all its ramifications. **Mucosal** lactase activity does not change with dietary lactose. The microflora of the small and large intestinal contents respond to increased dietary lactose by a doubling of lactase activity of the intestinal contents. Thus, some substantial fraction of dietary lactose may be hydrolysed by the bacteria in the intestinal contents. Lactose intolerance is a well-recognized dietary-associated complication. It is thought to be due to a decrease in the mucosal lactase activity such that a greater

fraction of the lactose is fermented, producing gas and short-chain **volatile fatty acid**s. Intestinal **fermentation** results in increased osmotic pressure in the intestinal contents, which results in water retention leading to **diarrhoea**. (NJB)

Key references

Misselwitz, B., Butter, M. and Verbeke, K. (2019) Update on lactose malabsorption and intolerance: pathogenesis, diagnosis and clinical management. *Gut* 68, 2080–2091.

Ugidos-Rodríguez, S., Matallana-González, M.C. and Sánchez-Mata, M.C. (2018) Lactose malabsorption and intolerance: a review. *Food and Function* 9, 4056–4068.

Lamb:

see **Sheep**

Lameness

Any imperfect use of limbs but generally excluding conditions in which the animal is systemically affected. In ruminants, most lameness arises in the feet but in young calves, lambs and goat kids it is commonly due to septic arthritis. In horses and pigs many cases of lameness arise from abnormalities of joints and tendons. Excessive **energy intake** is associated with **laminitis**, sole **ulcers** and white line disease, particularly if it is in the form of **starch**. Starch-based diets are responsible for toxin release into the bloodstream, which in the hoof cause laminitis. Low **dry matter** feeds, such as wet **silage**, are also associated with lameness, because of cows standing and walking in wet slurry for long periods. (WRW; CJCP)

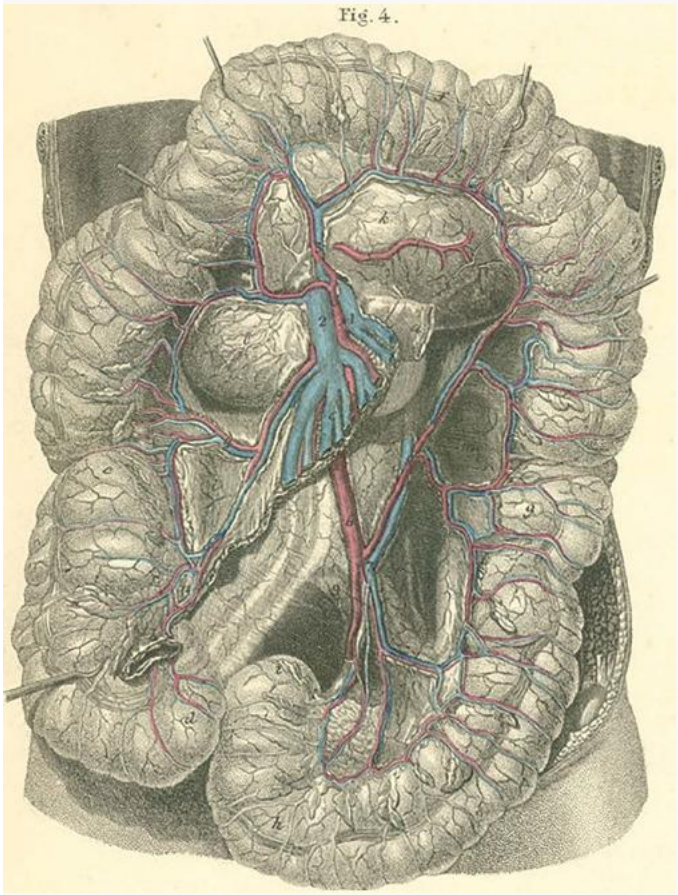
See also: Foot diseases

Laminitis
In acute laminitis, the laminae of the hoof separate from the interdigitating horn so that the pedal bone (third phalanx) drops, rotates or both. It is seen in horses on grass, and in cattle on concentrate feed, and may be associated with lack of exercise or toxaemia. In dairy heifers and cows fed large amounts of concentrates and living in restricted conditions, haemorrhage in the sole is very common and is often referred to as sub-clinical laminitis. (WRW)
See also: Activity, physical; Concentrate; Foot diseases; Hooves

Lard
The abdominal fat of pigs that has been rendered and clarified. The composition depends on diet but includes a high proportion of long-chain **saturated fatty acid**s. It is a rich source of **energy** (*c.* 38.5 MJ kg^{-1}) but deficient in other essential nutrients. In some countries it is used in pig, poultry and pre-ruminant diets to increase dietary energy concentration. The major **fatty acid**s in lard (g of total fatty acids kg^{-1}) are: 14:0 1.6; 16:0 25.5; 16:7 n-7 2.2; 18:0 16.8; 18:1 sum of *trans* **isomer**s 0.3; 18:1 sum of *cis* isomers 39.2; 18:2 n-6 10.0; 18:3 n-3 1.2; and saturated fatty acids 43.9, monounsaturated fatty acids 41.7 and **polyunsaturated fatty acid**s 11.2. (JKM)

Large intestine
The section of the digestive tract between the **small intestine** and

the anus. In most mammals it consists of the **caecum**, **colon** and **rectum**. Most birds have two caeca, both connected to the intestine at the ileocaecocolic junction. The large intestine is the major site for microbial activity in non-ruminants and is of particular importance for non-ruminant herbivores such as horses, **rabbits** and **ostrich**es. (SB)



The large intestine with its blood vessels, after removal of the small intestine. Image courtesy of Knowledge Collector. Licensed under Public Domain Mark 1.0.

Large yellow croaker (*Larimichthys crocea*)

An economically important **marine fish** distributed along the tropical and subtropical coast of East Asia. As a eurythermal fish, it usually lives in a **temperature** range of 10–32°C and grows best in 18–25°C (Qian and Xue, 2016). China is the main producing

country of cultured large yellow croaker in the world and the production reached 225,549 t in 2019, ranking first in mariculture fish of the country (Kong *et al.*, 2019; Zhou *et al.*, 2019). Nowadays, about 90% of the large yellow croakers grown in China are cultured using a floating sea-cage farming model in which the water depth is shallow (usually 4–6 m). (QS)



Floating sea cage in shallow sea water in Iceland. Photo courtesy of Luc Coekaerts. Licensed under CC0 1.0.

References

Kong, S.N., Ke, Q.Z., Chen, L., Zhou, Z.X., Pu, F., Zhao, J., Bai, H.Q., Peng, W.Z. and Xu, P. (2019) Constructing a high-density genetic linkage map for large yellow croaker (*Larimichthy crocea*) and mapping resistance trait against ciliate parasite *Cryptocaryon irritans*. *Marine Biotechnology* 21, 262–275.

Qian, B.Y. and Xue, L.Y. (2016) Liver transcriptome sequencing and *de novo* annotation of the large yellow croaker (*Larimichthy crocea*) under heat and cold stress. *Marine Genomics* 25, 95–102.

Zhou, Z.X., Han, K.H., Wu, Y.D., Bai, H.Q., Ke, Q.Z., Pu, F., Wang, Y.L.

and Xu, P. (2019) Genome-wide association study of growth and body-shape-related traits in large yellow croaker (*Larimichthy crocea*) using ddRAD sequencing. *Marine Biotechology* 21, 655–670.

Larval feeding:
see Fish larvae; Live fish food

Lathyrism
A paralytic syndrome of humans and livestock characterized by spastic paraplegia, pain, hyperaesthesia and paraesthesia. Historically, lathyrism occurred under conditions of poverty and **drought** when people were forced to subsist on diets composed largely of seeds of *Lathyrus* spp. Horses are highly sensitive, developing a hopping gait, stiffness and pain when moving. The onset of disease ranges from several days to months, depending on the dose. One identified toxin is directly neurotoxic, causing neurolathyrism (**muscle** rigidity and paralysis). A second toxin causes osteolathyrism by inhibiting **connective tissue** development (**lameness**). Many animals recover fully but chronically poisoned animals can develop permanent stringhalt-like signs. (BLS)

Lauric acid
Dodecanoic acid, $C_{12}H_{24}O_2$, molecular weight 222, shorthand designation 12:0. This 12-carbon, monocarboxylic, **saturated fatty acid**, with a melting point of 44.2°C, is a major component of **coconut** and palm **oils** and is also present in human **milk**, dairy **fat**, cinnamon and laurels. (JAM)
See also: Fatty acids

Laying hen

The term 'laying hen' refers to a female **chicken** that has been genetically selected over many generations to become efficient at table-**egg production**. In North America most consumers prefer white-shelled **eggs**, from breeds such as White Leghorn. Today's laying hen is dramatically different from the original red junglefowl of Southeast Asia. A mature junglefowl hen will lay only 10–12 white-shelled eggs during the breeding season. Today poultry breeding companies have strains that can lay white- or brown-shelled eggs all year long. Productivity will depend on the strain of hen. For white-egg laying hens, those kept in cages will lay 471–487 eggs in a 100-week period, with each hen eating about 100 g of feed per day. For the white-egg laying hens kept in non-cage systems, each hen will lay 456–473 eggs in the same 100-week period, consuming slightly more feed at 101–108 g per day per hen. For consumers preferring brown-shelled eggs from breeds such as Rhode Island Reds, those hens kept in cages will lay 468–483 eggs in a 100-week period, consuming 105–112 g of feed per day each. Similarly, hens laying brown-shelled eggs and kept in non-cage systems will lay 419–432 eggs each, while consuming 105–116 g of feed per day each.

There are non-commercial chicken breeds that are popular with those keeping laying hens in the backyard. People often prefer breeds that lay different-coloured eggs. For example, the Araucana is a South American breed that will lay a blue-coloured shell. When an Araucana is crossed with another breed the result is a chicken that can lay eggs with light blue, pink, or green shells. Other

popular breeds for backyard enthusiasts include Orpingtons, Wyandottes, Rhode Island Red and Plymouth Rock, which lay eggs with a range of brown colours. The Maran and Welsummer hens have become popular because of their dark chocolate-coloured eggs.



Araucana chicken in S. America. Photo courtesy of Chailey. Licensed under CC BY 2.0.

Nutrition

Hens that have been selected for efficient egg production typically lay more eggs on a reduced quantity of feed compared with unselected hens. To achieve their genetic potential for egg production, these hens must receive a well-balanced diet.

The **nutrient requirement**s for egg-type chickens were reviewed by the National Research Council (1994) and are summarized in the table. Combinations of different feed ingredients are mixed together to provide the nutrients the chickens need.

Nutrient requirements of egg-laying chickens[a].

Nutrient	Chick starter	Chick grower	Pullet developer	Prelay	Layers
Metabolizable energy, kcal kg⁻¹	2800	2800	2850	2850	2900
CP, g kg⁻¹	170	150	140	160	150
Lysine, g kg⁻¹	8.0	5.6	4.2	4.9	6.9
Methionine, g kg⁻¹	2.8	2.3	1.9	2.1	3.0
Methionine + cystine, g kg⁻¹	5.9	4.9	3.9	4.4	5.8
Arginine, g kg⁻¹	9.4	7.8	6.2	7.2	7.0
Histidine, g kg⁻¹	2.5	2.1	1.6	1.8	1.7
Isoleucine, g kg⁻¹	5.7	4.7	3.7	4.2	6.5

Nutrient	Chick starter	Chick grower	Pullet developer	Prelay	Layers
Leucine, g kg⁻¹	10.0	8.0	6.5	7.5	8.2
Phenylalanine, g kg⁻¹	5.1	4.2	3.4	3.8	4.7
Threonine, g kg⁻¹	6.4	5.3	3.5	4.4	4.7
Tryptophan, g kg⁻¹	1.6	1.3	1.0	1.1	1.6
Valine, g kg⁻¹	5.9	4.9	3.8	4.3	7.0
Calcium, g kg⁻¹	9.0	8.0	8.0	18.0	32.5
Avail. phosphorus, g kg⁻¹	4.0	3.5	3.0	3.5	2.5
Sodium, g kg⁻¹	1.5	1.5	1.5	1.5	1.5

Nutrient	Chick starter	Chick grower	Pullet developer	Prelay	Layers
Chloride, g kg^{-1}	1.2	1.1	1.1	1.1	1.3

[a] Adapted from data supplied by the NRC publication *Nutrient Requirements of Poultry*, 9th edition (1994), reproduced with permission from the National Academy of Sciences, courtesy of National Academies Press, Washington, DC.

For optimal performance, the diet must provide adequate **energy**, essential **amino acid**s (AA) and other essential nutrients. The **protein** requirement values outlined by the NRC (1994) assume a **maize**–soy diet of high **digestibility**. Therefore, it is advisable to adjust the dietary target values when diets based on feedstuffs of lower digestibility are formulated. Laying stock have the ability to regulate **feed intake** according to the energy level of the diet, making it important to adjust the concentration of other nutrients in relation to dietary energy level.

Cereal **grain**s, such as maize, **barley**, **wheat** and **sorghum**, are the main ingredients of poultry diets. They serve as an **energy source** and make up the largest portion of a layer diet and usually provide 30–60% of the total protein and AA requirements. Sources of protein such as **soybean** meal and canola meal must be provided to ensure adequate amounts, and a proper balance, of essential AA.

Methionine is important for feather formation and is generally the first limiting amino acid. It is important, therefore, that the required amount of methionine be included in the diet and in the correct proportion to the other essential AA.
Dietary fats are utilized mainly as a source of energy: common sources include **animal fat**, poultry fat and yellow grease. Poultry have a specific requirement for one fatty acid, namely **linoleic acid**, an **essential fatty acid**. Fat is also important in poultry diets to allow for the **absorption** of **fat-soluble vitamins** A, D, E, and K. Fat also helps control dust in the feed.

Maize is the most commonly used grain in North America and is the standard to which other grains are compared. It is the easiest for poultry to digest and the only grain that contains xanthophylls, making yellow maize a valuable component of layer diets when yellow-pigmented yolks are desired. Wheat is often used in poultry diets in western Canada and parts of Europe. The energy content of wheat is 94–96% that of maize but is higher in protein, **lysine** and **tryptophan**. Wheat also contains **gluten**, which is advantageous when making pellets because it eliminates the need for pellet binders. It also contains varying levels of **non-starch polysaccharide**s (NSPs), some of which are difficult to digest and can result in sticky droppings and **foo**t problems. The use of supplemental feed **enzymes** helps alleviate these problems.

Barley is commonly grown for **malting** but can also be grown for **poultry feeding**. It is grown in some parts of western North America and in many countries in Europe that are less suitable for maize production. Barley can be included in poultry feed, with

some restrictions. Some varieties contain β-**glucans** which, because of the chemical structure, cannot be easily digested by poultry and can lead to sticky droppings. Again, the use of supplemental feed enzymes helps alleviate this problem.

Sorghum, also referred to as milo, is one of the most **drought**-tolerant **cereal** crops. It is grown in some areas of southern USA and many areas of Africa. The nutrient profile of sorghum is similar to that of maize, although the ME value is slightly lower. In the past, the use of sorghum in layer diets had been restricted because of the presence of **tannins** which reduce nutrient availability and can cause poultry to refuse feed. The sorghum varieties grown in the USA are tannin-free, but many sorghum varieties grown in Africa can be high in tannins and should be used with care.

Oats and **rye** are lower in energy but can be used in poultry diets in small quantities. Caution must be used when including rye in chicken diets, because of the possibility of **ergot** contamination. Ergot is a toxic fungus**,** and rye is a grain that is particularly susceptible to ergot contamination. **Triticale**, which is a hybrid of rye and wheat, has also been used as a dietary **energy source** for poultry diets in some countries.
In addition to the use of whole grains, several grain **milling by-product**s are used in layers' diets. These include **gluten** meal, **bran** and middlings. **By-product**s from **ethanol** production are also used and are referred to a distillers' grains.

Protein sources can include both vegetable and animal sources

such as **oilseed** meals, **legumes** and slaughter or **fish** processing by-products. The vegetable sources usually come as meals or cakes. For **oil** meals, solvent extraction is used for oil removal. For oil cakes, mechanical extraction is used. The most commonly used oil meal in poultry diets is soybean meal, but canola meal and **sunflower** seed meal are used in various parts of the world. Canola is a variety of rapeseed that is low in **glucosinolate**s in the oil and **erucic acid** in the meal. The **crude protein** content of canola meal is lower than that of soybean meal but has a good **amino acid** profile. The fibre level of sunflower seed meal can limit its use in poultry diets. **Cottonseed** meal can also be used but it has less crude protein, dietary energy and available **lysine** content than soybean meal. The cottonseed meal needs to be developed from glandless varieties so that **gossypol** content is eliminated. **Sesame** seed meal is low in lysine, **isoleucine**, **leucine** and **valine** compared with soybean meal, but is a good source of **methionine**. **Groundnut** (peanut) meal is a poor source of essential amino acids and has a high risk for **mycotoxin** contamination.

Legume seeds being used in layer diets include field **peas** and field (faba) **beans**. Field peas have been referred to as 'feed peas' in Canada and as 'protein peas' in Europe. The relatively low levels of anti-nutritional factors in these seeds eliminates the need for **heat treatment** prior to inclusion in layer diets.

Two animal by-products commonly used in poultry feed include fish meal and meat and **bone meal**. Other by-products include poultry by-product meal, **blood meal** and **feather meal** (banned

in some countries). By-products are rendered to produce nutritional and economical feed ingredients.

Insect meals are becoming a popular, sustainable animal feed ingredient. Black soldier fly larvae meal is most popular. Black soldier fly larvae (BSFL) can be provided live for small layer flocks, but large-scale commercial production systems are being developed and can provide a variety of products, including the whole BSFL, BSFL meal and BSFL oil.

Typically, grains are finely ground before being mixed into poultry diets which can be fed as a **mash**, pellets, or crumbles. Some producers prefer to feed the grain whole (unground) since poultry have the ability to digest grains in this form. One benefit is that feeding whole grain results in improved **gizzard** development. If whole grain is fed, the chickens should also have a supply of non-calcareous grit available to assist with grinding in the gizzard.

Minerals are required in poultry nutrition for their vital roles in metabolic, enzymatic and biochemical reactions in the bird's body. Minerals are defined as macro- or micro-minerals depending on the quantities required in the diet. Micro-minerals, also referred to as trace minerals, are measured in milligrams (mg) per kg while macro-minerals are required in larger amounts. Although required in trace amounts, micro-minerals are essential to the health of poultry. For example, **iron** is responsible for binding **oxygen** in blood cells; **copper** is important for the **connective tissue**s; **manganese** is essential for **cartilage** formation; and **zinc** is important for **collagen** synthesis. Grains are low in available

minerals, therefore **mineral supplement**s are included in commercial poultry feeds. The enzyme **phytase** is often added to poultry diet to release the **phosphorus** bound to **phytate** in grains. This reduces the levels of inorganic phosphorus that need to be added. Phosphorus and **calcium** can be provided as **dicalcium phosphate**, **limestone**, **oyster shell**, etc. Most of the calcium in the diet of the growing bird is used for **bone formation**, whereas in the laying bird most of the dietary calcium is used for **eggshell** formation. An **egg** contains about 2 g of calcium in the shell; therefore, the calcium need of the laying hen is high. A deficiency results in soft-shelled eggs and reduced egg production. A weakness termed 'layer fatigue' has also been linked to calcium deficiency (as well as phosphorus or **vitamin D** deficiency), though it is usually reported only in caged birds.

Certain vitamins and trace minerals are typically included in the form of a premix, to ensure that requirements have been met. In the past, only inorganic **salts** of minerals were available for use in premixes**,** such as **zinc sulphate**, **copper** sulphate, etc. Unfortunately, inorganic salts are only partially absorbed by the birds. Today organic trace minerals are available. Mineral availability is much higher with the organic trace minerals, reducing the potential for environmental pollution from unabsorbed minerals.

Because of the high **metabolic rate** of the fowl, a continuous supply of feed is required. This is provided for by the crop that acts as a reservoir for the storage of feed prior to its **digestion**. Poultry tend to eat meals at about 15 min intervals throughout the daylight

hours and, to some extent, during darkness. They tend to eat larger portions at first **light** and in the late evening. A meal of normal feed takes about 4 h to pass through the gut in the case of young stock, 8 h in the case of laying hens and 12 h for broody hens. Intact, hard grains take longer to digest than cracked grain.

In **choice feeding** or 'free-choice feeding' the birds are usually offered a choice among three types of feedstuffs: (i) an **energy source** (e.g. maize, **rice bran**, sorghum or wheat as whole or cracked grain); (ii) a **protein source** (e.g. soybean meal, canola meal or fish meal) supplemented with vitamins and minerals; and (iii) in the case of laying hens, calcium in granular form (calcareous grit such as oyster-shell grit). Regular grit of a suitable granular size (to aid grinding in the **gizzard**) should also be made available. The basic principle behind choice-feeding is that birds possess some degree of '**nutritional wisdom**' which allows them to select from the various feed ingredients offered and construct their own diet according to their individual needs and production capacity.

Poultry are typically not able to digest **cellulose** and non-starch compounds very well. As a result, chickens do not digest most pasture crops effectively. The amount of nutrients they will get from pasture will depend on the type of crops and pasture management. Shorter, immature pasture will provide more nutrients than longer, mature pastures. Chickens kept on pasture will obtain some nutrients from earthworms and other small soil arthropods. Chickens are not able to digest **chitin** very well so do not obtain a lot of nutrients from mature insects. The quantity of insects that free-range chickens are able to obtain will depend on

the geography, **climate**, and density of chickens.

Water is often overlooked, but it is one of the most important nutrients. An animal can live without food longer than it can live without water. A hen will drink twice as much water as it will eat. In an egg-laying flock, a shortage of water for just a few hours can result in drop in egg production which can have long-term consequences. So, it is important that hens have clean water available at all times. A laying hen drinks about 25% of her daily water intake during the last two hours of daylight, therefore the amount of water given in the morning must be sufficient to last all day. (JPJ)

Reference

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Lead

The nutritional essentiality of lead has only been demonstrated under laboratory conditions in ultra-trace quantities. Lead is a potentially toxic element for farm animals. It is present in many forms on the farm, but most hazardous are old paints (made before lead was removed from paint in the latter part of the 20th century), discarded lead batteries and roofing material, and soil contaminated by industry and mine tailings. Cattle are most at risk, being inquisitive and likely to eat soil, paint, etc., when their diet is inadequate. Lead is the most common cause of cattle **poisoning** in the UK, accounting for about 200 deaths annually. The symptoms of acute lead poisoning are **blindness**, excessive salivation,

irritability and **convulsion**s, often accompanied by a stiff gait and impaired vision. Chronic lead poisoning may induce loss of **appetite**, osteoporosis and fractures, and neurological disorders, due mainly to the strong affinity of lead for the binding sites of **calcium** and other essential nutrients. (CJCP)

Leaf protein

Composed of hundreds of **enzymes**, leaf protein is dominated by a single polypeptide complex: Rubisco (ribulose 1,5-bisphosphate **carboxylase/oxygen**ase) (also known as RuBisCo). This protein comprises approximately 50% and 30% of **leaf protein** in C3 and C4 plants, respectively. It is a crucial component in the photosynthetic fixation of atmospheric carbon within green plants. Rubisco is the protein present in all green leafy plants. It can account for 50% of total leaf cell protein and it is rich in the essential **amino acid**s. In temperate regions, **forage** leaf is fed fresh, ensiled for winter feed or dried to produce **grass**, clover or **lucerne** (alfalfa) meal (see table). Lucerne meal is fed to racehorses and high-yielding cows. In tropical regions, the leaves of a wide range of plants, including ***Lablab purpureus***, **leucaena** and **glyricidium**, are fed fresh, wilted or dried into leaf meal. Typically these are used as **protein source**s for cattle, goats, sheep, poultry, fish and **shrimp**. They also supply **vitamins**, **minerals** and **trace element**s, as well as pigments. *Alchornia cordifolia* meal is fed to poultry as an egg and meat colorant, while *Sauropus androgynus* (Katuk) and tu-chung (*Eucommia ulmoides*) are used to reduce meat **lipid** content. Many leaves contain **antinutritional factor**s (ANFs) which limit dietary

inclusion levels. Levels of some ANFs can be reduced by simple processing such as **wilting** (*Gliricidia*), drying (***Cassava***) or by supplementing the diet with specific antidotes (such as adding **iodine**, **copper** or ferrous **sulphate** to leaves of *Leucaena leucocephala*). Selection and breeding of low-ANF plants is possible. (JKM; DB)

Dry matter (g kg^{-1}), nutrient composition (g kg^{-1}) and energy (MJ kg^{-1}) contents of leaves.

	Dry matter	**Crude protein**	**Crude fibre**	**Ash**	**Ether extract**	**NFE**	**ME**
Gliricidia spp. leaf meal	930	230–240	200	85–90	35–42	400–480	–
Leucaena leucocephala meal	950	292	192	105	–	–	–

	Dry matter	Crude protein	Crude fibre	Ash	Ether extract	NFE	ME
Alchornia cordifolia	950	190	164	25	51	575	–
Grass meal	930	155	220	85	35	480	9.3
Lucerne meal	930	160	240	95	25	425	8.0
Lucerne, fresh	945	230	243	83	48	396	–
Lucerne meal concentrate	951	370–420	7–30	13–16	30–69	360–423	–
Residue from lucerne	926	171	352	69	33	375	–

ME, metabolizable energy; NFE, nitrogen-free extract.

Reference

Edelman, M. and Colt, M. (2016) Nutrient Value of Leaf vs. Seed. *Frontiers in Chemistry* 4, 32. doi: 10.3389/fchem.2016.00032.

Lean body mass

The lipid-free mass of the body (excluding **digesta**). Lean body mass is normally calculated by subtracting fat (**lipid**) content from total body mass. It therefore includes **body water**. (MMacL)

Leaves:

see Leaf protein

LecithinPhosphatidylcholine, a major **phospholipid** in cell membranes. The *sn* 1 and 2 positions of the **glycerol** backbone $CH_2OH{\cdot}CHOH{\cdot}CH_2OH$ of lecithin are **long-chain fatty acid**s while the *sn* 3 position has phosphocholine, ${\cdot}O{\cdot}PO_3{\cdot}CH_2{\cdot}CN^+{\cdot}(CH_3)_3$, linked to it. The fatty acid in the *sn* 2 position of lecithin is generally a long-chain **unsaturated fatty acid** such as **arachidonic acid**. (NJB)

Lectins

Carbohydrate-binding proteins of non-immune origin that agglutinate cells or precipitate **polysaccharide**s or glycoconjugates. **Carbohydrates** are present on most cell membranes: if their structure fits the binding site of the lectin, agglutination will occur. Lectins were first termed **haemagglutinin**s because of their ability to cause the agglutination of human and animal **blood** *in vitro*. Lectins are

distinguished from **antibodies** that agglutinate cells by being found in plants, bacteria and viruses that do not have the ability to produce antibodies. In addition, lectins are a heterogeneous group of proteins that vary in size, composition and three-dimensional structure, in contrast to antibodies, which are structurally similar.

Lectins are distributed broadly throughout the plant kingdom and have been identified in moulds and lichens as well as higher plants. **Ricin** was the first to be isolated, extracted from castor beans in 1889 by P.H. Stillmark. Since Stillmark's discovery, lectins have been identified in more than 1000 plant species. The majority of the toxic lectins come from species of Euphorbiaceae and Leguminosae. Most lectins in higher plants are found in the seeds but they have also been found in tubers, plant saps, leaves, stems and bark. The highest concentrations of lectins are in the mature seeds of **legumes**, where they may constitute as much as 10% of the total **protein**.

Because of the broad distribution of lectins throughout the plant kingdom, they are present in most foods and feeds of plant origin. Not all are toxic to animals but many raw legume seeds are detrimental to animal performance. Ingestion of lectins can result in **diarrhoea**, decreased **nutrient absorption**, increased bacterial infection, **growth** retardation and death. Lectins binding to surface cells of the **intestinal mucosa** may cause lesions and disruption of the normal development of the microvilli. Apart from reducing nutrient absorption, such lesions may increase bacterial proliferation in the gut and infiltration via the bloodstream into internal organs. (SEL)

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Leg weakness

A term commonly used to describe specific syndromes in pigs and turkeys. In pigs, the pathogenesis includes osteochondrosis, epiphysiolysis and osteoarthrosis, but generally excludes infectious arthritis. It is a condition of rapidly growing pigs between 12 and 24 weeks of age. The affected pigs generally show a progressive **lameness**. Osteochondrosis (**dyschondroplasia**) involves abnormal differentiation of the **cartilage** of growth plates. It is found in subclinical form in the majority of pigs sold for meat. In epiphysiolysis, the epiphysis separates from the diaphysis (shaft) of the bone, often the proximal femur. In osteoarthritis (degenerative joint disease, DJD) the articular cartilage degenerates. The causes of leg weakness are uncertain but it appears to be more common in pigs selected for **growth** and **feed conversion** and fed on a high **plane of nutrition**. Predisposition may be inherited (heritability of up to 0.3), the Landrace breed being particularly affected. Lack of exercise is also a suspected risk factor and exercise appears to improve the gait of pigs, though it does not reduce the joint lesions.

High dietary concentrations of **calcium** and **phosphorus** are commonly advised methods of prevention. Signs of leg weakness include a short-stepping swaying gait, crossed legs, flexed carpal joints and difficulty in rising. Epiphysiolysis can cause sudden inability to rise and may be difficult to distinguish from a fractured femur. Leg weakness is a common reason for culling gilts and boars, often at the beginning of their breeding life.

The aetiology of leg weakness in turkeys is not understood. The birds show swelling of the hock joints. Osteochondrosis is also seen in young male purebred cattle as osteochondritis dessicans and as sub-chondral cysts, causing unilateral lameness but bilateral radiographic changes and a high rate of culling if not treated surgically. Osteodystrophia fibrosa (**bran** disease; miller's disease) is a condition seen in horses, pigs and goats in which bone is resorbed and weakened. It may be caused by a diet high in phosphorus and low in calcium. The animal shows shifting lameness with no pain and may have swollen upper and lower jaws. In **ostrich**es, leg weakness is commonly encountered. Adequate calcium, grit (3–6 mm for chicks, 6–20 mm for adults) and **protein** between 16% and 18% of the diet are normally recommended. (WRW)

See also: Bone diseases

Legume

Any plant of the family Leguminosae, which includes **lucerne** (alfalfa), clover, **peas** and **beans**. Bacteria (*Rhizobia*) colonize the roots of legumes and fix atmospheric **nitrogen**. (JMW)

Legume protein
The protein contained in leguminous plants such as **lucerne** (alfalfa), clover, **peas** and **beans**. (JMW)

Legume silage
The term **legume** (from *legere*, to gather) applies to many **nitrogen**-gathering plants which bear seeds in pods. The foliage of legumes is rich in **protein** compared with **cereal**s or **grasses**. Legumes are perceived as difficult crops to ensile, due to their high chemical buffering capacity. Legume silage plants include **lucerne** (*Medicago sativa* L.), **sainfoin** (*Onobrychis vicciifolia*), white clover (*Trifolium repens* L.), red clover (*Trifolium pratense* L.), vetches (*Vicia sativa* L.), field **beans** (*Vicia faba* L.), **peas** (*Pisum sativum* L.) and **lupin** (*Lupinus* spp.). (RJ)

Lehmann system
A system of feeding animals a bulky feed *ad libitum* with restricted amounts of a balancing concentrate feed given once or twice a day. It was developed in Germany about 100 years ago for feeding **potatoes** to pigs. It is well suited to feeding root crops, but can also be used with other perishable crops such as waste **bananas**, **sugarcane** juice, etc. (MFF)

Lentil (*Lens culinaris* Medik; *L. esculenta* Moench)
Also known as red dahl or split **pea**, lentils grow on a widely cultivated bushy herb about 50 cm tall, native to Asia. The seeds are used mainly for human consumption, particularly in the Near East and Asia. Harvested vines are valuable for ruminant feed. The

protein in raw lentils is inefficiently used as feed, with a ratio of body weight gain:protein consumed of 0.03, compared with 1.42 for **chickpea** (*Cicer arietinum* L.). The **digestibility** of lentil **straw** – 51.9 g digestible **organic matter** (DOM) 100 g^{-1} dry matter (DM) – in ruminants is higher than for most other straws, with a voluntary intake only 10% lower than that of **lucerne** hay. As with all **legumes**, the nutrient content and digestibility of the leaves (8–10% **crude protein** and 66.2% DM **digestibility**) are considerably higher than for other plant parts (see Tables 1 and 2). (LR)

Table 1. Nutrient composition (% dry matter) of lentil products.

	DM (%)	**CP**	**CF**	**Ash**	**EE**	**NFE**	**Ca**	**P**
Bran	87.6	26.4	8.4	2.8	1.1	61.3		
Pod husks	88.0	12.6	29.0	3.5	0.8	54.1		
Straw		5.8	37.1	9.0	2.4		1.65	0.07

CF, crude fibre; CP, crude protein; DM, dry matter; EE, ether extract; NFE, nitrogen-free extract.

Table 2. Digestibility (%) and ME content of lentil products.

	CP	**CF**	**EE**	**NFE**	**ME** (MJ kg^{-1})

	CP	CF	EE	NFE	ME (MJ kg^{-1})
Ruminant					
Pod husks	11.8	67.2	99.9	70.7	9.26
Straw					7.90

Further reading

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Leptin

A 16 kDa **protein hormone** produced in **adipose tissue** to signal **satiety** and reduce **appetite** in a negative feedback loop to control intake and **energy expenditure**. It is encoded by the obese (*ob*) gene. It also has roles in angiogenesis, **bone formation**, immune function and **fertility**. Its proinflammatory activity can trigger autoimmune responses in chronic inflammatory diseases. Cortisol and **insulin** are potent stimulators of leptin production. Leptin levels decrease soon after initiation of fasting and the hormone acts as a mediator of **adaptation** to fasting; indeed, this may have been how the molecule evolved. Leptin is expressed in higher concentration in obese animals and is directly correlated with animals' **body condition** score. (CJCP)

See also: Ghrelin; Hunger

Leucaena

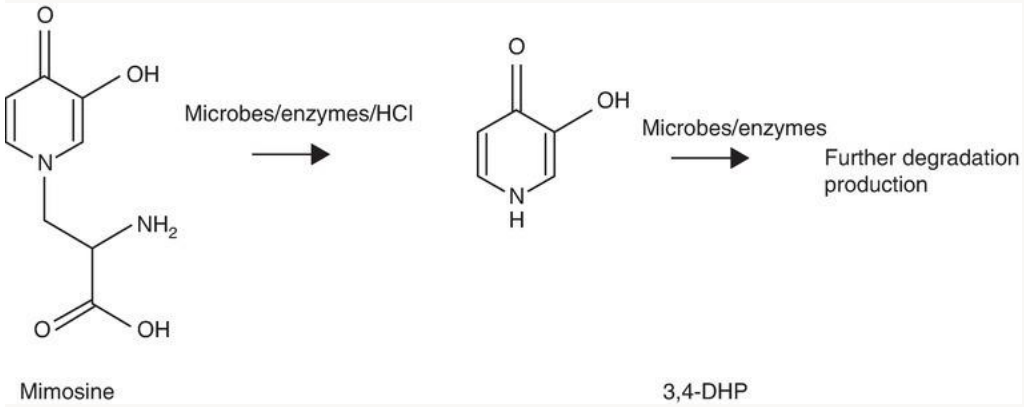
A tropical leguminous tree or bush of which the leaves, pods and seeds can be used to feed animals. It is grown to produce firewood, to stabilize and enrich poor soils and as a source of nutrients for animals, primarily ruminants. There are ten species and about 800 varieties of leucaena, some of which can produce over 100 t of **forage** per annum. Typically the forage has (g kg^{-1} dry matter (DM)): **protein** 250, **fat** 40, **crude fibre** 80 and neutral detergent fibre 600. It has adequate concentrations of **minerals** and is a substantial source of **carotenoid**s, which are important in **egg production**. The **metabolizable energy** of leucaena for ruminants is about 8.5 MJ kg^{-1}, while that for poultry is only about 2.5 MJ kg^{-1}, due to its **non-starch polysaccharide**s, **tannins** and the toxic amino acid, **mimosine**. Compared with the leaves, the seeds of leucaena are higher in protein and fat (300 and 80 g kg^{-1}, respectively) but they also contain more mimosine (60–100 g kg^{-1} in comparison with 40–60 g kg^{-1} for the leaf). Condensed tannins in this forage can promote **protein utilization** when they are present at low levels (< 35 g kg^{-1} DM), but at higher concentrations (e.g. 50 or 60 g kg^{-1} DM) they reduce **protein digestibility** and **nitrogen retention**.



Leucaena leucocephala, a deep-rooted legume used for cattle feeding. Photo courtesy of Forest and Kim Starr. Licensed under CC BY 3.0.

Mimosine (see structural figure) is a **non-protein amino acid** that causes numerous adverse effects when consumed by animals. It causes depilation (**hair** loss) and interferes in the **metabolism** of other amino acids to which it is structurally related. It is readily degraded by **rumen** bacteria to yield 3-hydroxy-4(1H)-pyridone, which is often referred to as 3,4-DHP and which interferes with thyroid function to cause **goitre**. The mimosine content varies with the variety of leucaena but is a deterrent to its use as a **fodder** (especially as the sole source) in some parts of the world. The value of leucaena as a forage for ruminants depends greatly on the presence or absence of certain **rumen microorganism**s (*Synergysti joneseii*) which degrade mimosine and 3,4-DHP to innocuous compounds within the rumen. In some areas of the

world (notably Australia) the rumen microflora are cultured and administered to cattle and sheep and they can then browse leucaena with impunity and grow well on leucaena-based diets.



Mimosine and its degradation by *Synergisti joneseii* and enzymes.

Leucaena meal, included in poultry diets at about 50 g kg^{-1}, increases egg **yolk pigment** in hens and provides protein for growing chicks. Higher inclusion rates tend to cause poorer performance, presumably due to the tannins and non-starch polysaccharides. Pigs appear to be able to tolerate about 50 g kg^{-1} in their diet without detrimental effects but the **digestible energy** of leucaena leaf meal for pigs is only about 5 MJ kg^{-1}. (TA; GMcLD)

Further reading

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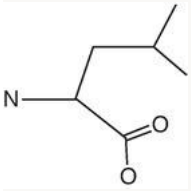
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Leucaena leaf meal:

see **Leaf protein**

Leucine

An essential amino acid ($(CH_3)_2{\cdot}CH{\cdot}CH_2{\cdot}CHNH_2{\cdot}COOH$, molecular weight 131.2) found in protein. It is one of the **branched-chain amino acid**s. Leucine is generally found in considerable excess in most plant proteins, so in practice a deficiency is rare. Leucine is purely ketogenic; it cannot be used in **gluconeogenesis**. **Catabolism** of leucine involves **transamination** followed by **oxidative decarboxylation** to a **coenzyme** A derivative, and these first two steps in leucine catabolism use the same enzymes that are used for the first two steps in **isoleucine** and **valine** catabolism. (DHB)



Leukotrienes

Lipid-based compounds derived from **arachidonic acid**, a 20-carbon unsaturated (20:4 n-6 $\Delta^{5,\,8,\,11,\,14}$) **fatty acid** synthesized in most mammals from **linoleic acid** (18:2 n-6 $\Delta^{9,\,12}$) except in cats, where arachidonate is an **essential fatty acid**. Arachidonate in the *sn*-2 position of the **glycerol** moiety of **phospholipid**s in cell membranes is released by **phospholipase** A_2. It can then be used in the biosynthesis of series 4 leukotrienes. This conversion is dependent on a lipoxygenase which facilitates the incorporation of molecular **oxygen** into arachidonate, forming an intermediate (5-

HPETE), which ultimately leads to formation of A_4, B_4, C_4, D_4, E_4 and F_4 forms of leukotrienes. Four of the leukotrienes are amino **lipids**. Leukotriene C_4 contains **glutathione** (x-glutamyl-cysteinyl-glycine); D_4 derived from C_4 contains **glycine** and **cysteine**; E_4 derived from D_4 contains cysteine; and F_4 derived from E_4 after addition of glutamic acid has cysteine and glutamic acid. These substances act as local **hormone**s and have short half-lives. They are chemically similar to **prostaglandin**s and thromboxanes but are involved in hypersensitivity and allergic responses. They are vasoactive, they produce bronchoconstriction and they are involved with counteracting the effects of asthma (Drazen *et al*., 1999). Two other series, 3 and 5, are identified but their functions are little understood. The series 3 leukotrienes are derived from **mead acid** (20:3 n-9 $\Delta^{5, 8, 11}$). The series 5 leukotrienes are derived from timnodonic acid (20:5 n-3 $\Delta^{5, 8, 11, 14, 17}$). (TDC)

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Level of feeding:

see Plane of nutrition

Lieberkühn's crypts:
see Crypts of Lieberkühn

Light
Electromagnetic radiation with a wavelength of 400–780 nm which, when received at the retina and neurally transferred to the brain, makes sight possible. Light also has a profound effect on the physiology and performance of farm animals, whether artificial light in indoor production systems or natural light for grazing livestock. For avian species, light influences sexual activity by directly penetrating the skull and tissues to the **hypothalamus**. Since farmed birds are reared typically in indoor systems, knowledge of the components of the artificial lighting regime that affect behaviour and performance is critical. These are **photoperiod** (day length), light intensity (illuminance) and spectral composition (colour balance or wavelength). Photoperiod has the strongest influence, affecting **growth** rate and skeletal integrity, rate of sexual maturation and all reproductive characteristics.

Light intensity also has a strong influence on bird behaviour and, to a lesser extent, bird performance. Activity and **energy expenditure** are positively correlated with intensity, together with the incidence of cannibalistic behaviour and its related mortality. A minimum intensity of 2 lux during rearing ensures that sexual maturity is not retarded, whilst maximum **egg production** in modern hybrids is achieved with a minimum intensity of 5–10

lux. Unexplainably, **feed intake** and **egg** weight decrease, though at a low rate, with increasing illuminance. Growth rate and feed conversion in modern broilers and turkeys are not significantly affected by light intensity, provided that the illuminance during the first week is sufficiently bright to allow the birds to find feed and water.

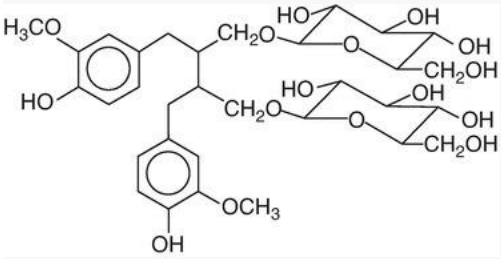
Spectral composition minimally affects egg production, despite longer wavelengths (red) penetrating to the hypothalamus more effectively than shorter wavelengths of light. This is inconsequential to birds given white light, because white includes all wavelengths of light. Birds are more active and tend to exhibit more aggression under red light and this might explain why body weight gain in broilers and turkeys is reduced under red light. Though not light in human terms, UVA ultraviolet radiation is important for poultry because they have a fourth retinal cone that is sensitive to UVA. As a consequence birds can see objects and plumage markings that reflect UVA, though these will be invisible to humans. Injurious **pecking** in growing turkeys is reduced when birds are given supplemental UVA concurrently with environmental **enrichment**.

Light affects reproductive activity, growth, food intake and pelage growth in mammalian species, with **photoperiod** rather than light intensity or wavelength being the key factor. Seasonal changes in natural photoperiod provide the major influence in largely outdoor production systems, but artificial lighting regimes during periods of housing can clearly be important. Deer, sheep and goats demonstrate the most pronounced seasonal changes in

physiology whereas cattle and pigs are less seasonal. In addition, within the diurnal period, whatever the time of year or photoperiod, animals preferentially eat more during the day than at night. Thus, in freely feeding cattle and sheep, meals are longer and more frequent during daylight than during darkness. (PDL; CLA)

Lignans

A class of secondary plant **metabolite**s. Lignans are oligomers of hydroxy **cinnamic acid**s ($C_6H_5CH{=}CHCOOH$). Unlike **lignin**, lignans are soluble and may be absorbed from the digestive tract of mammals. Lignans have post-absorptive physiological effects such as oestrogenic activity. For example, consumption of the lignan secoisolariciresinol diglycoside (shown here) in flaxseed is associated with a decreased risk of breast cancer. (JDR)



Lignin

An insoluble **polyphenolic compound** associated with **polysaccharide**s in the plant cell wall. Lignin makes the cell wall rigid and hydrophobic. It is formed by the oxidative polymerization of monolignols (hydroxycinnamyl alcohols). The polymerization process occurs outside the cell after monolignols are transported across the plasmalemma. The structure of lignin is complex and difficult to determine by traditional biochemical techniques.

Lignification of the cell wall occurs after cell elongation is complete and is associated with a decrease in the **digestibility** of cell wall polysaccharides. Lignin in the cell walls of **grasses** is cross-linked with polysaccharides through esters of two **cinnamic acid**s: *p*-coumaric, $HOC_6H_4CH{=}CHCOOH$; and ferrulic acid, $HOC_6H_3(CH_3O)CH{=}CHCOOH$. These esters are saponified by alkali treatment, which leads to an increase in the degradability of the **polysaccharide**s. This process is used to increase the digestibility of **cereal** crop residues. The cell walls of **legume** forages have fewer **ester** cross-linkages and alkali treatment has little effect on the degradability of their cell wall polysaccharides.

Lignin is indigestible and is negatively correlated with digestibility of the cell wall. Certain aerobic fungi are capable of degrading lignin through oxidative cleavage of the phenolic rings through the action of phenol oxidases and Mn^{2+} peroxidases. The degradation of lignin in anaerobic environments is too slow to occur in the digestive tract of mammals. (JDR)

Lignocellulosic waste

Waste products such as sugarcane **bagasse**, **yam** peel, **cocoa bean** shells and paper **milling** waste are used as animal feeds, as carriers for low-dry-matter feeds, or as **substrates** for bio-conversion into protein-enriched feed by cellulolytic fungus. Lignocellulosic wastes are used most frequently in ruminant diets. (JKM)

Lignoceric acid

Tetracosanoic acid, $CH_3{\cdot}(CH_2)_{22}{\cdot}COOH$, molecular weight 368.6,

shorthand designation 24:0. A 24-carbon **saturated fatty acid** found in **sphingolipid** and glycosphingolipid of animal tissues and in seeds of Leguminosae and Sapindaceae.(DLP)

Limestone
A sedimentary rock found in vast deposits throughout the world, usually formed from the exoskeletons of marine creatures and consisting mainly of **calcium** carbonate ($CaCO_3$). It is typically white or off-white. In a ground form it is used as a source of calcium in animal feeding stuffs. A common type of limestone is dolomite, in which some of the calcium is replaced by **magnesium**, $CaMg(CO_3)_2$. The availabilities of calcium and magnesium from dolomite are relatively low. (CRL)

Linamarin
A simple cyanogenic **glycoside** found in **linseed**, **cassava** and white clover. Its structure is $C_6H_{12}O_6{\cdot}C{\cdot}(CH_3)_2{\cdot}CN$. In the **gastrointestinal tract** it readily undergoes acid or enzymatic **hydrolysis** to yield **glucose** and cyanic acid (HCN). HCN is extremely toxic, inhibiting **cytochrome** oxidase activity and ultimately causing death. (TA)

Linear programming
Method of minimizing or maximizing a mathematical function, linear in a number of variables, subject to linear constraints on these variables. Primarily used in animal nutrition to minimize the total cost of a feed, subject to restrictions on its nutrient composition. (RG)

Key reference

van Dooren, C. (2018) A review of the use of linear programming to optimize diets, nutritiously, economically and environmentally. *Frontiers in Nutrition* 5, 48.

Linoleic acid

cis-9,12 Octadecadienoic acid, with molecular structure $CH_3(CH_2)_4(CH{=}CHCH_2)_2(CH_2)_6COOH$, molecular weight 280.4, shorthand designation 18:2 n-6. An **essential fatty acid** of the n-6 family and a metabolic precursor of many physiologically active **eicosanoid**s. It is found in high concentration in many **oil** seeds. (DLP)

Linolenic acid

cis-9,12,15 Octadecatrienoic acid, with molecular structure $CH_3(CH_2)(CH{=}CHCH_2)_3(CH_2)_6COOH$, molecular weight 278.4, shorthand designation 18:3 n-3. An **essential fatty acid** of the n-3 family and a metabolic precursor of many physiologically active **eicosanoid**s, it is highly susceptible to spontaneous **oxidation**. It is the major fatty acid in **linseed** oil; there are also significant amounts in **soybean** oil. (DLP)

Linseed (*Linum* spp.)

Plant grown for its fibre (flax) and the **oil** of its seed. Linseed oil is high in **unsaturated fatty acid**s, especially **linolenic acid**, and is therefore subject to **oxidation**. Consumption of linseed **oil**, especially by non-ruminants, makes the tissue **lipids** soft and subject to oxidation, with an undesirable flavour and smell. Linseed

cake or meal (the residue after the oil has been extracted) is used as a **protein concentrate** in animal diets, mainly for ruminants and horses. It is less useful in diets for non-ruminants because it contains up to 100 g of **non-starch polysaccharide**s (NSPs) kg^{-1} known as mucilaginous **gums**. They are essentially indigestible by non-ruminants and tend to absorb large quantities of water, increasing digesta **viscosity** and producing wet sticky faeces. Enzyme **supplementation** may reduce some of the effects associated with these NSPs but this is not necessary in ruminants, as the gums are degraded by the **rumen** microflora. Linseed meal also contains the cyanogenic **glycoside**, **linamarin**, which can yield HCN after ingestion.



Linseed flowers. Photo courtesy of Acradenia. Licensed under CC BY 2.0.

The apparent **metabolizable energy value**s of linseed meal for poultry, pigs and ruminants are about 8, 13 and 14 MJ kg^{-1}, respectively. The **crude protein** concentration is 300–400 g kg^{-1}. It contains factors that antagonize **vitamin** B_6 in poultry. The **protein** is relatively low in **lysine**, which may be made less available by heating due to the formation of Maillard products.

Inclusion levels of linseed in diets are usually less than 20 g kg^{-1} diet for poultry or 110 g kg^{-1} for other species. (TA)

Lipase

A class of hydrolytic **enzymes** that degrade **lipids**. Lingual lipase is present in the **saliva** of calves when they are on a **milk** diet but disappears when they mature. Pancreatic lipases are secreted into the **duodenum**.

Lipids are hydrophobic and, before they can be digested, most dietary lipids need to be emulsified, i.e. their lipid droplets are reduced to a size that forms stable suspensions in water. Emulsification is begun in the **stomach** by the higher temperature and intense mixing, which decrease the droplet size before the lipid enters the **small intestine**. In the duodenum the emulsification is completed by the detergent action of **bile** acids and **phospholipid**s secreted via the bile duct from the liver.

Lipase itself cannot penetrate the coat of bile products surrounding the droplets of triglyceride, the major dietary lipid component. The enzyme colipase, a relatively short **peptide**, is needed to make a path through the bile products, giving lipase access to the underlying triglycerides. Lipase then cleaves the **fatty acid**s from each end of the triglyceride molecule, but does not attack the central fatty acid. Thus, the **hydrolysis** products of one triglyceride are two fatty acids and one monoglyceride.

Other lipid-digesting pancreatic enzymes include **cholesterol** esterase and **phospholipase**. The hydrolysis products are non-esterified fatty acids, cholesterol and lysophospholipids. (SB)

Lipid

Low-molecular-weight (generally < 1000) substance of biological origin that are relatively more soluble in non-polar than polar solvents. Lipids are characterized by their low **oxygen** content and are therefore **energy** dense. Neutral lipids (**fats**, **oils**) are generally found as energy storage molecules, whereas the more polar lipids (**phospholipid**s, **sphingolipid**s) are key components of cellular and subcellular membranes. (DLP)

Lipid absorption

Because lipids do not dissolve in water they have first to be emulsified; they can then be hydrolysed by **lipases** in the **duodenum** and must then be formed into micelles before they can be absorbed into the **enterocyte**s of the **intestinal mucosa**.

Emulsification is achieved mainly in the duodenum by exposure to **bile**, which leads to the production of emulsified droplets. In the **jejunum** the combined actions of lipase, co-lipase and bile lead to the formation of micelles consisting of the **hydrolysis** products – **fatty acid**s and monoglycerides. The micelles diffuse through the unstirred water layer to the **brush border** of the enterocytes through which all the components, except the bile acids, are absorbed by **diffusion**. The bile acids pass down the intestinal tract to the **ileum**, where they are absorbed by a specialized **sodium** co-transport.

In the enterocytes, triglycerides are reformed and packaged into **chylomicron**s. These are complex aggregates also consisting of **cholesterol** esters, with a surface layer of **phospholipid** and cholesterol molecules with their hydrophobic ends towards the

centre and their hydrophilic ends facing the surface, which makes the chylomicrons water-soluble. A small number of **protein** molecules help to stabilize the surface and also to direct the **metabolism** of the particle.

Fatty acids containing fewer than 10–12 carbon atoms are not packaged in chylomicrons but pass from the mucosal cells directly into the portal **blood**, where they are transported as free (non-esterified) fatty acids (NEFA).

Chylomicrons are too large to pass through the basement membrane of the intestinal capillaries and cannot be absorbed through the intestinal blood system. Rather, they travel through the intestinal lymphatics to the thoracic duct which empties into the vena cava; in this way chylomicrons reach the blood vascular system.

Lipid absorption is greatest in the jejunum, but appreciable amounts may also be absorbed in the ileum. (SB)
See also: Gastrointestinal tract

Lipid metabolism
Consists of various metabolic processes involving or closely related to **fatty acid**s. These processes can be divided mainly into anabolic processes that create biologically important molecules such as triglycerides, **phospholipid**s, **hormone**s and **ketone** bodies; and catabolic processes that generate **energy**. They involve the **digestion**, transportation, storage and **oxidation** of dietary lipids, as well as the *de novo* synthesis and utilization of lipids.

During digestion, lipids enter the **small intestine** as lipid

droplets, which are emulsified by **bile** acids and pancreatic secretions. Triacylglycerides are hydrolysed by pancreatic lipase to fatty acids and monoglycerides and associate with bile acids to form micelles. Fatty acids with fewer than 10–12 carbon atoms pass directly from the epithelial cells into the portal **blood**, where they are transported as free (unesterified) fatty acids, whereas fatty acids with more than 10–12 carbon atoms are re-esterified to triacylglycerides. They are then coated with a layer of **protein**, **cholesterol** and phospholipid to form **chylomicron**s. These leave the cell by **pinocytosis**, enter the lymphatics and are transported by the lymphatic system to the systemic blood circulation through the thoracic lymph duct.

The water-insoluble **triacylglycerol**s from **intestinal absorption** are transported in plasma in bulk as chylomicrons and from the liver as very low-density **lipoprotein**s (VLDLs), the fatty acids of triacylglycerol being released by lipoprotein **lipase** activity of specific tissues. Removal of triacylglycerol from lipoproteins results in a dynamic remodelling in plasma of lipoprotein particles of differing **lipid** and protein content, brought about by exchange of phospholipid, cholesterol, cholesteryl esters and specific apoproteins of different particles.

De novo synthesis of fatty acids is limited to certain tissues. These differ between species: liver and **adipose tissue** are the major sites in rodents and pigs, liver in humans and avian species, adipose tissue in ruminants and the **mammary gland** in all mammals. Pigs, rodents and humans utilize **glucose** as the main carbon source for **fatty acid synthesis**, whereas ruminants rely

mainly on **acetate** from rumen **fermentation** for **lipogenesis** due to low dietary glucose availability. The process of fatty acid synthesis from acetyl-CoA and NADPH is mediated by the action of **fatty acid synthase**s. This process takes place in the cytoplasm of the cell. Most of the acetyl-CoA that is converted into fatty acids is derived from **carbohydrates** via the glycolytic pathway.

Fatty acids (mainly in the form of triacylglycerides) constitute the main storage form of energy in the animal body. In comparison with carbohydrates and protein, fatty acids yield the most ATP on an energy per gram basis when they are completely oxidized to CO_2 and water by β-oxidation and the TCA cycle.

Fuel supply and **energy balance** of the animal are maintained by deposition of lipid, especially in adipose tissue during energy surplus, and by mobilization in deficit; the frequency of such cycles may be hours, days or months, depending upon nutrient supply and energy demands. Mobilization of stored fatty acids is mediated by **hormone**-sensitive lipase; fatty acids are transported to tissues by association with serum **albumin**. Though **muscle** and other tissues may utilize mobilized fatty acids directly, the bulk is taken up by the liver in a concentration-dependent manner. In the liver, fatty acids are oxidized to **ketone** bodies (**acetone**, acetoacetate and β-OH **butyrate**), which are exported for energy by extrahepatic tissues. Excessively rapid mobilization and oxidation of fatty acids may lead to **ketosis**, a condition in which the supply of strongly acidic ketone bodies exceeds the capacity of tissues to oxidize them. In such conditions ketone bodies are excreted by the kidneys, accompanied by equimolar quantities of base, causing the

animal to become acidotic.

Gluconeogenesis supplies the needs for plasma glucose between meals. Gluconeogenic **substrates** include **glycerol**, **lactate**, **propionate** and certain **amino acid**s. PEP carboxykinase catalyses the rate-limiting reaction in gluconeogenesis. Glucose cannot be synthesized from fatty acids, since they are converted by β-oxidation to acetyl CoA, which subsequently enters the TCA cycle and is oxidized to CO_2. An exception is the three-carbon fatty acid, propionate, which is carboxylated, converted to succinyl-CoA and enters the TCA cycle as a four-carbon intermediate, not as acetyl CoA. Gluconeogenesis occurs mainly in the liver and kidney cortex and to a lesser extent in the **small intestine**, stimulated by **glucagon**, **growth hormone**, **epinephrine** and cortisol. Gluconeogenesis is extremely important to neonatal pigs and neonatal and adult ruminants, because it provides about 70–90% of their total glucose needs.

Though quantitatively the major role of lipid **metabolism** is to match energy supply to demand, many lipid components are essential to the healthy function of the body. These include cholesterol metabolism to form bile acids and hormones and to aid in lipid transport, **essential fatty acid**s for membrane function and as precursors of the **prostaglandin**s that provide many regulatory functions, and **sphingolipid**s as essential components of cell membranes and nerve tissue. (RB)

Further reading

Nafikov, R.A. and Beitz, D.C. (2007) Carbohydrate and lipid metabolism in farm animals. *Journal of Nutrition* 137, 702–705. doi:

10.1093/jn/137.3.702

Lipid peroxidation

Generally a chain reaction that leads to the degradation of **unsaturated fatty acid**s with the formation of multiple oxidized products. There are three phases: (i) initiation, whereby an electron is abstracted from a reactive carbon of the fatty acid molecule, usually by a **metal** ion (such as **copper**) or by a hydroperoxide product of the chain reaction, to form a **free radical**; (ii) propagation, whereby the free radical combines with **oxygen** to form a peroxy free radical, which in turn may abstract **hydrogen** from another unsaturated molecule to yield a **peroxide** and a new free radical, thus initiating the chain reaction, which may be repeated several thousand times; and (iii) termination, which occurs by free radicals reacting with themselves to yield inactive products, or by introduction of a chain-breaking **antioxidant** (e.g. **vitamin E**). The methylene groups adjacent to double bonds are most susceptible to abstraction of electrons, thus the methylene-interrupted diene system of **polyunsaturated fatty acid**s is most reactive and susceptible to **oxidation**. (DLP)

Lipids in animal diets

Lipids are organic molecules, generally with limited **solubility** in water but highly soluble in organic solvents. In animals, lipids comprise non-esterified **fatty acid**s, neutral lipids, polar lipids and **cholesterol**.

Fatty acids

Fatty acids are the primary components of neutral and polar lipids

and, like cholesterol, are synthesized from the two-carbon building block, acetyl-**coenzyme** A (AcCoA). **Glucose** is the primary dietary precursor of AcCoA in non-ruminants, and the conversion of glucose into AcCoA involves production of **pyruvate** by **glycolysis**, conversion of pyruvate carbon to citrate in mitochondria by the initial steps of the **tricarboxylic acid** cycle, and generation of AcCoA in the cytoplasm via ATP-citrate lyase. AcCoA is converted into fatty acids in the cytoplasm by the sequential actions of AcCoA **carboxylase** and the **fatty acid synthase** complex, which produces **palmitic acid** (16 carbons with no double bonds; 16:0). In most mammalian tissues, the proportion of palmitic acid is relatively constant (25–30% of total fatty acids), because palmitic acid is effectively elongated to **stearic acid** (18 carbons, no double bonds; 18:0) by fatty acid elongase and desaturated to **oleic acid** (18 carbons, one *cis*-double bond; 18:1 n-9) by the Δ9 desaturase, stearoyl-CoA desaturase. The fatty acid elongases and stearoyl-CoA desaturase are located in the endoplasmic **reticulum** (ER); hence, the complete conversion of glucose carbon into oleic acid requires **enzyme** systems in the cytoplasm, mitochondria and ER. **Fatty acid synthesis** can occur in the liver (humans, poultry, rodents and many fish) and/or **adipose tissue** (pigs, ruminants and rodents), whereas virtually all vertebrate tissues have some capacity for fatty acid elongation and desaturation (with the notable exception of erythrocytes).

Although animals can produce **saturated fatty acid**s (e.g. palmitic and stearic acid) and monounsaturated fatty acids (e.g. oleic acid), **linoleic acid** and α-linolenic acid cannot be produced

by animal tissues. Thus, linoleic acid and α-linolenic acid must be supplied in the diet (i.e. they are nutritionally **essential fatty acid**s). Linoleic acid contains 18 carbons with two *cis*-double bonds (18:2*cis*-9, *cis*-12; or 18:2 n-6), and α-linolenic acid contains 18 carbons with three *cis*-double bonds (18:3*cis*-9, *cis*-12, *cis*-15; or 18:3 n-3). Linoleic acid subsequently is converted to **arachidonic acid** (20:4 *cis*-5, *cis*-8, *cis*-11, *cis*-14; or 20:4 n-6) by the sequential actions of Δ6 desaturase, fatty acid elongase, and Δ5 desaturase, and α-linolenic acid is converted to **eicosapentaenoic acid** (20:5 *cis*-5, *cis*-8, *cis*-11, *cis*-14, *cis*-17; or 20:5 n-3) by the same series of reactions. It is apparent that, in animal tissues, n-6 fatty acids remain n-6 fatty acids however much they are elongated and desaturated, and n-3 fatty acids remain n-3 fatty acids. These very long-chain, **highly unsaturated fatty acid**s are important precursors of **prostaglandin**s (via cyclooxygenase and peroxidase) and **leukotriene**s (via lipoxygenases). Prostaglandins are involved in steroidogenesis, gastric secretion, inflammation, **blood** clotting and other essential biological processes; leukotrienes are pro-inflammatory mediators.

Another important very long-chain, highly unsaturated fatty acid is **docosahexaenoic acid** (22:6 *cis*-4, *cis*-7, *cis*-10, *cis*-13, *cis*-16, *cis*-19; or 22:6 n-3). Eicosapentaenoic acid and docosahexaenoic acid can be converted to the recently described resolvins, and docosahexaenoic acid can be converted to resolvins and protectins. Resolvins and protectins reduce cellular inflammation by inhibiting production and transportation of inflammatory cells and **cytokines** to sites of inflammation.

Neutral lipids

Neutral lipids include monoacylglycerols (MAGs), diacylglycerols (DAGs) and **triacylglycerol**s (TAGs), which have in common the three-carbon backbone, **glycerol**, to which is attached one (MAG), two (DAG), or three (TAG) fatty acids in **ester** linkage. TAGs are the most abundant neutral lipids in animal tissues (> 90% of total neutral lipids), followed by DAGs and then MAGs. Neutral lipids are concentrated in lipid vacuoles of **adipocyte**s, liver and type I **muscle** fibres. Neutral lipids are heterogeneous, and each TAG contains a mixture of saturated, monounsaturated, and **polyunsaturated fatty acid**s. The position of the fatty acids in a neutral lipid is indicated by the stereospecific number (sn), and sn-1,2, sn-1,3 and sn-2,3-DAGs can exist. However, sn-2,3-DAGs are the most abundant DAGs, produced by partial **hydrolysis** (**lipolysis**) of TAGs. Similarly, sn-2-MAGs are the most abundant MAGs, produced during TAG **digestion** in the **small intestine**, or by **hormone**-sensitive **lipase** in animal tissues. Complete hydrolysis of TAGs yields glycerol and three fatty acids, but this only occurs during long-term fasting or **starvation**, or perhaps long-term, aerobic exercise such as marathon running.

Polar lipids

In animal tissues, polar lipids consist primarily of **phospholipid**s and **sphingolipid**s. Phospholipids are similar in structure to neutral lipids in that they contain a glycerol backbone; hence, phospholipids, TAGs, DAGs and MAGs all fall under the classification of **glycerolipid**s. Phospholipids are distinct from neutral lipids in that they contain a phosphate group at the sn-3

carbon in a phosphoester linkage, and the phosphate group typically is linked to another highly charged moiety such as choline. **Phosphatidylcholine** is the most abundant phospholipid (hence, most abundant polar lipid) in animal cells. In membranes, phospholipids provide a barrier to water-soluble molecules and, as such, encapsulate cells and subcellular organelles. They provide the surface for **lipoprotein**s such as high-density and low-density lipoproteins, allowing the transport of TAGs, cholesterol and cholesterol esters in the aqueous environment of the circulatory system.

Less abundant are the sphingolipids, which contain a sphingosine base backbone rather than glycerol. Sphingosine is synthesized in animal tissues from **serine** and a long-chain, saturated fatty acid, saturated palmitic acid. A major class of sphingolipids is the ceramides, which contain an **amide**-linked fatty acid that can be a saturated or monounsaturated fatty acid (e.g. **oleic acid**), 16–26 carbons in length. In mammals, the most abundant sphingolipids are the sphingomyelins (ceramide phosphocholines), which are enriched in neuronal membranes.

Cholesterol

Cholesterol is the precursor for **bile** salts, **vitamin D** and steroid hormones such as estradiol and **aldosterone**. The liver is the primary site of cholesterol synthesis, which is elegantly regulated. Eighteen AcCoA molecules undergo a series of condensations, **phosphorylation**s and **decarboxylation**s to form the 30-carbon lanosterol, which subsequently loses three methyl groups to yield cholesterol. The activity of 3-hydroxy-3-methylglutaryl-CoA

(HMG-CoA) reductase, the rate-limiting enzyme in the cholesterol biosynthetic pathway, is depressed by phosphorylation via AMP-dependent protein kinase, and expression of the HMG-CoA reductase gene is depressed by high levels of intracellular free cholesterol. The concentration of free cholesterol is reduced by the action of acyl-CoA:cholesterol acyltransferase (ACAT), which attaches a fatty acid to the hydroxyl group of cholesterol in an ester linkage. The preferred fatty acid for the ACAT reaction is oleic acid, formed by stearoyl-CoA desaturase (described above). Cholesterol esters are among the most hydrophobic lipid molecules in animal tissues. (SBS)

Lipogenesis
The metabolic process whereby non-**lipid** substances (**carbohydrates** and some **amino acid**s) are converted to **fatty acid**s. Acetyl CoA is a key intermediate. (DLP)

Lipolysis
The process whereby glycerides are hydrolysed and released as **fatty acid**s and **glycerol** by the action of a **lipase** enzyme. Most commonly this involves **triacylglycerol** as the **substrate**. **Phospholipase**s hydrolyse the constituents of **phospholipid**s at specific bonds, yielding products differing according to the specificity of the phospholipase. (DLP)

Lipopolysaccharide
A complex component of the cell wall of Gram-negative bacteria. Lipopolysaccharides contain a lower proportion of **lipid** than do

glycolipids. The toxic lipid moiety (lipid A) contains a high proportion of 3-OH **myristic acid**; other **fatty acids** of 10–22 carbons may be present, as well as glucosamine, ethanolamine and phosphate. A **polysaccharide** core links lipid A to the O-polysaccharide moiety which designates specificity. Various structural models have been presented. (DLP)

Lipoprotein lipase
A lipolytic **enzyme** secreted from capillary endothelial cells. It hydrolyses the **triacylglycerol** of triacylglycerol-rich **lipoprotein**s (**chylomicron**s, VLDLs) in serum, thus releasing **fatty acid**s to be taken up by tissues. It requires specific activating peptides found in circulating lipoproteins. The lipoprotein lipase of **milk** is identical to that of serum. Regulation of the expression of the enzyme differs among tissues. (DLP)

LipoproteinsProtein–lipid complexes that solubilize neutral lipids so that they can be transported in an aqueous medium, such as the **blood**. **Particle size** (75 to > 1000 Å) and molecular weight (0.2–100 × 10^6 daltons) are inversely related to density. Larger, less dense particles contain > 80% **triacylglycerol** and only 1–2% protein, whereas the smallest and most dense particles are > 50% protein with most of the lipid being **cholesterol** and phospholipid. Large particles have a central core predominantly of triacylglycerol and some cholesteryl ester, surrounded by a thin film of **phospholipid**, free cholesterol and protein. Major classes of lipoproteins are commonly classified according to hydrated density (triglyceride content decreasing as density increases) and

electrophoretic mobility into: (i) **chylomicron**s (density < 0.94 g ml^{-1}, produced by the **small intestine** to transport dietary lipid); (ii) very low-density lipoproteins (VLDLs) (density 0.94 to < 1.006 g ml^{-1}, produced by the liver, and to a lesser extent the small intestine); (iii) low-density lipoproteins (LDLs) (density 1.006–1.063 g ml^{-1}, created by the **metabolism** of VLDLs); and (iv) high-density lipoproteins (HDLs) (density 1.063–1.20 g ml^{-1}). These classes may be further subdivided on the basis of lipid or protein content. The protein components are called apoproteins and are responsible for signalling the **metabolism**, transport and cellular uptake of lipoproteins. (DLP; JAM)

Liquid diets

Liquid feeding systems allow higher **feed intake**s and, as a consequence, pigs fed liquid diets have faster **growth** rates. Fermented liquid feed given to weaned piglets has the potential to reduce disease in the **gastrointestinal tract** and improve the performance of weaners. Calves are fed various liquids after their initial colostrum, including whole **milk**, surplus colostrum, waste or discarded milk and milk replacer, some of which are specifically formulated for *ad libitum* intake. **Sugarcane** juice and **by-product**s such as **molasses** and condensed solubles from **fermentation** (*see* Yeast) can be fed to ruminants. Such products can be part of a multi-component diet and they can be processed to increase **palatability** or to provide an appropriate feed to utilize **urea**. The addition of **oil** can increase the **energy** concentration; **protein**, **vitamins** and **minerals** may also be added. Liquid feed

has a low replacement rate and cows fed on **whey** will consume approximately two-thirds of their normal water intake as whey. The use of liquid feed requires some form of storage and feeding equipment, which can, depending on cost, be prohibitive to the economical use of liquid feeds. (JKM)

Lithium (Li)

A highly alkaline **metal** with an atomic mass of 6.941, present in the earth's crust at about 20 mg kg^{-1}. The natural lithium content of feed ingredients is probably very low. One study found < 3 μg kg^{-1} in whole ground **maize**. Although there is no known dietary requirement for any farm animal, there is evidence that low concentrations of dietary lithium are essential for the support of maximal reproductive efficiency and **birth weight** in rats. Rats maintained on diets containing 0.6 μg lithium kg^{-1} for three generations had significantly lower **litter size** and weights than similar rats maintained on 500 μg dietary lithium kg^{-1}. (PGR)

Further reading

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Litter

Animal bedding. The central function of poultry litter is to provide bedding for birds (broilers and turkeys) so that they may grow well, remain comfortable and be free from blemishes when slaughtered. Litter may also act as an insulation material, reducing heat transfer through the floor of the poultry house. The litter must absorb by admixture all excreta and convert it to a drier and more

manageable material. The degradative processes in litter and the exchanges with the poultry house environment must maintain both a proper litter moisture level and good air quality. Bacteria and other **microorganisms** are essential components of litter but the qualities of the medium also necessitate consideration of the role of litter in pathogen maintenance and transmission and recycling of drugs and toxins.

Whilst the provision and management of litter appears to be a simple technology, the material is actually an important dynamic component of the poultry house environment. Thus, any analysis of litter problems, including 'wet litter', will reveal a multiplicity of causes, factors and complex interactions that may underlie the aetiology of the difficulty. Litter management involves choice of material (and availability), depth of litter to be used, supplementary additions and frequency, litter stirring and the use of chemical additives and of course litter removal, disposal and/or re-use. A global calculation based on 1998 figures suggested a world broiler **meat production** of 52 million tonnes, requiring approximately 25 million tonnes of litter and resulting in 100 million tonnes of used litter for disposal. Used litter, with or without composting, may be employed as a fuel or fertilizer or as the base for ruminant feedstuffs.

The choice of litter material must be based upon the ability to absorb water, decomposability, freedom from toxins and contaminants, availability and cost. In use, the litter should be dry and friable; there should be no caking or capping and the **ammonia** content should remain low. Materials frequently used

as litter include wood shavings, sawdust, **wheat straw**, **oat** straw, papyrus straw, peat moss, newsprint, cardboard, **rice** hulls, **groundnut** hulls, **maize** cobs and vermiculite.

An important feature of the litter material is moisture content. Many raw materials have an initial moisture content of 10–15% and in use this falls by between 25–50%. Litter moistures of 40% are considered satisfactory but caking will occur at 45% and severe wet litter problems will occur at 50% or greater. Perhaps the most important chemical transformation taking place in active litter is the conversion of uric acid to ammonia via **allantoin** and **urea** by bacterial degradation. This process can be accelerated in high-moisture conditions and this will have serious consequences for the poultry house environment. Wet litter is a major problem occurring under production conditions around the world; thus, understanding the water relations of litter and the factors precipitating wet litter is essential. Water added to the litter from any source is either retained in the litter or evaporated into the air and ultimately is removed by ventilation. For any litter material and set of conditions it is necessary to define the equilibrium moisture content – equilibrium relative humidity relations between the litter and the air in the poultry house. These relationships facilitate the prediction of litter moisture and therefore litter quality from a knowledge of relative humidity and **temperature** and can form the basis of calculations of ventilation rates required to control litter condition.

Wet litter is usually identified by caking or sealing of the surface. This condition will influence **growth** rate, **carcass** quality

and disease status. There is a wide range of possible causes, several of which may contribute to the problem in any situation and all of which must be considered when seeking a solution. They include: external climatic conditions (e.g. high temperature associated with high humidity); inadequate ventilation; condensation (poor insulation); disturbances in bird water intake or water balance; diseases producing **diarrhoea**; dietary effects; **water quality** and composition; the use of some anti-coccidial drugs; inappropriate use of evaporative cooling and fogging; and poorly maintained and leaky drinkers and pipes. In most modern commercial poultry (broiler) facilities, production is operated close to the limiting conditions and an interaction of two or more of these variables can precipitate a very rapid deterioration in litter conditions. To optimize litter quality, it is necessary to pay close attention to these factors and in particular to understand litter–water relations and the principles of ventilation control. (MMit)
See also: Poultry droppings

Litter size
The number of piglets born during a single farrowing. Litter size may be influenced by the nutrition of the sow at critical stages. '**Flushing**' (providing a high feed level, 3–4 kg per day of a high-quality diet) in the 10–14 days prior to service can increase ovulation rate in gilts. A similar result can be obtained in young sows by preventing excessive loss of **body condition** in **lactation** and achieving a high **feed intake** between **weaning** and service. After service, reduction of feed level is also important, because giving excessive feed to gilts and young sows at this time can impair

implantation and reduce embryo survival. Once the implantation period has passed and pregnancy has progressed beyond 3 weeks, nutrition has little further effect on litter size. After farrowing, the litter size that a sow is nursing will exert a major influence on her nutritional requirements during lactation, since milk output increases with the number of piglets that are **suckling**. (SAE)

Litter weight

The total weight of piglets nursing a single sow. The litter weight at birth may be influenced by nutrition during gestation, when an increased level of **feed intake** can increase piglet **birth weight**. Increased **feed allowance** in the last third of pregnancy is especially beneficial if the sow is in poor **body condition**, since low-birth-weight piglets are at much greater risk of neonatal mortality. However, giving extra feed to the sow in order to increase birth weight is a relatively inefficient process; it requires about 100 kg of extra sow food during pregnancy to give an increase of 0.1 kg in average piglet birth weight. The litter weight in the first 3 weeks of **lactation** is determined by the **milk** yield of the sow, which in turn depends on her body condition at the start of lactation and her ability to consume the large amount of feed necessary to meet the demands of milk production. Litter growth rate increases by about 9 g for each additional **megajoule** of **digestible energy** consumed by the sow. After 3 weeks of age, the suckling piglets will eat increasing amounts of solid feed, and provision of an appropriate **creep feed** will increase litter weight. (SAE)

Live fish food

Many **fish larva**e at the time of initial exogenous feeding have a short, rudimentary digestive tract and lack a functional stomach (gastric glands). Generally, formulated diets do not meet the nutritional requirements of these larvae and thus may lead to poor growth and survival. Live food organisms are required during the first feeding stages. Live foods are more attractive than inert formulated feeds to first-feeding fish larvae, which are visual predators. These live food organisms also contain high amounts of digestible nutrients (e.g. free amino acids) and enzymes, which allow for autolysis (self-digestion of the live food).

Rotifers

(*Brachionus plicatilis*) and brine **shrimp** (*Artemia* spp.) are the most commonly mass-cultured **zooplankton** for use as live food for fish larvae as well as for the early juvenile and larval stages of crustaceans (shrimp). Most species of **marine fish** larvae are initially reared on a diet of rotifers followed by the larger brine shrimp, after which formulated feeds are introduced. The development of a functional stomach (around metamorphosis) determines when **weaning** will take place.

The best live food is the natural prey of the larvae but copepods, the natural prey of marine fish larvae, are not suitable for intensive culture because of their longer growth period and culture at low density levels. The harpacticoid copepods such as *Tigriopus* and *Tisbe* spp. are better suited for mass culture than calanoid copepods (e.g. *Acartia* spp.). Since these benthic organisms do not swim in the water column, larvae cannot easily locate them. The

use of captured wild zooplankton (i.e. copepods) is limited because of variations in both quality and quantity. Other live foods include freshwater cladocerans (*Moina* and *Daphnia* spp.), bivalve larvae (trochophores) and various **protozoa**n species.

Fish larvae are sensitive to dietary deficiencies of n-3 **polyunsaturated fatty acid**s (PUFAs). **Eicosapentaenoic acid** (20:5 n-3) and in particular **docosahexaenoic acid** (22:6 n-3) are essential for proper functioning of the cell membranes in the rapidly developing neural and optical systems of the larvae. **Arachidonic acid**, the major precursor of **eicosanoid**s, is also thought to be essential for fish larvae. Copepods contain high amounts of these **essential fatty acid**s (EFAs), whereas rotifers and brine shrimp must be enriched in these EFAs before being fed to fish larvae. Commercial EFA **enrichment**s commonly consist of either **marine oils** containing an **emulsifier** (**lecithin**) or concentrated spray-dried algal products. Live food organisms are fed these enrichments in aerated water baths for a short period of time (< 24 h) before being fed to the fish larvae.

Cultured **phytoplankton** or micro-**algae** (e.g. *Isochrysis* and *Nannochloropsis* spp.) are often used directly as a food source for **shellfish** and the early larval stages of some fish and crustacean species. Phytoplanktons are also fed to live food organisms to feed larval fish, with the species selected depending upon their nutrient composition. Phytoplankton in larval fish tanks also provide essential nutrients to live food organisms, scatter incoming **light** (possibly enhancing visualization of live food prey) and supply enzymes, feeding stimulants and unidentified compounds with

properties of immunostimulants to larvae. (DN)
See also: Aquatic organisms

Liver diseases
Disease of the liver can be caused either by direct damage to the cells of the liver or by damage to the **bile** secretory system (e.g. blockage of the bile duct). The liver can be affected by primary infectious disease, caused by viruses or bacteria, parasitic disease caused by liver fluke, the larval stage of tapeworms, ascariasis in pigs, toxic damage from pathogens (e.g. **aflatoxin**s, clostridial toxins), toxic products of **metabolism** or poisonous plants, such as ragwort. Signs of liver disease include weight loss and **inappetence** but are generally non-specific and a laboratory diagnosis may be required. Damage to the liver may include fatty change, inflammation (hepatitis), neoplasia, necrosis or atrophy. Some liver diseases have a nutritional aetiology. Fatty liver disease (hepatic lipidosis) is seen in overfat animals. If these animals are subjected to high energy demands, inefficient **fat** utilization leads to a build-up in **ketone**s. Liver abscesses are more common in cattle fed high-**carbohydrate**, low-**roughage** diets. Hepatosis dietetica in fast-growing pigs is associated with **vitamin E** and **selenium** deficiency. Hepatic necrosis can be caused by **aflatoxin**s, particularly in pigs and ducklings. (EM)

Liver function
The liver is a multifunctional organ that is responsible for regulating: (i) the **metabolism** of **carbohydrates**, **lipids** and proteins; (ii) the production of important plasma proteins,

including **albumin** and **fibrinogen**; (iii) the synthesis and release of **bile** acids; (iv) the storage of certain **vitamins** and **iron**; (v) the **detoxification** and excretion of many drugs and toxins; (vi) the production of **hormone**s, including **growth hormone**; and (vii) the degradation of certain hormones.

The liver is a major storage site for **glycogen** which, when broken down by glycogenolysis, releases **glucose** into the **blood**. It is also the primary site of **gluconeogenesis**, which converts certain **amino acid**s, **propionate** and **glycerol** into **glucose**. These processes are tightly controlled by the hormone**, glucagon**. In regulating **lipid metabolism**, the liver is the primary site of remnant **chylomicron** absorption from the circulation and the synthesis of **very low-density lipoprotein**s (VLDLs). Liver hepatocytes are the principal source of **cholesterol** in the body, where it is used to produce **bile** acids. Bile secretion into the **small intestine** is the major route of **cholesterol** excretion from the body and plays a pivotal role in controlling serum cholesterol levels. (GG)

Liver meal

Produced from condemned livers, which are dried at a low temperature and then ground. Liver meal can be included in small amounts in poultry and pig feeds as a source of **B-complex vitamins** and **vitamin A**, but it is also a source of high-quality **protein** and reduces the need for inorganic mineral **supplement**s in the **diet**. The use in animal foods of animal **by-product**s, including liver, is banned in the EU. **Fish** liver oils are rich sources of vitamins A and D and of **essential fatty acid**s and

are used in animal feeds. The dry matter (DM) content of liver meal in Uganda is 921 g kg^{-1} and the **nutrient** composition (g kg^{-1} DM) is **crude protein** 732, **crude fibre** 0, **ash** 104, **ether extract** 94, NFE 70, **calcium** 0.2 and **phosphorus** 0.7 (FAO, 2002). (JKM)

Reference

FAO (2002) Feed resources information service. Available at http://www.fao.org/ag/AGA/AGAP/FRG/AFRIS/Data/318.htm

Liveweight

The weight of the live animal at a particular time. This includes the weight of gut contents, which varies with diet and feeding pattern. Liveweight is therefore distinct from empty body weight (total weight minus gut contents) and deadweight or **carcass** weight, which refer to the weight of the eviscerated animal, often with other parts such as feet or head also removed. (MFF)

Llama meat:

see South American camelids meat, effects of nutrition

Lobster

A name applied to various species of large decapod crustacea in the class Malacostraca, characterized by: a large carapace enclosing the thorax; five pairs of thoracic walking legs, the first of which is frequently specialized as **claws**; a highly muscularized abdomen designed for strong ventral flexion of the tail fan; and movable stalked eyes. There are four families of lobsters: clawed lobsters (Nephropidae, including the European, American and Norwegian

lobsters); spiny lobsters (Palinuridae); slipper lobsters (Scyllaridae); and coral lobsters (Synaxidae). (RHP)



A Maine lobster. Photo courtesy of John Stracke. Licensed under CC BY-SA 2.0.

Lobster culture:
see Crustacean feeding; Shellfish culture

Locust bean
Properly the fruit of the African locust bean tree (*Parkia filicoidea*) but the name is frequently applied to the fruit of the **carob** tree (*Ceratonia siliqua*). The latter originated in the eastern Mediterranean region and is also found in the subtropics. The fruit are thick, fleshy (more so in the carob) pods, each containing about a dozen seeds. The seeds are tough and must be crushed before feeding. The resulting meal has a high **sugar** and **energy** content and is very palatable but is low in **protein** (42–54 g kg^{-1}). (JKM)

Long-chain fatty acids
The **fatty acid**s containing 14–20 carbon atoms, as distinct from short-chain (4–8 C), medium-chain (10–12 C) and very long-chain (> 20 C) fatty acids. They may contain other functional groups (e.g.

double bond, hydroxyl or methyl branch). (DLP)

Long-chain triacylglycerols
The high-molecular-weight fraction of **fat**. **Triacylglycerol**s contain three **fatty acid**s, with a total carbon number > 50. The term most commonly refers to a fraction of **milk** fat. (DLP)

Lordosis
A common degenerative condition of the **connective tissue**s forming the spinal column in which the affected animal develops a hollow-backed or sway-backed appearance. It can be caused by deficiencies of **micronutrient**s, including **vitamin D** and **tryptophan**. Deficiency of **copper** can cause 'swayback' in sheep. (DS)

Lucerne (*Medicago sativa* L.)
Also known as alfalfa, lucerne is a perennial herb with deep roots, trifoliate leaves and purple flowers, requiring sunshine and high **temperatures**. It can be grown alone or mixed with **grasses** or other **legumes**. Drier leaves are friable and leaf loss is high during haymaking. In lucerne-growing areas, green **forage** is used to feed high-producing animals as it is highly palatable and contains sufficient **protein**, **calcium** and **vitamins** not to require concentrate **supplement**s. As with many forage legumes, the **nutritive value** declines with age and lucerne should be harvested before the flowers mature. Stage of **maturity** has the most influence on nutritive value of irrigated lucerne at first cutting. A rotational system is recommended for **grazing** animals.

Hay can be harvested to separate leaf from stem. Stems can then be used as **roughage** and the dried leaves included in concentrate mixtures. There is a danger of young lucerne causing **bloat** in grazing ruminants if they consume too much; this can be avoided by using wilted material – cutting in the morning and feeding in the afternoon – or allowing grass grazing before access to the legume. **Dried lucerne** leaf has a high **vitamin A** content and 2–5% can be included in layer rations to ensure a good yolk colour. Lucerne can be used as pasture for pigs, and lucerne meal can be included in concentrate mixtures. (LR)



Lucerne. (a) A leafy shoot; (b) an inflorescence.

Nutrient composition of lucerne (% dry matter).

	DM (%)	CP	CF	Ash	EE	NFE	Ca	P
Fresh: pre-bloom	17.0	25.3	23.5	11.8	2.9	36.5	2.41	0.35
early bloom	22.7	22.9	26.0	11.5	3.5	36.1	2.56	0.31

mid-bloom	29.0	19.0	30.0	10.3	3.4	37.3	1.76	0.24
Fresh: 1 year old	20.3	17.1	19.4	12.6	2.7	48.2		
2 years old	21.4	16.5	21.3	11.5	2.8	47.9		
3 years old	21.4	16.2	22.3	10.8	2.7	48.0		

CF, crude fibre; CP, crude protein; DM, dry matter; EE, ether extract; NFE, nitrogen-free extract.

Digestibility (%) and ME content of lucerne.

	CP	CF	EE	NFE	ME (MJ kg^{-1})
Ruminant					

Fresh: pre-bloom	89.0	45.0	50.0	76.0	10.35
early bloom	79.0	49.0	38.0	78.0	9.89
mid-bloom	69.0	45.0	50.0	61.0	8.42
Fresh: 1 year old	85.9	68.4	59.6	80.7	11.10
2 years old	87.4	79.5	55.6	76.7	11.23
3 years old	88.1	70.8	33.9	80.5	11.15
Leaf meal	79.4	59.9		77.7	9.51

Lupin (*Lupinus* spp.)

Lupins are becoming increasingly important as an alternative feed ingredient to **soybean** meal, especially in Australia, which is also an exporter of this product. Benefits of this crop are that the plant is an N-fixing **legume** and, like **peas**, can be grown and utilized on-farm with minimal processing. Another advantage of lupins is that the seed stores well. A recurring shortage of protein feedstuffs in Europe has stimulated interest in lupins as an alternative **protein source** there. Lupins are also being grown as **forage crop**s and **silage** for **ruminant feeding**.



Lupins, a legume providing a valuable protein feed for livestock. Photo courtesy of Liz West. Licensed under CC BY 2.0.

The development of low-**alkaloid** (sweet) cultivars in Germany in the 1920s allowed the seed to be used as animal feed. Prior to that the crop was unsuitable for animal feeding because of a high content of toxic alkaloids in the seed. In Australia, where much of the research on lupins as a feedstuff has been done, the main species of lupins used in livestock and poultry diets are *Lupinus angustifolius* and *L. luteus*. *Lupinus luteus* (yellow lupin) is also regarded as having significant potential as a feedstuff. One of the remarkable features of the breeding of improved genotypes of lupins for livestock and **poultry feeding** is that it has been achieved without the use of genetic engineering, making the crop of particular interest to organic farmers.

Nutritional composition

Table 1 shows a comparison of the main lupin seed varieties used in poultry and livestock feeding, and a more detailed nutritional

composition of sweet white lupin seed meal for poultry is shown in Table 2 (Blair, 2018). Lupin seed is lower in protein and **energy** contents than soybean meal or soybeans, and more similar to peas in energy content. The hull amounts to about 25%, therefore dehulling the seed increases the **crude protein (**CP**)** content and results in a feedstuff more comparable to soybean meal. The **amino acid** pattern is not well balanced, and pig and **poultry** diets containing significant quantities of lupin seed meal require **supplementation** with **methionine** and usually **lysine**.

Table 1. Nutrient and energy values of three lupin species (whole seed, air-dry basis) (from Petterson *et al.*, 1997)

	L. angustifolius	*L. albus*	*L. luteus*
Crude protein %	32	36	38
Crude fibre (%)	15.4	10.6	16.3
ADF (%)	19.7	14.6	24.9
NDF (%)	23.5	17.6	34.3
Calcium (%)	0.2	0.2	0.2
Phosphorus (%)	0.3	0.36	0.43
Alkaloid (%)	0.02	0.02	0.04
DE Pigs (MJ kg^{-1})	14.6	16.9	16.4

	L. angustifolius	*L. albus*	*L. luteus*
ME Cattle (MJ kg^{-1})	12	11.9	n/a
ME Sheep (MJ kg^{-1})	12.2	12.5	n/a
AME Poultry (MJ kg^{-1})	10.4	13.2	11.4

Table 2. Average nutritional composition of lupin seed meal (sweet white) for poultry, air-dry basis. North American feed regulations require that it must contain less than 0.3 g total alkaloids/kg. Also, the species of seed must be listed after the name (from Blair, 2018).

Component	Amount	Component	Amount
Dry matter (g kg^{-1})	890	**Trace minerals** (mg kg^{-1})	
ME (kcal kg^{-1})	2625	Copper	10.3
ME (MJ kg^{-1})	11	Iodine	NA
Crude fibre (g kg^{-1})	110	Iron	54.0

Neutral detergent fibre (g kg^{-1})	203	Manganese	23.8
Acid detergent fibre (g kg^{-1})	167	Selenium	0.08
Crude fat (g kg^{-1})	97.5	Zinc	47.5
Linoleic acid (g kg^{-1})	35.6	**Vitamins** (IU kg^{-1})	
Crude protein (g kg^{-1})	349	Beta-carotene (mg kg^{-1})	NA
Amino acids (g kg^{-1})		Vitamin A (IU kg^{-1})	NA
Arginine	33.8	Vitamin E (IU kg^{-1})	8.0
Glycine + serine	NA	**Vitamins** (mg kg^{-1})	
Histidine	7.7	Biotin	0.05
Isoleucine	14.0	Choline	NA
Leucine	24.3	Folacin	3.6
Lysine	15.4	Niacin	21.9
Methionine (Met)	2.7	Pantothenic acid	7.5
Met + cystine	7.8	Pyridoxine	3.6

Phenylalanine (Phe)	12.2	Riboflavin	2.2
Phe + tyrosine	25.7	Thiamin	6.4
Threonine	12.0	**Vitamins** (μg kg^{-1})	
Tryptophan	2.6	Cobalamin (vitamin B_{12})	0
Valine	10.5		
Major minerals (g kg^{-1})			
Calcium	3.4		
Phosphorus (total)	3.8		
Phosphorus (non-phytate)	1.6		
Chloride	0.3		
Magnesium	1.9		
Potassium	11.0		
Sodium	0.2		

The type of **carbohydrate** in lupins is different from that in most legumes, with negligible levels of **starch** and high levels of soluble and insoluble NSPs and **oligosaccharide**s (up to 500 g kg^{-1} seed). These compounds increase the **viscosity** of the

digesta, influencing **feed transit time** through the gut of pigs and poultry and the utilization of nutrients, as well as the microflora and morphology of the **gastrointestinal tract**. They also result in an increase in water intake, which can result in wet droppings in poultry and a reduction in the quality of the **litter**. One of the main ways of addressing the adverse effects of the NSPs and improving the utilization of lupin seed is to include a **supplement** of exogenous **enzymes** in the diets.

Antinutritional factors

Non-ruminant animals are known to be sensitive to alkaloids in lupins, but the average alkaloid content of cultivars of *L. angustifolius* and *L. albus* now used is generally low. The levels of **saponin**s in *L. albus* appear to be of less than 12 mg kg^{-1} and 55 mg kg^{-1} in *L. luteus*, suggesting that it is unlikely that saponins are responsible for reduced **feed intake**s of diets containing *L. albus*. The levels of **tannins** in *L. angustifolius* are considered to be low enough for this not to be a problem in poultry diets. Data on the tannin levels in *L. albus* and *L. luteus* appear to be more limited. Low-alkaloid lupins appear to contain zero or very low levels of **trypsin inhibitor**s and **haemagglutinins**.

Livestock, poultry and human diets

Results indicate that lupin seed meal can effectively replace soybean in ruminant feed (Abraham *et al*., 2019). Complete replacement can also be accomplished in diets for pigs and poultry, provided that the NSP content of the particular cultivar of lupin seed used is low, or the diet can be supplemented with an NSP-degrading enzyme. **Supplementation** with **lysine** and

methionine is also necessary, to optimize the AA balance in the diets and ensure efficient production.

According to Prusinki (2017), white lupin seeds are regarded as a valuable component of healthy diets for humans because of their content of protein, **fatty acid**s with a desirable ratio of omega-6 to omega-3 acids, fibre, **oligosaccharide**s, **antioxidant**s and NSPs, and they are being used in a range of food products as a replacement for other proteins. (RB)

See also: Antinutritional factors.

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Lupinosis
A mycotoxicosis caused by ingestion of toxins (phomopsin A and B) produced by the fungus *Diaporthe toxica* (anamorph *Phomopsis* spp.), which colonizes domestic **lupin** stubble in Australia. The phomopsins are hepatotoxic hexapeptides and the severity of the disease is dose related. Lupinosis affects livestock that graze 'sweet' (i.e. low-**alkaloid**) lupin stubble and limits the use of this animal **feed** in Australia. Phomopsis-resistant lupin cultivars are available but, in spite of their increasing use, lupinosis is still a major limitation to the full utilization for feed of the millions of hectares of sweet lupin stubble. Lupinosis is not to be confused with lupin **poisoning** caused by ingestion of 'bitter' (high-alkaloid) lupins, which contain the toxic quinolizidine and piperidine alkaloids. In the western USA after the early 1900s, there were extensive losses of sheep that were grazing lupin pastures; these rarely occur now but lupin-induced skeletal defects in cattle ('crooked calf disease') is still a major cause of economic loss to cattle producers. Certain quinolizidine (anagyrine) and piperidine (ammodendrine) alkaloids in these lupins are responsible for the skeletal defects and cleft palate in the calf when ingested by pregnant cows during days 40–100 of gestation. (KEP)

Lutein
A yellow **carotenoid** pigment ($C_{40}H_{56}O_2$, **xanthophyll**) widely spread in plants and found in animals in **body fat** and **egg** yolk. It is not a precursor of **vitamin A**. (NJB)

Luteinizing hormone (LH)
A glycoprotein hormone produced by the anterior pituitary. In females, LH stimulates the maturation of follicles, the final rupture of the follicle to release an **ovum**, the production of follicular **progesterone** and the development of the ruptured follicle into the corpus luteum. In males, LH stimulates the testes to produce testosterone. (JRS)

Lychnose
An **oligosaccharide**, 1-α-galactosylraffinose, molecular weight 666. Carbon 1 of the **fructose** of **raffinose** is linked to an α-D-galactopyranose residue. Found in roots of members of the *Carophyllacea*. (JAM)
See also: Carbohydrates

Lycopene
An aliphatic hydrocarbon **carotenoid** ($C_{40}H_{56}$) with 11 conjugated double bonds. Natural plant sources are predominantly all-*trans* but the *cis* **isomer**s predominate in many human tissues. Found predominantly in the chromoplast of plant tissues, especially **tomato**, but high also in fruit. Among the biological carotenoids, lycopene is the most efficient quencher of singlet **oxygen**. Clinical studies suggest that it is an anti-**carcinogen**. (DLP)
Further reading
Nguyen, M.L. and Schwartz, S.J. (1999). Lycopene: chemical and biological properties. *Food Technology* 53(2), 38–45.

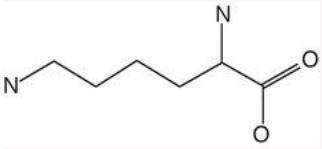
Lymphocytes:

see Immunity

Lysine

An essential **amino acid** ($H_2N^+ \cdot (CH_2)_4 \cdot CH \cdot NH_2 \cdot COOH$, molecular weight 146.2) found in protein. Lysine is generally the most limiting amino acid in the food supply of both animals and humans. It is produced commercially as L-lysine·HCl, L-lysine·SO_4, or L-lysine free base. Virtually all cereal **grain**s and their **by-product**s are first limiting in lysine, and most **oilseed** meals, with the exception of **soybean** meal, are deficient in lysine. In addition to its use in **protein synthesis**, lysine, as protein-bound **trimethyllysine**, is a precursor of **carnitine** in the body.

Both protein-bound lysine and free lysine can react with free carbonyl groups such as those existing on **reducing sugars** to form **Maillard reaction** products. Heat and humidity promote the Maillard reaction in stored feeds and feed ingredients. Also, under alkaline conditions and heat, lysine in feeds or feed ingredients can react with dehydroalanine (produced from **serine**) to form the cross-linked amino acid, lysinoalanine. Neither lysino**a**lanine nor Maillard-bound lysine have lysine bioactivity. (DHB)



Lysolecithin

Generally, a **phospholipid**, but specifically phosphatidyl **choline**, from which a fatty acyl chain has been removed by **hydrolysis** or

acyl transfer, e.g. 1-acyl or 2-acyl lysolecithin. So named for its ability to lyse erythrocytes. (DLP)

Lysozyme
A protein, also called muramidase, present in **milk**, tears, **saliva**, **body fluid**s, leukocytes and other cells. It is an antibacterial **enzyme** acting on the peptoglycans found in bacterial cell walls. (EM)

M

MacronutrientsNutrients required in the largest amounts. The six major classes of nutrients are **carbohydrates**, **lipids**, **proteins**, water, **vitamins** and **minerals**. Those that make up the greatest fraction of foods are carbohydrates, lipids and proteins and are called the macronutrients. (NJB)

Magnesium (Mg)
An alkaline **metal** with an atomic mass of 24.305. It is an essential dietary component for all farm animals. Its metabolic function centres on reactions involving **phosphorylation** and energy transfer with ADP and ATP. About 60% of body Mg is found in

bone, where it forms **salts** of phosphate and carbonate, but its exact function there is not known. Magnesium is also involved in the dampening of nerve impulses and **muscle** contraction and is antagonistic to **calcium**, which is stimulatory. In Mg deficiency, if the plasma concentration drops to low levels, muscle spasms, or **tetany**, may result. Acute Mg deficiency (**hypomagnesaemia**) often occurs in cattle during **lactation** when there is a shift in Mg distribution in the body brought on by the consumption of forages low in Mg and the need for Mg for **milk** production.

In most non-ruminant animals, Mg is absorbed primarily from the upper **small intestine**; ruminants can absorb Mg from the ruminoreticulum and **omasum**. Body balance of Mg is controlled by excretion in both the **urine** and lower intestine. Plasma Mg concentration (about 20 mg l^{-1}) is sensitive to the amount of Mg consumed. Most common forages and seeds contain variable amounts of Mg, and although Mg deficiency is not common in grazing animals, **feedlot** animals sometimes require Mg **supplementation**. The US National Research Council recommends 1000 mg Mg kg^{-1} diet for growing beef cattle, 1200 mg kg^{-1} during gestation and 2000 mg kg^{-1} in early lactation. For dairy cattle the requirements are 1600, 2000 and 2500 mg Mg kg^{-1} diet for similar stages. The Mg requirement for pigs is approximately 400 mg kg^{-1} diet and for poultry it is 400–600 mg kg^{-1} diet. For horses it ranges from 800 mg kg^{-1} diet for growth to 1300 mg kg^{-1} for adults engaging in moderate to intense work. For sheep, it is between 1200 and 1800 mg kg^{-1} diet. (PGR)

See also: Bone density; Bone formation; Phosphorus

Magnetic resonance imaging (MRI)
The use of **nuclear magnetic resonance** (NMR) to produce images of the internal structures of the body. Nuclear magnetic resonance occurs because certain atomic nuclei (especially **hydrogen**) have a dipolar magnetic moment and align with an externally applied magnetic field. Image production is based on the **absorption** and emission of **energy** in the radio frequency range of the electromagnetic spectrum. Each scan produces an image of a single plane through the body so, for a complete description of **body composition**, images at multiple planes are needed. (MMacL)

Mahua (*Madhuca longifolia*)
A large evergreen or semi-evergreen tree native to southern Asia, cultivated for its edible oil-containing fleshy seeds. The fruit seeds contain 169 g **crude protein** kg^{-1} and 515 g **oil** kg^{-1}, comprising 46% **oleic acid**, 18% **linoleic acid**, 18% **palmitic acid** and 14% **stearic acid**. The meal is obtained after extraction of oil. It is high in **saponin**s (98 g kg^{-1}), which are toxic at this concentration. These levels are reduced by treatment with isopropanol, following which the **flour** has an **organic matter digestibility** *in vitro* of 810 g kg^{-1}. (JKM)



Mahua tree (*Madhuca longifolia* var Latifolia). Photo courtesy of J.M. Gard. Licensed under CC BY 3.0.

Nutrient composition of mahua products (g kg^{-1} dry matter).

	Dry matter	**Crude protein**	**Crude fibre**	**Ash**	**Ether extract**	**NFE**
Oilcake						
Extracted	–	160	310	57.0	109	643
Extracted and detoxified	922	290	126	105	77.0	492
Defatted mahua seed flour	940	294	–	–	–	–

	Dry matter	Crude protein	Crude fibre	Ash	Ether extract	NFE
Fresh leaves	–	91	190	76	39	604
Fresh flowers	–	50	16	42	18	874

NFE, nitrogen-free extract.

Maillard reaction

A **browning** reaction that occurs when proteins are heated in the presence of **reducing sugars**. This involves condensation of an **amino acid** with the carbonyl group of a **hexose** sugar in the open chain form to give a Schiff base. Subsequent Amadori rearrangement forms an N-substituted 1-amino-1-deoxy-2-ketose (ADK). This compound enolizes to either a 1,2-eneaminol or a 2,3-enediol. The former is degraded to 5-hydroxymethyl furfural (HMF), the latter to a methyl α-dicarbonyl intermediate that in turn rearranges into maltol, methyl reductones and α-dicarbonyls such as 2-oxopropanal, acetol, diacetyl and hydroxydiacetyl. A third pathway known as the Strecker degradation can arise in which a dicarbonyl compound reacts with an amino acid to yield CO_2, an **aldehyde** with one less carbon than the amino acid and pyrazine heterocyclic ring compounds. Heating **molasses** with **ammonia** or **urea** or the treatment of **straw** with ammonia can similarly form imidazoles, which cause neurological disease in

cattle known as 'bovine bonkers'.

Of the large number of compounds formed by Maillard reactions, some are reductones having an enediol conjugated with a carbonyl group. This structure is the same as that in L-**ascorbic acid** and such compounds are strong reducing agents in acid solution. Brown-coloured polymeric melanoidins are formed from reactions between carbonyls and **amine**s. These have variable structure and **solubility** and have strong UV absorbance and fluorescence, due to unsaturated **nitrogen** heterocyclic rings. Some Maillard products, such as maltol, are volatile and impart a caramelized flavour. The free amino group of **lysine** in proteins is particularly likely to be involved in Maillard reactions, often leading to loss of **availability** of this essential amino acid. As this amino acid is often the most limiting amino acid in animal diets, damage to lysine by overheating high-protein foods, especially in the presence of **sugars**, can impair their nutritional value. (IM)

Maintenance

The state in which an animal is in **energy** equilibrium, neither productive nor losing weight. It is then said to be on a maintenance ration. The terms half-maintenance, 2 × maintenance, etc., are sometimes used to describe feeding levels. Although growing animals are also considered to have a maintenance requirement, its definition and measurement are more problematic. (JAMcL)
See also: Energy balance

Maize (*Zea mays*)

Also called **corn** or Indian corn, probably the most important

cereal plant of the **Gramineae** (**grass**) family. Maize may have yellow, white or red **grain**s. It is a tall, annual grass having stout, erect and solid stems with large narrow leaves spaced alternately on opposite sides of the stem. The main stem axis is terminated by a 'tassel' which bears the staminate (male) flowers. The pistillate inflorescence, which matures to form the ear, is a spike with a thickened axis, bearing paired spikelets in longitudinal rows, each row of paired spikelets normally producing two rows of grain. The spike is enclosed by modified leaves, called husks.



Maize grain is used for both livestock and human food, and as a raw material for several industries. Photo courtesy of Johan Neven. Licensed under CC BY 2.0.

Based on kernel texture, maize may be classified commercially as dent, flint or **flour**. For dent types, the kernel is composed of a mixture of hard and soft starches, while flint types contain little soft **starch**. For flour types, the kernels are composed largely of soft starch, which is easily processed by grinding. Sweetcorn is unlike other types since the plant **sugars** are not converted to starch. Popcorn is an extreme form of flint that is characterized by

small, hard kernels devoid of soft starch. During heating, popcorn kernels explode due to the expansion of the moisture within the cells.

Maize grain (see table) is used for both livestock and human food and as a raw material in the manufacture of starch and **glucose**. Although the overall **digestibility** of the nutrients is high, the protein content, as **crude protein** (CP), of the grains (90–140 g kg^{-1} dry matter (DM)) is lower than that found in **barley** and **wheat** grains. Maize kernels contain two main proteins: **zein** is the most important and is found in the **endosperm**; maize glutelin occurs in the endosperm, but at lower levels than zein, and also in the germ. Zein protein is deficient in the two essential **amino acid**s, **lysine** and **tryptophan**, and this fact contributes to the overall poor quality of maize protein. Higher levels of these two essential amino acids are found in maize glutelin. One recent objective of plant breeders has been to produce new varieties with better amino acid profiles (e.g. improved lysine content).

Chemical composition of maize grain and maize by-products (as g kg^{-1} DM unless stated).

Maize product	DM (g kg^{-1})	CP	EE	Starch	NDF	GE[a]	ME[a]	DE[a]	AME[a]
Maize grain	873	102	39	700	117	18.9	13.8	16.5	15.9

Maize germ meal	879	108	82	532	224	19.7	14.5	–	14.3
Maize gluten meal	904	669	29	155	84	23.7	17.5	–	17.9
Maize gluten feed	885	220	44	186	383	19.1	12.9	–	9.2
Maize fibre	378	147	31	181	538	19.9	13.4	–	–

Distillers' dark grains (maize)	889	317	110	24	342	22.4	14.7	–	–
Maize silage	251	101	29	206	480	20.2	10.5	–	–

[a] As MJ kg^{-1} DM. Source: MAFF (1990) UK Tables of Nutritive Value and Chemical Composition of Feedingstuffs. AME, apparent metabolizable energy; CP, crude protein; DE, digestible energy; DM, dry matter; EE, ether extract; GE, gross energy; ME metabolizable energy; NDF, neutral-detergent fibre.

The '**gluten**' proteins in maize are of poorer quality than those in wheat. Maize flour is therefore not used in bread making but is widely used throughout Latin America in the preparation of food products such as tortillas. Maize is rich in starch (range 661–755 g kg^{-1} DM) and is more slowly degraded in the **rumen** than the starch from other cereal grains. Maize grain contains low levels of fibre (as NDF, 91–176 g kg^{-1} DM) and the oil content varies from 22 to 51 g kg^{-1} DM and comprises mainly oleic and linoleic **fatty**

acids (23% and 57% of total fatty acids, respectively). Maize grains generally have the highest **energy value** of all cereals, owing to the high oil and low fibre levels.

In addition to the use of whole maize grain for livestock feeding, the grains may also be ensiled at an average DM content of ~700 g kg^{-1}. Finely ground grains can be ensiled either alone (ground maize **silage**) or following processing of the whole ear (including husks) (ground ear maize). Maize grains, like other cereal grains, may also be processed prior to feeding using 'cold' processing methods (including grinding, rolling, cracking or crimping, and cold **pelleting**) or 'hot' processing methods (including steam-**flaking**, micronization, roasting and hot pelleting).

Maize grains are an excellent feed resource for ruminants and are commonly used in **compound feed**s and **total mixed ration**s. 'Hot' processed maize grains, containing gelatinized starch, may be used for feeding high-yielding dairy cows requiring high amounts of concentrates. In certain countries maize is an important cereal fed with **oats** to horses. Feeding maize to poultry is important in countries where the grain is commonly grown and the use of yellow varieties promotes a yellow pigmentation in the **egg** yolk and tissue **fat**. Maize may also be grown as a **forage crop** and fed fresh (maize forage) or following preservation by ensiling at a grain DM content of about 350 g kg^{-1} (maize silage).

The processing of maize grains in the manufacture of starch and glucose results in the production of three main **by-product**s: maize germ, maize **bran** and maize gluten, for use in livestock feeding (see table). Maize germ is separated from the kernel by

coarsely grinding cleaned maize grains that have been soaked in a dilute acid solution. The germ is very rich in **oil**, which is mostly extracted for use in the human food industry prior to producing maize germ meal. Maize bran is separated by wet screening of the finely ground degermed grain. The remaining solution comprises a suspension of starch and protein (gluten), which are separated by centrifugation.

Maize gluten meal, also known as prairie meal, is a high-protein feed (about 669 g CP kg^{-1} DM), produced by drying the protein (gluten) fraction to a DM content of about 900 g kg^{-1}. It is suitable for feeding most livestock species; for ruminants the protein fraction is largely undegraded in the rumen but overall the protein is deficient in lysine. Feeding maize gluten meal to laying birds increases egg **yolk pigment**ation. Processing the degermed kernel also gives white fibres, which are mixed with corn steep liquor, and sometimes variable amounts of maize germ meal, to produce maize gluten feed. The **protein quality** of maize gluten feed generally limits its use to ruminant rather than pig and poultry diets. For mature beef and dairy cattle it may be included to about 40% of a concentrate ration. The composition and **nutritive value** of maize gluten feed is variable, owing to differences in the proportion used in the mixing process and the amount of germ meal added.

Grain distilleries using maize (for description of distillation process and by-products, *see* Barley) also produce a number of by-products for use in livestock feeding, including maize distillers' dark grains, which may be fed either as a meal or following pelleting. These products are very palatable to livestock and are

widely used in proprietary compound feed manufacture or for feeding as a coarse mixture of feed ingredients. (ED)

Further reading

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Malabsorption:

see Digestive disorders

Malate

Malate or malic acid ($HOOC{\cdot}CH_2{\cdot}CHOH{\cdot}COOH$) is one of the intermediates in the conversion of **citric acid** to oxaloacetic acid in the **tricarboxylic acid cycle**. (NJB)

Malic acid:

see Malate

Malnutrition

Deficiencies, excesses, or imbalances in the dietary intakes of energy and/or nutrients (amino acids, carbohydrates, fatty acids, vitamins, minerals and water). Malnutrition is classified as either **undernutrition** (underfeeding) or overnutrition (**overfeeding**). Malnutrition can occur in farm, zoo and companion animals, as

well as humans, depending on the availability of food and other environmental factors (such as disease, ambient temperature and air quality). In 2018, about 60% of cats and 56% of dogs in the USA were overweight or obese.



Obese dog in the USA. Photo courtesy of Mr TGT. Licensed under CC BY-ND 2.0.

According to the World Health Organization, more than 1 billion people worldwide were obese in 2016: 650 million adults, 340 million adolescents and 39 million children, numbers that had nearly tripled since 1975. (GW)

Malt:
see Brewery by-products; Distillers' residues

Maltase
An **enzyme** found in the **brush border** membranes of epithelial cells in the **duodenum** and **jejunum**. Also known as **glucoamylase**, it breaks down malto-**oligosaccharide**s (repeating α(1→4) **glucose** units) into single glucose units. (GG)

Malting
The process in which cereal **grain**, predominantly **barley**, is soaked and germinated under controlled conditions to activate the natural **amylase** of the grain. This in turn hydrolyses the **starch**, producing mainly the **disaccharide** sugar, **maltose**, with some dextrins and other **sugars**. **Germination** is allowed to proceed for several days, during which there is some development of the radicle (root). The process is then terminated by kiln drying and removal of the rootlets (malt culms). Typically, **hydrolysis** of the starch is only partial but it continues to completion when the malt is re-wetted (mashing). (CRL)

Maltodextrin
Mixture of **glucose**, **maltose** and higher **oligosaccharide**s of glucose, usually not exceeding ten glucose units. It is commonly produced by controlled enzymatic **hydrolysis** of **starch**, as in partially hydrolysed **maize** syrups. Time, temperature and the type of α-**amylase** used in hydrolysis determine the mix of monomers to polymers. Molecular weight range 180–1800. (JAM)
See also: Carbohydrates; Isomaltose; Maltotriose

Maltose
A **disaccharide**, $C_{12}H_{22}O_{11}$, molecular weight 342, consisting of two D-**glucose** residues joined by glycosidic α(1→4) linkage. It is produced in the enzymatic **digestion** of starch, in which it is the repeating unit. (JAM)
See also: Carbohydrates; Maltodextrin; Starch

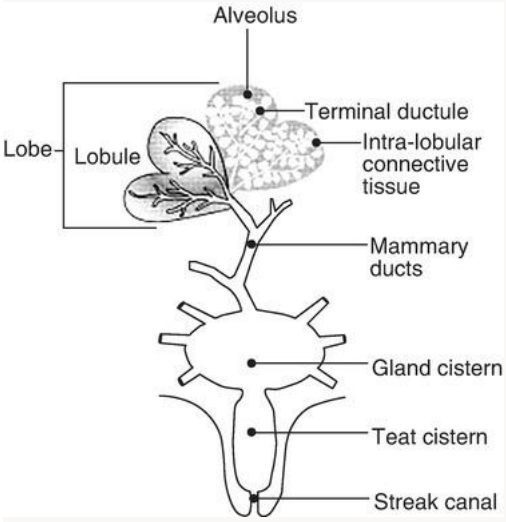
Maltotriose

An **oligosaccharide**, $C_{18}H_{32}O_{16}$, molecular weight 504, consisting of three D-**glucose** residues joined by α(1→4) linkages. (JAM)
See also: Carbohydrates; Starch

Mammary gland

The **milk**-producing gland of female mammals, derived from epithelial cells under the skin. Cows have four mammary glands; sheep, goats and horses have two; pigs have 10–14. A group of mammary glands is called an udder.

Each mammary gland consists of thousands of secretory (alveolar) cells, arranged like bunches of grapes, which drain into small ducts. The ducts lead to the gland cistern, where milk is stored until milking or **suckling**. Milk is expelled from the gland cistern through a teat. The tissue surrounding the alveolar cells is elastic and contracts during milking, under the influence of **oxytocin**. Alveolar cells are closely associated with **blood** vessels, from which nutrients are absorbed for milk synthesis.



Diagrammatic representation of mammary duct and lobular–alveolar system.

The udder is rudimentary in males and young females, but enlarges in females after **puberty**. During the first pregnancy, mammary cells differentiate and become most active after parturition. (PCG)
See also: Lactation

Mandarin fish (*Siniperca chuatsi*)
Freshwater fish belonging to the class Osteichthyes and the order Perciformes. It is a very ferocious species that is very hard to adapt to an artificial diet. It is mainly distributed in East Asian countries such as China, Vietnam and North Korea (Sun *et al*., 2017). It is popular among consumers owing to its flavour and the absence of intermuscular bones. Consequently, it has become an important high-quality freshwater cultured fish species in China, with a production of 336,000 t in 2018, which are mainly farmed by using **fish fingerling**s or trash fish (fish caught but too young or small to be consumed by humans) in China. (QS)

Reference

Sun, C., Niu, Y., Ye, X., Dong, J., Hu, W., Zeng, Q. and Lu, M. (2017) Construction of a high-density linkage map and mapping of sex determination and growth-related loci in the mandarin fish (*Siniperca chuatsi*). *BMC Genomics* 18, 446.

Manganese (Mn)
An essential **trace element** for animals, including humans. It is involved in the **metabolism** of **carbohydrates**, **amino acid**s, **protein** and **lipid** as a constituent or activator of several **enzymes**. Mn is also essential for the synthesis of chondroitin

sulphate, required for the organic matrix of bone. Manganese is found in many foods and feedstuffs, therefore a deficiency is less likely than that of other trace minerals.

According to the US NRC publications, the dietary requirement for Mn ranges from 10 to 40 mg kg^{-1} in **laboratory animal**s, 20 mg kg^{-1} in pigs, 28–30 mg kg^{-1} in chickens, 20 mg kg^{-1} in **beef cattle** and 40 mg kg^{-1} in **dairy cattle** (Milatovic and Gupta, 2018). The estimated adequate intake for adult humans is around 2 mg per day.

Mn deficiency has been reported in ruminants, pigs and poultry, resulting in retarded **growth**, skeletal abnormalities, **ataxia** of the newborn and reproductive failure. A deficiency in poultry results in **perosis**, bone shortening (chondrodystrophy) and retarded down formation in the embryos, bowing of the legs, reduced hatchability of eggs and poor **eggshell** quality. No cases of Mn deficiency appear to have been documented in humans.

Mn toxicity may occur in livestock and humans as a result of environmental **contamination**. In addition to reproductive and developmental effects, toxicity is primarily associated with neurological effects (Milatovic and Gupta, 2018). Treatment involves removal of contaminated feed and water, followed possibly by chelation therapy. (RB)

Reference

Milatovic, D. and Gupta, R.C. (2018) Manganese. Ch 3 in: *Veterinary Toxicology: Basic and Clinical Principles*, 3rd edn. Elsevier, Amsterdam, pp. 445–454.

Mango (*Mangifera indica* L)

A large evergreen tree cultivated throughout the tropics for its fruit, which has a large fibrous seed. Five mango products are potentially available for animal feeding: the fresh whole fruit, residue after juice extraction, mango kernel meal (after **oil** extraction), peelings and **forage**. The kernel constitutes about 15% of the weight of the fruit. The kernels contain **tannins**; increasing rates of inclusion in pig and poultry diets progressively reduce **growth** rate and feed conversion. Ruminants have been shown to tolerate up to 50% inclusion of kernels in concentrates without adverse effects on performance. Mango fruit is readily eaten by cattle and pigs, but the whole fruit has caused obstructive **bloat** and **rumen** impaction in cattle and buffalo. Fruit gluts can be conserved by ensiling with 1% **salt** and the **silage** can be fed to pigs. Mango fruit and fruit products have high water contents and very low protein and mineral contents (see table) (Heuzé *et al*., 2015, 2019).

Nutrient composition of mango

Constituent	Forage	Whole fruit	Kernel meal
Dry matter (g kg^{-1})	339	171	937
Protein (g kg^{-1} DM)	94	47	69
Crude fibre (g kg^{-1} DM)	268	146	29

Constituent	Forage	Whole fruit	Kernel meal
Calcium (g kg^{-1} DM)	16.9	2.3	2.1
Phosphorus (g kg^{-1} DM)	1.5	1.0	2.7



Mango tree with ripening fruit. Photo courtesy of Nutrilover. Licensed under CC BY 2.0.

Mango forage can be fed to ruminants but it is not very palatable, and it contains a phenolic substance, mangiferin (2,4,5.7-tetrahydroxy-3-glucosylxanthone), which poisons cattle if fed in excess for long periods (greater than 7 days). (EO; GMcLD)

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Mannans

Linear or branched homo- or heteropolysaccharides of α- or β-D-**mannose** residues. Present in the cell walls of most **yeasts**. Some cell surface or extracellular mannans are phosphorylated and appear to have immunological properties. Mannans in plant cell walls or **endosperm** virtually all contain some **galactose**. Many are **gums** and are viscous in aqueous solutions, e.g. **guar** gum. Water-soluble **galactomannan**s are found in the endosperm of many leguminous plants. Mannans, glucomannans and glucuronomannans are also the principal food-reserve **polysaccharide**s in **algae**. (JAM)

See also: Carbohydrates; Dietary fibre; Storage polysaccharides

Mannitol

A polyol or **sugar** alcohol, $C_6H_{14}O_6$, molecular weight 182, a reduction product of **mannose**. It occurs in **algae**, lichens and bacteria and in mountain ash berries. It is a normal constituent of **silage**, where it is formed by bacterial reduction of the **fructose** moiety of **sucrose**. (JAM)

See also: Carbohydrates; Mannose

Mannose

A **hexose monosaccharide**, $C_6H_{12}O_6$, molecular weight 180, an

epimer of **glucose** in which the bond at carbon 2, containing the hydroxyl group, is inverted. Mannose does not occur free in nature but is widely distributed in hemicellulosic **polysaccharide**s. (JAM)
See also: Carbohydrates; Dietary fibre; Hemicelluloses

Marasmus
In its report *The State of Food Security and Nutrition in the World 2020*, the United Nations Food and Agriculture Organization (FAO) in collaboration with other international agencies reported that almost 690 million people (8.9% of the global population) were undernourished in 2019, 60 million more than in 2014. Child mortality globally is estimated at around 9 million annually, a main cause being **malnutrition** (Forrester *et al*., 2012; WHO, 2022).

The World Health Organization (WHO, 2021) categorized **undernutrition** of humans into four types: wasting; stunting; underweight; and deficient in certain **vitamins** and **minerals**. Undernutrition makes children in particular much more vulnerable to disease and death. Low weight-for-height is known as wasting. It usually indicates recent and severe weight loss, because a person has not had enough food to eat and/or has an infectious disease, such as **diarrhoea**. A young child who is moderately or severely wasted has an increased risk of death, but treatment is possible. Low height-for-age is known as **stunting**. It is the result of chronic or recurrent undernutrition, usually associated with poor socioeconomic conditions, poor maternal health and nutrition, frequent illness, and/or inappropriate infant and young child feeding and care in early life. Stunting holds children back from

reaching their physical and cognitive potential. Children with low weight-for-age are known as underweight. A child who is underweight may be stunted, wasted, or both. Of those affected, 149 million children under 5 years of age were estimated to be stunted and 45 million were estimated to be wasted.

Micronutrient-related malnutrition is related to a deficient intake of vitamins and minerals that are essential for proper **growth** and development; these are mainly **iodine**, **vitamin A** and **iron**, which are the most important in global public health terms. Deficiency of these nutrients represents a major threat to the health and development of populations worldwide, particularly children and pregnant women in low-income countries. Most of those affected live in countries with high rates of food insecurity. Chronic undernutrition manifests primarily as protein-energy malnutrition (PEM), also known as protein-**calorie** malnutrition. Frequently children are affected. Traditionally two main conditions have been described: (i) kwashiorkor, characterized by signs of a severe **protein deficiency** associated with oedema and **ascites**; and (ii) marasmus, involving grossly inadequate intakes of energy (mainly) and protein leading to loss of muscle and subcutaneous fat. It is now clear that there is considerable overlap in the causation and effects of these two conditions. Kwashiorkor is less common than marasmus but is associated with a much higher mortality rate (Forrester *et al*., 2012). The term marasmus is derived from a Greek word meaning a wasting away, withering and decay. The term kwashiorkor is derived from an African word meaning 'first child – second child' because a first-born child often

develops kwashiorkor when the second child is born and replaces the first-born child at the mother's breast. Because children tend to develop kwashiorkor after they are weaned, they are usually older than those who have marasmus. Patients with kwashiorkor and marasmus differ in **body composition**. Children who die of kwashiorkor have significant tissue reserves of protein and fat, as these stores are mobilized inadequately during the disease process. On the other hand, children with marasmus are better able to sustain mobilization from protein and **lipid** stores. This difference in metabolic response to severe undernutrition probably explains the ability of marasmic patients to sustain **amino acid** and lipid supply for intermediary metabolism during the period of decreased dietary intake. In kwashiorkor, the greater suppression of protein breakdown creates shortages of essential and conditionally essential amino acids, and these insufficiencies impair **protein metabolism**, while the reduced availability of lipid impairs **energy metabolism**. Patients with kwashiorkor are thus likely to suffer metabolic disorganization even while retaining greater tissue stores than in marasmus. Following recovery, **protein turnover** is approximately 30% faster, and oxidative disposal of lipids is approximately 35% higher, in kwashiorkor survivors than in marasmus survivors.

With effective treatment, most adults recover fully from malnutrition. Affected children usually recover well following the provision of an adequate diet, but may never reach their full growth potential and may be shorter than their peers.

Kwashiorkor tends to be confined to certain areas of the world

where staple foods and foods used to wean infants are deficient in protein even though they provide enough calories as **carbohydrates**. In addition these foods are often bulky, rather indigestible foods not well suited for post-**weaning** diets.



Kwashiorkor is characterized in humans by oedema in the ventral region. It is common in children with a protein deficiency. Photo courtesy of C. Heitz. Licensed under CC BY 2.0.

Pham *et al*. (2021) provided additional findings on kwashiorkor and marasmus in a review of current evidence. Depletions of **antioxidant**s, vitamins and minerals are more severe in kwashiorkor than in marasmus. This is consistent with a severe and uncontrolled oxidative stress associated with the depletion of gut anaerobes; and the invasion and relative proliferation of gut microbes belonging to the aerotolerant Proteobacteria phylum and pathogens suggest a specific microbial process critical in the pathogenesis of kwashiorkor. These researchers postulated that liver mitochondrial and peroxisomal dysfunction could be

secondary to toxic microbial compounds produced in the gut, such as **ethanol**, **lipopolysaccharide**s and **endotoxin**s produced by Proteobacteria, particularly *Klebsiella pneumoniae*, and **aflatoxin** produced by *Aspergillus* species. The gut–liver axis alteration is characterized by oedema and a fatty and enlarged liver and is associated with a dramatic depletion of **methionine** and **glutathione**, an excessive level of free circulating iron and frequent lethal bacteraemia due to enteric pathogens. This is consistent with the fact that antibiotics improved survival only in children with kwashiorkor but not in those with marasmus. The specific pathogenic characteristics of kwashiorkor identified in this review suggest new approaches to developing more targeted and effective treatments for both marasmus and kwashiorkor. Urgent correction of plasma glutathione depletion, together with a supply of specific essential amino acids, particularly methionine and **cysteine**, early detection of pathogens and an antibiotic more efficient than amoxicillin in supressing gut Proteobacteria (including *K. pneumoniae*), and **probiotic**s to restore the human gut anaerobic mature microbiota were suggested as being potentially beneficial in saving many more children with kwashiorkor.

In 2016, the United Nations (UN) General Assembly proclaimed 2016–2025 to be the United Nations Decade of Action on Nutrition. This period was regarded as an unprecedented opportunity for addressing all forms of malnutrition. It set out a concrete timeline for implementation of the commitments made at the Second International Conference on Nutrition (ICN2) to meet a set of

global nutrition targets and diet-related NCD targets by 2025, as well as relevant targets in the Agenda for Sustainable Development by 2030, in particular Sustainable Development Goal (SDG) 2 (end **hunger**, achieve food security and improved nutrition and promote sustainable agriculture) and SDG 3 (ensure healthy lives and promote wellbeing for all at all ages).

Led by WHO and the Food and Agriculture Organization of the United Nations (FAO), the UN Decade of Action on Nutrition called for policy action across six key areas:

i. creating sustainable, resilient food systems for healthy diets;
i. providing social protection and nutrition-related education for all;
i. aligning health systems to nutrition needs, and providing universal coverage of essential nutrition interventions;
v. ensuring that trade and investment policies improve nutrition;
v. building safe and supportive environments for nutrition at all ages; and
i. strengthening and promoting nutrition governance and accountability, everywhere.

Unfortunately there is no clear evidence that these aims will be achievable within the stated timeframe in all regions affected by food insecurity, given the current rate of progress. For instance, according to the Africa Regional Overview of Food Security and Nutrition (OCHA, 2021), Africa is not on track to meet the Sustainable Development Goal (SDG) 2 targets to end hunger and ensure access by all people to safe, nutritious and sufficient food all

year round, and to end all forms of malnutrition. The most recent estimates show that 281.6 million people on the continent (over one-fifth of the population) faced hunger in 2020, 46.3 million more than in 2019. This deterioration continues a trend that started in 2014, after a prolonged period of improving food security. In addition to hunger, millions of Africans suffer from widespread micronutrient deficiencies. The overview concluded that progress towards achieving the global nutrition targets in Africa by 2030 remains unacceptably slow. (RB)

See also: Kwashiorkor under 'History of nutritional sciences'

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Mare

An adult fertile female horse or pony: as a foal's mother she is described as its dam. A female ass or donkey is a jenny. The mare may be non-breeding, pregnant, lactating, or lactating and pregnant.

Under natural conditions the mare is a seasonal breeder, influenced particularly by **light**. The **gestation period** normally lasts 335–345 days but **lactation** length depends on management and under more intense farming it is restricted to 6 months or less. Most of the fetal **growth** occurs during the last 90 days of gestation but the mare's **energy requirement** increases during that period by only 10–20% above **maintenance**. An average lactation requires approximately eight times as much **energy** above maintenance as is required above maintenance by a normal pregnancy at term. However, the daily **milk** yield of a healthy mare

may be altered by varying her daily **feed intake** during late pregnancy, or lactation, and by the extent of her **fat** stores at parturition.

During the first 8 months of her gestation period the mare has a **digestible energy** (DE) maintenance requirement (zero body weight change plus normal activity of the non-working horse) similar to that of the non-breeding animal. This requirement is directly proportional to body weight and for mares ranging in size from 125 kg to more than 600 kg the requirement accords to the relationships given under '**Horse feeding**' (equations 1 and 2). During the 9th, 10th and 11th month of pregnancy the DE requirement rises by 1.11 DE, 1.13 DE and 1.20 DE, respectively. The minimum **nutrient requirement**s of the mare are given in 'Horse feeding' (Tables 1, 2 and 3). (DLF)

Marine environment

The marine environment comprises the complex physical, chemical and biotic factors (temperature, salinity, living things, etc.) of the sea that act upon an organism or group of organisms and determine their function, form and survival. The surface of the earth is approximately 361 million km^2 and interconnected bodies of **sea water** cover about 71% of this area. Wave action, tides and vertical and horizontal ocean currents produce a continuous mixing of sea water and maintain relatively little fluctuation in the concentration of dissolved gases and **salt**. **Oxygen** is usually available and the salinity of the open ocean is relatively constant, ranging from 33 to 37 parts per 1000 ($g\ kg^{-1}$), depending on the

latitude. **Light** and **temperature** vary greatly, mainly due to depth. In turbid coastal waters, the yellow-green wavelengths commonly penetrate furthest, dwindling to 1% at about 16 m. Sunlight not only illuminates but also warms the water it penetrates. A thermocline describes the rapid transition between a warm surface layer and the cooler, denser water beneath. In unproductive areas such as tropical or temperate regions in summer, these layers are stabilized and the surface layers become depleted of **nutrients**, reducing primary productivity. In shallow temperate waters, mixing of the water layers in the autumn and better growing conditions in the spring cause seasonal increases (e.g. algal blooms) in productivity. (DN)
See also: Freezing

Marine fish
There are obvious differences between **fish** and terrestrial farm animals as subjects for production in captivity. Fish are cold blooded and so significant amounts of dietary **energy** are not used in maintaining body **temperature**; life in water means that fish do not need the large anti-gravity **muscles** that are characteristic of birds and mammals (nor do they need the heavy skeleton on which these muscles hang). **Ammonia**, the main excretory product of **protein metabolism**, can be excreted directly into the surrounding water, so energy does not have to be expended in converting it to non-toxic compounds. On the other hand, respiration in water necessitates having permeable surfaces in contact with the aqueous environment. Thus, marine fish risk **dehydration** from a hyperosmotic medium while **freshwater**

fish face hydration from a hypotonic environment. In both cases energy has to be expended in controlling the osmotic problem. The balance of these differences indicates that fish convert food energy to **carcass** energy more efficiently than do mammals or birds.

Several species of wholly marine fish are either being cultivated, or are soon to be cultivated, on a commercial scale. These include **yellowtail** (*Seriola quinqueradiata*), **Asian sea bass** (*Lates calcarifer*), **European sea bass** (*Dicentrarchus labrax*), **gilthead sea bream** (*Sparus aurata*), **red drum** (*Sciaenops ocellatus*), **cod** (*Gadus morhua*) and several **flatfish**, such as Atlantic **halibut** (*Hippoglossus hippoglossus*). They are mainly warm- or temperate-water fish, only the marine flatfish being genuine cold-water fish. Most fish are carnivorous but this is especially so in the **marine environment**, where they lie at the head of a food pyramid, consume a high-protein diet and rely on diet to provide all nutrients in their most active form. Thus, the capacity to modify certain nutrients to more metabolically active forms is absent. For example, the capacity to transform **linolenic acid** to eicosapentaenoic or **docosahexaenoic acid** with full **essential fatty acid** activity has been lost.



Marine fish farming in the Saronic Gulf in Greece. Photo courtesy of Artur Rydzewski. Licensed under CC BY 2.0.

Marine fish are not domesticated in the sense that **rainbow trout** (*Oncorhynchus mykiss*) is domesticated; consequently, hard dry pellets are rarely acceptable as food. For yellowtail, a **casein**-based diet with 40% moisture and containing **taste attractants** (inosinic acid, **alanine** and **prolactin**) has been found to be suitable (Shimeno, 1991). The use of casein-based defined diets has been less successful with other marine species in attempting to quantify **nutrient requirement**s. Precise requirements for these species, therefore, remain to be established.

There is also a dearth of information on the **digestibility** of the major dietary components – **protein**, **carbohydrate** and **fat**. The absence of such data for different feedstuffs makes for difficulties

in assessing both the available energy density of experimental diets that have been used and the **energy requirement** of the fish. Making reasonable assumptions it can, however, be inferred that the energy density of food given to marine fish is in the range 17–23 MJ kg^{-1}. Dietary protein levels are high, usually of the order of 50% of the dry matter (DM) and sometimes in excess of this value. These levels appear to provide 25–30 g protein MJ^{-1} '**digestible energy**'. At these concentrations, much of the protein would be used as an **energy source**; there may also be a substantial **heat increment of feeding** but the magnitude of this in fish remains controversial. Essential **amino acid** requirements of marine fish are qualitatively similar to those of rainbow trout. Few, if any, attempts have been made to quantitate essential amino acid requirements. At the levels of dietary protein in use, amino acid deficiencies are unlikely to arise if a good quality fish meal is the main source of dietary protein. **Carbohydrates** are not well utilized by marine fish; they have limited amylolytic activity in the digestive tract and a limited capacity to metabolize **glucose** that is absorbed. **Dextrin** or pre-gelatinized **starch** are better utilized than is raw starch; even so, dietary concentrations of the former materials rarely exceed 20% of the dry matter.

As indicated above, marine fish have little capacity to modify 18C dietary **fatty acid**s metabolically. Their natural diet contains a luxus of polyunsaturated **long-chain fatty acid**s of the (n-3) series and sufficient of the (n-6) series to meet their dietary needs. **Essential fatty acid** requirements of marine fish are therefore met by using a **marine oil** (e.g. **cod liver oil**, pollock liver oil,

menhaden fish oil) in the diet. These oils are highly digestible. **Lipid** is the main non-protein energy source and levels in the diet are usually in the range 10–15%. The very high-energy (lipid) diets used in salmonid rearing have not found favour in the cultivation of wholly marine fish.

The **vitamin** requirements of yellowtail have been studied in detail (Shimeno, 1991) but few data are available for other species of marine fish. It is generally assumed that these species have a requirement for vitamins similar to that of salmonids and a vitamin pre-mix based on that used in salmonid diets is included as a component of diets for marine fish. No requirement for *p*-amino **benzoic acid**, **menadione** or **cholecalciferol** was found in yellowtail (Shimeno, 1991). Requirements for other vitamins were not greatly dissimilar from those of salmonids; specific **vitamin deficiency diseases** were described. It may be noted here that L-ascorbyl-2-monophosphate, a water-stable form of **vitamin C** but which is fully available to the fish, is especially useful in studies where diets of high moisture content are necessary.

Investigation of the **mineral** requirements of marine fish is complicated because some minerals are obtained from the **sea water** they drink to counter the osmotic problem arising from life in sea water (excess **salt** is excreted through the gills). Studies indicate the absence of a dietary requirement for **sodium**, **potassium** and **chloride** and a definite requirement (as yet unquantified) for **phosphorus**, **iron** and **zinc**, but there is no certain information on **calcium**, **magnesium** and **trace element** needs.

A special need in marine fish cultivation is live food for the rearing of larvae. Marine **fish larvae** are very small, generally less than 3 mm, and, despite numerous efforts with artificial foods (such as diets in microparticulate, microencapsulated and microbound form), it has not been possible to rear them without live food. **Rotifers** are an important live food and, in Japan, mass production of *Brachionus plicatus* makes fish larvae production possible. Newly hatched larvae (body length 2–3 mm) are given rotifers as the starting diet and this is continued for about 30 days. Thereafter other live food, in particular brine **shrimp** (*Artemia salina*), is substituted, as rotifers tend to become too small for larvae of 7 mm or so in length. Larvae larger than 10–11 mm may be fed on minced waste fish or, more usually, an artificial diet.

Problems were encountered initially over the nutritional quality of the rotifers; these were related to the food organisms used in the rotifer culture. When grown on a marine ***Chlorella***, rotifers of high nutritional value resulted; but if other organisms such as baker's **yeast** or a freshwater *Chlorella* were used, the *Brachionus* produced were of variable and often inadequate nutritional quality for marine fish larvae. The problem was resolved with the realization that marine fish larvae require long-chain **polyunsaturated fatty acid**s of the (n-3) series, i.e. 20:5(n-3) and 22:6(n-3), for normal development. The **fatty acid** profile of the *Brachionus* reflected that of the organisms on which it was grown and while marine *Chlorella* contained high levels of the required polyunsaturated fatty acids the other organisms that were tried did not. Similar problems occur with the brine shrimp.

Freshly hatched *Artemia* nauplii contain very low levels of (n-3) **highly unsaturated fatty acid**s and various **enrichment** methods are now available to enhance their content of these nutrients. These methods include feeding the nauplii on liposomes or microencapsulated diets, all with an appropriate fatty acid profile, or a fatty acid emulsion. (CBC; QS)

See also: Cod; Halibut; Rainbow trout; Salmon culture; Salmonid fishes

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Marine fouling

The attachment of marine micro- and macro-organisms to netting, lines and floats. Common fouling organisms include **seaweeds**, mussels, tunicates and sponges. Problems of fouling include increased drag in currents, reduced water flow through nets, increased net weight, and provision of a reservoir for wastes and pathogens. Remedial and preventive measures include treatment with anti-foulants (**copper** or **zinc** compounds), high-pressure spray, drying and biological controls (e.g. use of crabs as predators). (RHP)

Marine oils

Marine oils are made up of at least 65 **fatty acid**s but, by ignoring minor **saturated fatty acid**s and pooling the different **isomer**s of monounsaturated fatty acids, this can be reduced to about 50

and about 90% of the mass of fatty acids can be described simply in terms of about 12. These can be grouped as follows:

Saturated	**Monounsaturated**
14:0	16:1
16:0	18:1
18:0	20:1
	22:1
Polyunsaturated	**Long-chain poly-unsaturated**
18:2 n-6	
18:3 n-3	20:5 n-3
18:4 n-3	22:6 n-3

Fatty acid composition of fish and whale oil. (Unpublished data reproduced by courtesy of W. Schokker and H. Boerma, Unilever Research, Vlaardingen.)

Fatty acid	**Herring, North Sea**	**Anchovy, Peru**	**Whale, Antarctic**	**Pilchard, South Africa**	**Sardine, Portugal**	**Menhaden, USA**	**Pilchard**
12:0	0.10	0.10	0.20	0.20	0.10	0.15	0.10
14:0	6.10	7.45	7.45	7.75	6.70	7.30	7.30

Fatty acid	Herring, North Sea	Anchovy, Peru	Whale, Antarctic	Pilchard, South Africa	Sardine, Portugal	Menhaden, USA	Pilchard
14:1	0.15	–	0.75	0.15	–	–	–
16:branched	0.40	0.40	0.40	0.40	0.50	0.45	0.55
15:0	0.40	0.60	0.65	0.40	0.75	0.65	0.60
16:0	10.8	17.5	13.4	15.7	17.8	19.0	15.6
16:1	7.30	9.00	10.50	8.50	6.00	9.05	9.00
16:2 ω7	0.20	0.20	0.20	0.55	0.40	0.50	0.40
16:2 ω4	0.40	1.00	0.65	1.45	0.65	1.25	1.55
16:3 ω4	6.70	2.05	0.10	2.00	0.40	1.45	1.70
16:3 ω3	–	–	0.20	–	0.20	0.20	0.15
16:4 ω4	0.10	–	–	–	0.10	0.15	0.20
16:4 ω1	1.20	2.45	0.95	3.20	1.60	2.30	2.60

Fatty acid	Herring, North Sea	Anchovy, Peru	Whale, Antarctic	Pilchard, South Africa	Sardine, Portugal	Menhaden, USA	Pilchard
17:branched	0.30	0.35	0.25	0.25	0.20	0.20	0.15
17:0	0.35	0.55	0.95	0.80	0.80	0.90	0.85
17:1	0.30	–	0.25	–	0.30	–	–
18:branched	0.80	0.70	1.10	0.60	0.60	0.45	1.00
18:0	1.40	4.00	2.70	3.65	3.60	4.20	3.45
18:1	10.3	11.6	27.6	9.25	13.0	13.2	10.4
18:2 ω9	Tr.	0.10	0.10	0.15	0.15	0.30	0.20
18:2 ω6	0.95	1.20	1.90	0.80	1.20	1.30	1.30
18:2 ω4	0.10	0.60	0.20	0.50	0.30	0.40	0.50
18:3 ω6	0.05	0.30	0.20	0.35	0.20	0.25	0.30
18:3	Tr.	0.20	0.10	0.30	0.10	0.30	0.20
18:3 ω3	2.00	0.75	0.85	0.45	1.00	1.30	0.65

Fatty acid	Herring, North Sea	Anchovy, Peru	Whale, Antarctic	Pilchard, South Africa	Sardine, Portugal	Menhaden, USA	Pilchard
18:4 ω3	3.15	3.05	1.05	2.05	3.15	2.75	2.65
18:4	0.15	0.20	0.20	0.15	0.10	0.15	0.20
19:branched	–	0.10	–	–	0.20	0.20	–
19:0	0.20	0.10	0.60	0.20	0.40	0.40	0.10
19:1	0.10	–	0.40	–	–	–	–
20:0	0.10	0.30	0.20	0.60	0.40	0.35	0.30
20:1	13.4	1.55	6.75	2.50	4.30	2.00	1.45
20:2 ω9	–	0.30	0.10	0.40	0.15	0.45	0.15
20:2 ω6	0.15	0.35	0.15	0.25	0.20	0.35	0.30
20:3 ω6	0.10	0.10	0.20	0.30	0.10	0.15	0.20
20:3 ω3	0.30	1.10	0.60	1.35	0.85	0.80	1.00
20:4 ω6	Tr.	0.10	0.25	0.10	0.10	0.15	0.15

Fatty acid	Herring, North Sea	Anchovy, Peru	Whale, Antarctic	Pilchard, South Africa	Sardine, Portugal	Menhaden, USA	Pilchard
20:4 ω3	0.75	0.70	1.30	0.70	1.05	1.35	0.80
20:5 ω3	7.45	17.0	4.70	19.3	11.0	11.0	18.3
21:0	0.10	Tr.	0.05	0.15	0.10	0.05	0.10
21:5 ω2	0.25	0.70	0.15	0.90	0.50	0.60	0.90
22:0	0.05	0.05	0.10	0.20	0.20	0.20	0.15
22:1	21.3	1.15	2.40	3.10	3.80	0.55	1.55
22:2	0.20	0.10	0.05	0.05	0.10	0.20	0.10
22:3 ω3	–	0.15	0.25	0.15	0.15	0.15	0.20
22:4 ω3	0.25	0.55	0.20	0.40	0.70	0.50	0.60
22:5 ω3	0.75	1.60	2.40	2.35	1.30	1.90	1.80
22:6 ω3	6.75	8.75	5.70	6.45	13.0	9.10	9.60
23:0	0.10	0.05	0.05	0.10	0.10	0.10	0.15
24:0	0.15	0.05	Tr.	0.15	0.10	0.15	0.10

Fatty acid	Herring, North Sea	Anchovy, Peru	Whale, Antarctic	Pilchard, South Africa	Sardine, Portugal	Menhaden, USA	Pilchard
24:1	0.75	0.50	0.30	0.50	0.60	0.35	0.70

The saturated fatty acids usually total 20–30% of a marine oil, the monounsaturated 30–50%, the polyunsaturated (PUFAs) < 10% and the long-chain PUFAs (LCPUFAs) 10–30%. These are bound in various combinations to **glycerol**, hence oils are **triacylglycerol**s. The mixture may be such that some fish oils, for example **menhaden oil**, can be readily 'winterized', with a solid layer, containing a higher total of saturated fatty acids, settling out. On the other hand, oils high in 22:1, such as herring or capelin oil, solidify evenly. Most marine triacylglycerols are probably 95% digested by fish and mammals but shark liver oils, which sometimes also contain the hydrocarbon squalene or diacylglyceryl ethers, may be less digestible. A few marine invertebrate oils may have wax esters, which can be digested by fish but not necessarily by higher animals, and some whale oils are also rich in wax esters. **Freshwater fish** oils from cold climates are usually similar to marine oils in fatty acid composition but may be higher in PUFAs and lower in LCPUFAs.

The monounsaturated fatty acids are readily digested and used for **energy** by most animals, although 22:1 and to a lesser extent

20:1 may be excreted as **calcium** soaps. They are, however, quite stable towards **oxidation**. The LCPUFAs readily oxidize and produce a variety of **aldehyde**s, most of which are offensive and their **rancidity** is popularly identified as distinctively 'fishy'.

The C_{18} PUFAs of marine oils are of nutritional importance in the diets of chickens and non-ruminant farm animals. The LCPUFAs (and the 18:4 n-3, invariably only 1–2%) are responsible for a new interest in fish oils as human health **supplement**s. This is a relatively small market sector for fish oils and seal oil, which must be refined to a high quality. In the past 20 years, eating fish has been repeatedly demonstrated to reduce the risk of mortality from heart attacks. This benefit is attributed to the LCPUFAs in the fish, although their muscle fats have not only the same saturated fatty acids shown above, but about 1% **cholesterol** as well.

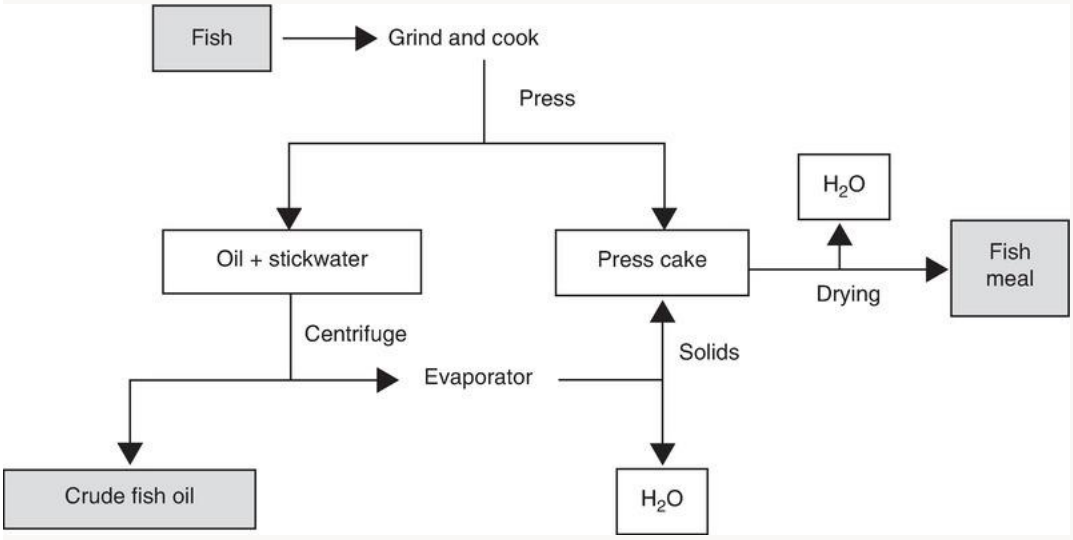
Ironically, the worldwide salmonid **aquaculture** industry requires the LCPUFAs as a dietary component. Some may be supplied through fish meal **lipids** (10% by weight and containing 20–30% LCPUFA), but usually up to 10% of an oil is added to the diet. The marine oil LCPUFAs are truly essential for salmonids at the level of 1% of the diet. Without LCPUFAs, **growth** may be limited since new cells require membranes that are approximately 40% LCPUFAs. Some allowance for use of 18:3 n-3 instead is possible, but it is not common in marine oils. A variety of other fats can be used for energy, provided that the requirement of LCPUFAs is met and excessive **linoleic acid** (18:2 n-6) is avoided. Conversely, the n-6 fatty acids are a staple part of diets for **tilapia** and channel **catfish** but so are 18:3 n-3 or LCPUFAs at a lesser

level than for salmonids. The dietary fatty acid requirements of broodstock and fish larvae may not be obvious but LCPUFAs should be carefully considered in terms of essentiality.

Partially hydrogenated marine oils contain ***trans* fatty acid**s, which are now considered undesirable in human diets. In consequence, more of the marine oils that were previously hydrogenated have become available for **aquaculture** feeds. Only limited use can be made for these in chickens, pigs, etc., because of the risk of **oxidation** and **taint** in the **meat** produced.

Fish oils are produced from a wide variety of fish, usually in conjunction with the production of fish meal (see schematic figure). Fish meal is nominally 65% protein with lipid and moisture contents of 8–10% each, plus some salt and minerals. To provide this, the modern fish plant grinds up the fish and cooks it. Most of the free oil and some of the water are squeezed out, and the solids are then dried to the desired moisture level. Grinding and addition of an **antioxidant** follow. The oil and water are separated by a centrifuge, usually desludging, although decanters are now sometimes used, and the water phase is concentrated so that any protein and other solids can be added back to the basic meal at the drying stage. The oil is commonly sold 'as is'. The quality of the marine oils is heavily dependent on the quality of the raw material. With the operation of a fish reduction plant on a scale of up to 1000 t per day, prompt processing of fish landed after a variable period on board ship is not always possible. **Enzyme activity** in both **muscle** and viscera of long-dead fish can produce **free fatty acid**s (FFAs), a useful index of the quality of the oil and to some

extent of the protein in the associated meal. An FFA content of up to 3% is probably acceptable as the FFAs are quite digestible and not apt to cause rejection of feeds by either fish or mammals on grounds of flavour. Oxidation products, assessed as the **peroxide** value (PV or POV), is often another criterion in assessing oil quality, because peroxides eventually break down to **aldehyde**s. Without being dogmatic, for fish oil from colder regions a POV of 5 or less should be considered acceptable.



Schematic of a modern fish reduction plant.

Unlike fish meals, usually no stabilizing antioxidants are added to marine oils. Whole fish or fish waste (offal) is always rich in autolytic enzymes. If the basic product is ground up ('minced') and left in storage, it will be contaminated by bacteria. To prevent this a strong acid, often **formic acid**, is added to keep the pH below 4. In a few days enzymatic cellular breakdown is sufficient for de-oiling and a liquefied protein product called fish **silage** is obtained. Although easily stored in tanks, pumped or transported, fish silage may only be suitable for manufacturing moist fish feeds, pig rations, etc. Fish silages used to be popular in fish aquaculture but

are now suspect for sanitary reasons, as disease has become one of the major industry problems.

Chile and Peru can produce 750,000 t of fish oil, half the world's production, but are subject to irregular disastrous years from **climate** changes. At these times fish meal and oil prices soar but other countries can make up some of the shortfall, e.g. South Africa, Norway, Japan, Iceland or the USA and Mexico. Overfishing is endemic and production of fish meal and fish oil is regarded by some people as an undesirable way to use the resources of the oceans. In the future these socioeconomic factors will become more important. (RGA)

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Marine plants

Marine plants, in the broad sense, are those vascular plants, **algae** and fungi that live and reproduce in the sea and associated **brackish water**s. Some authorities also include seaside vascular

plants whose roots are exposed to **sea water** to some degree but whose shoots are aerial and habit essentially terrestrial, e.g. mangroves and salt-marsh species. Vascular marine plants are chiefly the seagrasses, of which there are 58 species worldwide in four families; they are not true **grasses** but often with grass-like leaves and having submerged flowers and fruit. They typically populate the shallow soft bottom of temperate and tropical coasts. Marine algae are a much more diverse group, both morphologically and taxonomically. They range from microscopic unicells (**phytoplankton**, endophytes) to the tallest vegetation known, the giant kelps, and comprise many thousands of species in about 11 divisions or phyla. The multicellular algae, or **seaweeds**, are mainly confined to coastal shallows, but the planktonic microalgae form a huge biomass throughout the photic zone of the world's oceans. Marine fungi are the least conspicuous of the marine plants, being microscopic filamentous species in soft substrata, or forming intertidal lichens.

Marine plants are important contributors to oceanic production and coastal stability. A number of species are commercially valuable, including some seaweeds used to **supplement** livestock feed (e.g. *Ascophyllum nodosum*, *Laminaria digitata*) and microalgae cultured for herbivorous invertebrates in **aquaculture** nursery operations (e.g. *Isochrysis galbana*). Others have achieved notoriety as aggressive weeds or sources of toxins. (CB)

Marine toxins

Naturally occurring **organic compound**s produced by organisms in the **marine environment** that have inimical effects on other

species. A wide array of toxigenic invertebrate species are involved in the biosynthesis, transfer or propagation of such toxins within marine food webs, including protists (unicellular organisms), porifera (sponges), coelenterates (jellyfish, anemones, corals), echinoderms (**sea urchin**s, starfish), **mollusc**s (snails, bivalves, gastropods) and various worms and marine arthropods (joint-legged animals). In addition, marine toxins are widely distributed among vertebrates, such as **fish** and reptiles, particularly sea snakes. Certain marine toxins are reputed for their extreme potency – the high-molecular-weight compound, palytoxin, first isolated from the zoanthid *Palythoa* and now associated with a marine dinoflagellate, is among the most potent known biotoxins.

Toxic effects to humans and other mammals can vary from simple dermal irritation, as in the case of casual exposure to certain jellyfish and anemones, to severe physiological disturbances resulting from consumption of contaminated teleost fish, such as those associated with **histamine** fish **poisoning** (scombroid) causing an 'allergic' response, and other fish-borne diseases, e.g. puffer-fish poisoning (*fugu*; tetrodotoxicity). In extreme cases, mortalities can result; for example, in mammals, death by tetrodotoxin poisoning often occurs by respiratory paralysis following blockage of **sodium** channels in the neuromuscular system. (AC)

See also: Algal toxins

Marker

An indigestible substance used for the measurement of **digestibility**, or the rate of passage of **digesta**. A marker may be

an inert substance added to a diet, such as **chromic oxide**, titanium dioxide or polyethylene glycol, or it may be a substance that occurs naturally in feeds, such as acid-insoluble **ash**. Marker**s** may be chosen to follow either the solid components of the diet or the liquid phase. (MFF)

Mash feeding for poultry and pigs

Mash is the simplest feed form for use in **poultry feeding** and **pig feeding**. Preparation consists of grinding all the ingredients to a similar grist size, to allow for homogeneous blending of the ingredients during mixing and to prevent sorting and inadequate or excessive intake of some ingredients during feeding. A further step in feed preparation – **pelleting**, or pelleting followed by crumbling – reduces these problems associated with mash diets.

Feed intake in poultry takes longer with mash diets compared with crumbled or pelleted diets (e.g. Savory, 1974; Howlider and Rose, 1992). In the Savory (1974) study, newly hatched hybrid and Brown Leghorn chicks were fed on diets in either pellet or mash form and their **growth** and **feeding behaviour** were studied. The mash had been made by re-grinding the pellets, so that the **metabolizable energy** (ME) levels of the two feed forms were similar. Chicks fed on pellets were heavier after 40 days, even though they had eaten no more than those fed on mash. The apparent digestibilities of pellets and mash were about the same in the hybrid chicks but were greater for mash than pellets with the Leghorn birds. Chicks fed on mash spent about twice as much time feeding as those fed on pellets. Chicks given a choice of feed form

consistently preferred mash to pellets. Pellets may confer an advantage to chicken growth because of the reduced time feeding, and hence **energy expenditure**, on the pellets, and in the case of the Leghorns there may have been improved **digestibility** when the feed was pelleted. A follow-up study by Savory (1988) showed that, on average following a period of feed withdrawal, fowl took 1.8 times as long to reach two consecutive minutes with < 0.2 g eaten with mash as they did with pellets. That finding agreed well with the twofold difference between times spent feeding on mash and pellets by young chickens reported by Savory (1974).
In a related study, Jensen and McGinnis (1952) evaluated the response of **laying hen**s to different inclusion levels of dehydrated **lucerne** (alfalfa) (from 100 to 150, 200 and 250 g kg^{-1}) in mash and pelleted diets and found that increasing the inclusion level of alfalfa reduced bird weights with mash diets, whereas hens fed pelleted diets gained weight. These researchers also found that hens fed mash diets consumed less feed than the corresponding pelleted diets, with the intake difference being greater with diets containing high concentrations of dehydrated lucerne (200 and 250 g kg^{-1}) that increased the fibre content.

These findings on mash feeding in relation to poultry feeding behaviour can be applied beneficially with flocks of flighty or aggressive strains and breeds of chickens, in that longer feeding times can reduce the amount of aggressive behaviour such as **feather pecking** and **cannibalism**.

The beneficial effect of feeding pelleted diets to fast-growing birds, such as broilers, has been well established. Voluntary feed

intake is increased in birds fed crumbled or pelleted diets compared with mash diets (Jahan *et al*., 2006). The increase in feed intake, which is by between 2.5% and 6% (e.g. Bolton and Blair, 1977; Abdollahi *et al*., 2014, 2018), increases growth rate, which is largely attributed to the increased **bulk density** of pelleted diets, which facilitates easy prehension and increased feed consumption. However, the advantage of pelleting declines with increasing dietary nutrient density of the feed mixture (Hamungalu *et al*., 2020).

In addition to these benefits of pelleting and crumbling over mash feed, textured feed has the practical advantage of being more compact and less likely to deteriorate during storage or to break down during transportation, and less likely to incur spillage loss during feeding, particularly on deep-litter housing systems, resulting in less dust in the poultry barns. Banerjee (1998) reported that ground feeds did not retain their **nutritive value** as well as **pelleted feed**s. It is advisable to avoid mash diets with **automatic feeding** systems since they can cause bridging in the feed lines and inconsistent feed delivery. A further disadvantage of mash diets is that if the mash is too fine it may build up on the beaks and impede the entry of air into the nasal openings situated on the upper surface of the **beak**, resulting in distress in the birds.

Modern broiler production based on fast-growing strains fed high-energy crumbled and pelleted feed is a very efficient system of **meat production** but is associated with an increase in the incidence of **welfare**-related issues such as metabolic, circulatory and skeletal disorders (Abeyesinghe *et al*., 2021). Sudden death

syndrome may occur in flocks of rapidly growing broilers. The aetiology is uncertain, but the problem is considered to be a **metabolic disorder** that predisposes birds to cardiac arrhythmia (Sander, 2020). Reducing the growth rate, particularly during the first 3 weeks of life, by adjustment of the lighting cycle to reduce the periods of feeding or by feed restriction is known to be beneficial in lowering the incidence of metabolic diseases such as **ascites**, **lameness**, mortality and sudden-death syndrome (e.g. Sahraei, 2014). In one study, the incidence of skeletal disease was significantly lower in birds given restricted amounts of feed compared with birds fed *ad libitum*. These findings have led to consultations by several agencies and industry groups on how codes of practice relating to broiler production can be modified so that the welfare of the birds can be improved and regulated. Possible amendments to current codes may involve the use of mash diets to slow growth at certain stages of the production cycle, although this approach does not appear to have been well researched. Hasani *et al*. (2018) found that the occurrence of ascites was lower with mash diets than with crumbled or pelleted diets, post-mortem examination of affected broilers showing a right ventricular dilation whereas hearts from healthy broilers had normal right and left ventricles. Hamungalu *et al*. (2020) reported that **liveweight**s were reduced by 16% with mash diets compared with pelleted diets and were more variable with mash diets than with pelleted diets. No significant effect of diet form on overall mortality was found (total 4.4%: 2.5% in weeks 1–3 and 1.92% in weeks 4–6), although there was a tendency for an increase in

mortality with increasing nutrient density.

Similar reductions in growth rate with mash feed, compared with pelleted feed, have been reported for pigs (Longpré *et al*., 2016), which were associated with higher butyric and **propionic acid** concentrations in the intestines, reducing the pH to around 6. This has antibacterial activity, which can reduce the proliferation and virulence of pathogens, such as *E. coli* and salmonella. These bacteria are most likely to challenge pigs around stressful periods, such as at **weaning**. As well, the number of gastric lesions is reduced. Most benefit is likely to be seen with diets containing a large **particle size**, which is more slowly digested.

Mash feeding, as the simplest form of feed processing for feeding to chickens and pigs, precludes the possibility of **extrusion** of the cereal **grain**s, which adds steam and pressure to improve the availability of nutrients. This is used as part of the pelleting process in preparation of feed which, although being an expensive process, has particular benefit for digestion of **starch**.

Mash feeding therefore reduces growth rates in both chickens and pigs but can contribute to improved health in both species. (RB; CJCP)

See also: Restricted feeding systems

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Mass spectrometry (MS)

An analytical tool used to gain information about the elemental composition of samples and the structure of organic, inorganic and biological molecules. In addition, the qualitative and quantitative composition of complex molecules, the structure and composition of solid surfaces and the isotopic ratios of atoms in samples can be obtained. The technique involves the atomization of a sample and formation of ions followed by the separation of these ions based on their mass-to-charge ratio and the measurement of each ion produced. It is an extremely powerful technique. (JEM)

Mastication
A process of **chewing** feed in preparation for swallowing. This is a sideways, or circular, movement of the lower jaw. Feed is ground between the lower and upper molars and premolars. The time taken to form a bolus of small feed particles with **saliva**, suitable for swallowing, is much greater for long **hay** than for cereal **grain**s and so the bolus of grain contains much less fluid, i.e. saliva. (DLF)

Mathematical models
A mathematical description of the composition and behaviour of a system under study, intended to provide an understanding of the system, predictions of its future behaviour, or a guide to its optimal utilization. In agriculture, one can distinguish between models intended for research and those intended for management.
Models for research
The purpose of these models is to provide a clear, descriptive summary of the researcher's beliefs about the qualitative or quantitative behaviour of a system. Such models can draw attention to deficiencies in knowledge of the system and so indicate future research directions. A simple example will illustrate the main principles. Consider the problem of describing the dependency of food intake of an animal on the animal's ambient **temperature**. The simplest description, or model, is that of no dependency: the food intake is constant, independent of the temperature. A second, more realistic model may be that food intake decreases with an increase in temperature. A mathematically clear description of this dependency may be, for example, a linear relationship: for each

degree increase in temperature, food intake decreases by a fixed number of grams. Each of these two models has parameters: numbers that describe specific instances of the models while the general form remains unchanged. The first model has a single parameter: the constant food intake of the animal. The second can be described by two parameters: the food intake at some particular temperature and the change in food intake, in grams, for each degree increase in temperature.

Model fitting is the process of estimating values for, or fitting, the parameters in the model based on empirical measurements. Under the best choice of parameters the model may still be found to be an inadequate description of the data, in which case the model may itself need to be replaced. On the other hand, a model may be more complex than needed to describe a given situation. The principle of Occam's razor calls for the selection of the simplest model that adequately describes the data. This principle is justified by the predictive power of models: in general, a simpler model that describes a system adequately is a better predictor of future behaviour of a system than a more complex one. The complexity of mathematical models is often described, roughly, by the number of parameters in the model. The second model above is more complex than the first, and would only be selected once the first was shown to be inadequate. The process of model selection is therefore an iterative one: a model is formulated, its parameters fitted to data, and the model reformulated as necessary until an adequate fit is found.

The range of applicability of a model is the range of conditions

over which the model has been tested against empirical data and found to be adequate. There is usually little justification for trusting extrapolations of the model, or predictions about the behaviour of the system under study outside of this applicable range. The model above of a linear response to temperature variation, whatever the parameters, will clearly only be acceptable over a limited range of temperatures.

An empirical model relies primarily on data from the observed behaviour of the system for its formulation. Either of the food intake models discussed above fall into this category if chosen purely through experimental data on food intake at a number of temperatures. A mechanistic or simulation model attempts to represent mathematically something of the physical state or composition of the underlying system and to deduce behaviour of the system from its internal behaviour. For example, a model that measured the heat produced by an animal through **metabolism**, together with the heat able to be lost under ambient temperatures, and predicted a food intake response to temperature from this is mechanistic in its approach.

Models for management

The terms and methods described above under models for research apply equally to management models. However, here the goal of understanding the system is secondary to that of using it more effectively. A model for management must have a known, and useful, range of applicability. While a research model may be speculative, and built purely from mechanistic assumptions about the system, the model must be well tested empirically before it can

be used for management. Since others may use the management model besides the creator of the model, it should be robust to misuse or misunderstanding. In the food intake example above, while the researcher may be interested more in the overall pattern of intake response to temperature, linearly increasing, decreasing or otherwise, the manager's interest is clear: which temperature should I use? Management models are not restricted to biological models: farm planning, conservation and resource allocation (for example, in **feed formulation**) are all based on some underlying model of the behaviour of an economic system. A manager may use a model to try out a range of operational scenarios and judge which is optimal. This may be done by hand with simple models. Inferring optimal actions based on more complex models, with many inputs, may require adding a mathematical optimization component to the model. In the simplest form of this optimization, an objective function is specified that calculates a single number, representing the benefit of any behaviour of the system predicted by the model, and therefore the ultimate benefit of the management input that caused this behaviour. Various mathematical or computational optimization techniques may be used to find inputs that maximize this benefit.

Hill-climbing techniques are some of the simplest of these. The inputs to the model are varied repeatedly one by one, to see what will increase the objective. More sophisticated methods such as dynamic, linear or integer programming may be used too, depending on the underlying mathematical structure of the model. (RG)

Maturity

The stage of plant **growth** at which seeds and grain are developing and ripening. Maturity signifies the period between 50% flower emergence and completion of the transfer of nutrients, particularly protein and carbohydrates, from the stem to the grain or seeds. This is associated with a fall in **digestibility** of the plant, associated with increased **cellulose**, **hemicellulose** and **lignin** in the stem, in order to support the increased weight of the floret or cob. As the seeds ripen the plant **dry matter** increases, which can result in loss of leaf material through shattering, further depleting the nutritional value of the non-seed fraction of the plant. **Grass** crops are usually grazed at a young stage, when **nutritive value** is high. Grass for **silage** is also cut before the full flower stage is reached. **Hay** is cut at a later stage to facilitate air-drying (sometimes barn-drying). **Cereal** crops, usually grown for their grain with residues as a **by-product**, are normally harvested when the grain has dried sufficiently to be stored. By this time, the residues have reached the stage of senescence and, if to be carried and stored, care is necessary to minimize leaf loss. (TS)

Mead acid

Eicosatrienoic acid, a long-chain **unsaturated fatty acid** of the n-9 series with *cis* double bonds at the 5, 8 and 11 positions, 20:3 n-9($\Delta^{5,8,11}$). When the diet is deficient in **essential fatty acid**s, the same enzymes that desaturate linoleic and α-**linolenic acid**s will desaturate eicosenoic acid to produce eicosatrienoic acid (mead acid). It is not an essential fatty acid and will not replace

arachidonic acid or alleviate the symptoms of essential fatty acid deficiency. (NJB)

Meal frequency
When food availability is unlimited, animals concentrate their spontaneous feeding in discrete meals, which can be defined by establishing a criterion for distinguishing intra- from inter-meal intervals. Meal frequency is the number of meals thus defined per unit of time, and food intake equals meal frequency multiplied by mean meal size. When food availability is intermittent, meal frequency refers to the number of times food is provided per unit of time. (JSav)

Meat
Animal flesh, mostly the **muscle** tissue of an animal, prepared by humans and consumed as food. Most meat worldwide comes from domesticated animals raised on farms, mainly large industrial complexes that often house thousands of animals at a time. (DB)
See also: Body composition; Meat production; Meat products; Meat quality; Meat yield; Poultry meat

Meat and bone meal:
see Meat products

Meat composition
Water is the main constituent of **meat**. The other components are **protein** (**muscle**), **fat** (**adipose tissue**), **minerals** and **vitamins**. The major variable factor is the fat content, which is affected by species, gender, age, stage of **growth** and nutrition.

The composition of the fat is also affected by the dietary **fatty acid** profile, particularly with non-ruminants. (KJMcC)

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Meat meal:

see Meat products

Meat production

This term refers to the farming of animals and birds for the production of **meat** for human consumption. The major sources of meat are cattle, pigs, poultry and sheep. Of several avian species used for meat production, the commonest are broiler chickens, reared from hatching to around 4–10 weeks, depending on market outlet (size, further processing). Other avian species include turkeys, ducks, guinea fowl, quail, pheasant, partridge, ostrich and emu. Other ruminant species include goats and deer. Production systems for non-ruminants are generally intensive with control of breed, nutrition, health and environment. Extensive systems are found both in developing countries and where **welfare** considerations are important to consumers and they are prepared to pay for the extra costs involved. **Ruminant animal**s are normally reared in extensive systems, though at least part of the production cycle may be indoors for one of several reasons, for example weather conditions, land distribution or the use of '**feedlot**s' as practised particularly in the USA. (JW)

Composition of a range of meat products (g kg^{-1}).

Meat source	Moisture	Crude protein	Fat	Saturated fat	Energy (MJ kg^{-1})
Chicken breast	744	218	32	10	4.9
Chicken thigh	745	191	55	18	5.3
Pork chop	543	159	295	109	13.6
Lamb loin chop	495	146	354	176	15.6
Lamb leg (deboned)	631	179	187	93	10
Sirloin steak	594	166	228	97	11.8
Minced steak (lean)	645	188	162	69	9.2

Meat products

Primarily **by-product**s of **rendering** carcass material. They

include meat meal, meat and **bone meal**, fish meal, hydrolysed **feather meal**, bone meal and **blood meal**. Meat meal is manufactured from **carcass** trim and condensed carcasses. It is a brown, slightly fibrous meal and the term meat meal normally refers to products with a **crude protein** value > 60%. The product should be free from **hair**, bristle, feathers, horn, **hoof**, skin and viscera. The **fat** may be extracted either mechanically or with solvents. Solvent extraction removes more fat (leaving < 5%) but the final product should be free from solvent residues. EU legislation also requires that the product is described as 'rich in fat' if the **oil** content is > 11%. Meat and bone meal differs from meat meal in the quantity of bone found in the processed material. Meat and bone meal is manufactured from pieces of meat and carcass with a high proportion of bone but selected to result in a finished product with 40–55% **protein**. The nutritional characteristics of these meals can vary enormously as the nature of the material being processed influences protein and **ash** content and the treatment affects the amount of oil. The protein has a good **amino acid** balance and is highly digestible.

Fish meals are widely accepted as excellent **protein source**s but they vary with origin. Originally, fish meal was produced from the trimmings and **by-product**s of fish-processing plants. This still occurs in the UK, where white fish meal is made predominantly from **cod** and haddock. However, the world demand for fish meal cannot be met solely from waste, and fish are caught specifically for making into fish meal. These include South American-type fish meals, manufactured from purpose-caught small fish like Spanish

pilchards. In northern Europe herring-type meals are often produced from purpose-caught sprat. Fish meal is a high-protein (> 72%) feed with an excellent amino acid composition for non-ruminant animals. The **protein** is resistant to **rumen** microbial **catabolism** and therefore excellent for feeding to high-performance **ruminant animal**s, particularly dairy cows. The oil fraction is particularly high in long-chain n-3 **fatty acid**s, which are considered healthy.

Feathers contain a high level of the protein **keratin**, a poor source of protein for animals. However, the digestibility is increased when feathers are cooked under pressure. The product is dried and ground to make hydrolysed feather meal, which is a useful source of protein (89%).

Bone meal is primarily used as a source of **dicalcium phosphate** after the bones have been defatted, ground, treated with **hydrochloric acid** and precipitated with lime. This process is now tightly controlled within the EU under The Processed Animal Protein Regulations 2001 and in practice is not frequently used.

Blood meal is a deep red/brown granular powder made by drying **blood**. It is a good food material, high in protein, and is readily eaten by all animals, although it can be unpalatable at first.

Poultry meat meal (**poultry offal meal**) is a by-product of poultry processing plants. All body parts, including head, feet, carcass and fat, may be included. The final product varies in oil content and sometimes hydrolysed feathers may be included. The meal has a high protein content (65%) and can have a very high oil

content (up to 30%), depending on the carcass parts that are included. (MG)

Meat quality

The overall quality of meat encompasses the sensory attributes of quality (appearance, flavour and texture), nutritional quality and wholesomeness (microbiological quality, **contamination** and residues). The term 'meat quality' is often used in a more restricted sense to cover those aspects, whether measured subjectively or instrumentally, that relate to sensory attributes. The appearance of meat (which has two aspects: the amount and colour of the **fat**; and the colour of the lean meat) is a critical factor influencing selection by consumers. The amount of fat and its colour can be influenced by dietary factors prior to slaughter; for example, **maize** meal may impart a yellow colour to the fat as the pigments are fat soluble and are deposited in the subcutaneous fat. The colour of the lean meat is determined by the amount of haem pigment (myoglobin) in the **muscle** prior to slaughter and the form of the pigment. For example, **beef** is redder than **pork**, and poultry leg meat is redder than breast meat because in each case the former contains more haem pigment. In pigs that are sensitive to stress, or are subjected to stress just before slaughter, a rapid fall in the muscle pH as the **carcass** goes into rigor produces meat that is pale, soft and exudative (PSE). In all species, feed deprivation sufficient to deplete muscle **glycogen** reserves before slaughter or prolonged stress (for example long transport journey, mixing of animals, lairage) results in meat that is dark, firm and dry (DFD). The muscles do not undergo full **acidification** and the pH of the

muscle remains high. Due to the high ultimate pH (> 6.0), the meat has poor keeping quality and should not be vacuum packed.



High-quality meat on display in a New York restaurant. Photo courtesy of Grant Hutchinson. Licensed under CC BY-NC-ND 2.0.

The initial appearance of the whole carcass is important. Poor handling both in production and before slaughter, between farm and abattoir, can result in skin blemishes and bruising in all species and in hock burns and keel bone abrasions in poultry. Meat inspection involves examining the carcass and viscera for evidence of gross pathology. The inspection and clipping of cattle before slaughter has become increasingly important in order to reduce potential microbial contamination with pathogens being carried into cutting-plant operations. Hazard analysis critical control point (HACCP) schemes are applied to reduce contamination and maintain quality standards.

The tenderness of the meat depends on the age of the animal and post-slaughter chilling regimes. Meat that is chilled either too fast or too slowly results in shortening of the muscle fibres and

subsequent toughening (cold shortening and hot shortening). The toughness of the meat can be measured by a range of devices that quantify the force required to shear a piece of cooked meat (e.g. Warner-Bratzler Shear).

Flavour development in cooked meat is complex, depending both on the biochemical composition of the meat and on the method of cooking. **Taints** in meat can be a quality problem and may arise naturally from husbandry practices (e.g. **boar** taint) or from contamination after slaughter (e.g. disinfectant taint). Two compounds, **skatole** and androstenone, which accumulate in **adipose tissue**, have been identified as causes of taint in boars.

Nutritional quality of meat is becoming increasingly important, particularly in relation to fat content and the **fatty acid** profiles of the adipose tissue. The desires and requirements of consumers vary considerably and the aim is to produce meat that is safe and of a quality desired by the target consumer group. (BMM; JW)
See also: Poultry meat

Meat yield
The proportion of an animal **carcass** that is edible **meat**. This is different from the **dressing percentage**, which is the weight of the eviscerated carcass as a proportion of **liveweight**. Meat yield is affected by a large number of factors, including breed and gender (particularly for ruminants), stage of **maturity**, nutrition, etc, with the effects expressed through differences in **fat** content and to a lesser degree in bone content. The double-muscled Belgian Blue breed of cattle, for example, gives a much higher meat yield than other beef breeds, which in turn give higher yields than dairy

breeds. Meat yields of bulls tend to be about 2% higher than those of heifers and the same effect is evident when rams are compared with ewes. There is little interest in lean and fat ratios in meat from avian species, but there are differences in the proportional weight of breast meat between avian species, with turkeys exhibiting heavier breast muscles than broilers as a proportion of carcass weight. In reality the derivation of meat yield is dependent on the components included in the calculation. (DLH)
See also: Meat composition

Medicated feed
Foods containing added drugs intended to be fed to animals suffering from, or at threat from, various types of disease, particularly infectious disease. Some medication (e.g. antibiotics) is to enhance efficiency of production, some (e.g. coccidiostats) is to protect against disease and some (e.g. antibiotics) is to combat existing disease. (JMF)

Mediterranean diet
This focuses on the diet of the Mediterranean countries of Italy, Spain, Croatia and Greece in the 1960s. It emphasizes consumption of fresh fruit and vegetables, including nuts, pulses and herbs, some consumption of fish, and restriction of intake of red meat and dairy. Limited intake of red wine is permitted. The inclusion of **olive oil** is an important component. Claimed benefits include improved heart health, protection against Alzheimer's disease, improved cognition and reduced depression. (CJCP)



The Mediterranean diet is characterized by fresh fruit and vegetables, limited intake of fish and restriction of red meat and dairy products. Photo courtesy of Angel Ros Die. Licensed under CC BY 2.0.

Medium-chain fatty acids

Fatty acids, usually saturated, of chain lengths ranging from six (caproic or hexanoic acid, $C_6H_{12}O_2$, molecular weight 116) to 12 carbons (lauric or dodecanoic acid, $C_{12}H_{24}O_2$, molecular weight 222). Absorption from **small intestine** of mammals does not involve transport through lymph as **lipoprotein**s; their relatively hydrophilic character allows direct transport from intestine to liver via the portal vein. They are major constituents of **coconut** and palm **oils** and are also present in human **milk** and dairy **fat**. (JAM)

See also: Capric acid; Caproic acid; Caprylic acid; Fatty acids; Lauric acid

Medium-chain triacylglycerols

In **triacylglycerols,** the constituent **fatty acid**s are usually

saturated and range in chain length from six (caproic or hexanoic acid, $C_6H_{12}O_2$, molecular weight 116) to 12 carbons (lauric or dodecanoic acid, $C_{12}H_{24}O_2$, molecular weight 222). Typically, the triacylglyceride consists of fatty acids of more than one chain length. (JAM)
See also: Capric acid; Caproic acid; Caprylic acid; Fats; Lauric acid; Medium-chain fatty acids

Megacalorie
1 megacalorie (Mcal) = 1,000,000 **calorie**s or 1000 kcal. (JAMcL)
See also: Energy; Energy system

Megajoule
1 megajoule (MJ) = 1,000,000 **joule**s or 1000 **kilojoules** (kJ) (JAMcL)
See also: Energy; Energy system

Melatonin
A **hormone**, *N*-acetyl 5-methyoxytryptamine, synthesized in the pineal gland from the amino acid, **tryptophan**. Melatonin is involved in the regulation of seasonality. Its secretion is stimulated by darkness and inhibited by **light** and is thus sensitive to day length. Season-related behaviour and physiology, such as mating and **fertility**, are influenced by its pattern of secretion. (JRS)

Melibiose
A **disaccharide**, $C_{12}H_{22}O_{11}$, molecular weight 342, of α-D-galactopyranose linked to the 6-hydroxyl of D-glucopyranose. It is

produced, together with **fructose**, by **hydrolysis** of **raffinose**. (JAM)

Melitose:
see Raffinose

Melitriose:
see Raffinose

Melon (*Cucumis* spp.)
Members of the gourd family, Cucurbitaceae, which includes cucumbers, **pumpkin**s, squashes and watermelons. They are annual trailing plants with runners up to 2.5 m long. The yellow bell-shaped flowers require bees for pollination. Watermelons (*Citrullus lanatus* (Thunb.) Matsum & Nakai) are creeping annual plants with large round fleshy fruits with a high moisture content. Melon seeds are used in Africa for human consumption, but may be pressed to obtain **oil**. The resultant oilcake can be used at up to 20% in ruminant feed. (LR)

Nutrient composition (% dry matter) of melon

	DM (%)	**CP**	**CF**	**Ash**	**EE**	**NFE**
Water melon rind, boiled	93.0	7.3	36.5	1.6		

	DM (%)	CP	CF	Ash	EE	NFE
Seeds with hulls	88.0	24.4	31.6	4.2	35.4	4.4
Seeds without hulls	91.9	34.0	8.2	6.2	46.7	4.4

CF, crude fibre; CP, crude protein; DM, dry matter; EE, ether extract; NFE, nitrogen-free extract.

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Menadione

A synthetic compound, 2-methyl-1,4-**naphthoquinone**, also called menaphthone, used in animal feeds as a source of **vitamin K** activity. It is alkylated by animal tissues to a specific **menaquinone**, menaquinone-4. (JS)

Menaquinone
A series of compounds, 2-methyl-3-polyisoprenyl-1,4-**naphthoquinone**s, with **vitamin K** activity produced by anaerobic bacteria in the lower bowel. (JS)

Menhaden oil
An oil extracted from large herring-like fish (*Brevoortia* spp.) caught off the east coast of North America. Menhaden oil contains a high proportion of long-chain **polyunsaturated fatty acids**, particularly C_{20} and C_{22}. Refined menhaden oil has a **fatty acid** profile of ≤ 12:0 trace, 14:0 7–11, 16:0 12–31, 16:1 7–13, 18:0 2–5, 18:1 9–11, 20:0 trace, 20:1 1–2, 20:4 1.5–2.5, 20:5 11–14, 22:0 trace, 22:1 trace, 22:5 1–3, 22:6 7–11. (JKM)

Mercury
A **heavy metal**, not nutritionally essential, that is potentially toxic in farmed animals, particularly fish. In nature it exists mainly in low, non-toxic concentrations but its widespread use in industry and in particular its use as a seed dressing in agriculture has led to many **poisoning** incidents in farm animals and to its accumulation in lakes and waterways. It is used industrially mainly in the inorganic form, which is not well absorbed by animals, but this is readily converted into the organic forms, methyl and dimethyl mercury, by **microorganism**s. The organic form is more soluble and is easily absorbed via the **gastrointestinal tract**. It is neurotoxic and accumulates in liver and muscle, being particularly attracted to **cysteine**-rich molecules such as **metallothionein**s. (CJCP)

Metabolic disorder
A disease caused by a disturbance in one or more metabolic processes that may result in a deficiency or excess of a normal **metabolite**. Metabolic diseases include **milk fever** (**parturient paresis**, **hypocalcaemia**), **ketosis** (acetonaemia), pregnancy toxaemia and **hypomagnesaemia** (grass staggers). (ER)
See also: Poultry metabolic disorders related to nutrition

Metabolic hunger
Animals may have feed available to them *ad libitum*, but they are still unable to meet the requirements for **lactation**, **growth** and **maintenance** because of the inadequate concentration of nutrients in their diet. In these circumstances they may experience a metabolic hunger. (CJCP)

Metabolic rate
The sum of all oxidative processes in the body, equated to the rate of **heat production**. It may be measured directly as heat, or indirectly from **oxygen consumption** and **carbon dioxide** production using a formula such as **Brouwer's**. Basal metabolic rate and resting metabolic rate are measurements made under standardized conditions, which may be difficult to achieve in farm animals. (MFF)

Metabolic weight
The fractional power of **liveweight** to which **metabolic rate** tends to be proportional. It is most commonly expressed as live body weight (kg) raised to the power 0.75 (kg $W^{0.75}$) because the

relationship between metabolic rate (*M*) and body weight (*W*) in adults of species with a wide range of mature body weights has the form $M = aW^{0.75}$. Within a species, however, metabolic rate tends to be proportional to a lower power of body weight. (MMacL)

Metabolism

(1) The physical and chemical processes occurring within a living cell or animal that are necessary for life. (2) The changes involving a specified element, substance or attribute within the body (e.g. **nitrogen metabolism**, **protein metabolism**, **energy metabolism**). These changes involve biosynthesis (anabolism), uptake and excretion (transport) and breakdown (**catabolism**) carried out in a living cell, tissue or organ or in the whole animal. (JAMcL; NJB)

Metabolites

Compounds that are used in or produced by **metabolism**. A metabolite is thought of as a **substrate** or product of an **enzyme** system, although this applies as well to transport systems (uptake and excretion). A metabolite can be organic (e.g. **glucose** or glucose-6-phosphate) or inorganic (e.g. **sulphate** SO_4^{2-}, or phosphate PO_4^{3-}). (NJB)

Metabolizable energy (ME)

That part of the **gross energy** (GE) of the food that is not excreted as the gross energy of waste products (i.e. faeces, urine and combustible gases). **Metabolizability** is the proportion ME/GE of the complete ration.

A ration that maintains a non-working, non-pregnant, mature animal without **fattening** or production of milk, eggs, etc., is called a **maintenance** ration. At the maintenance level of feeding, all of the ME is converted into heat, i.e. the basal **heat production** (HP) plus the heat increment of the maintenance ration.

The ME system for estimating food requirements uses ME for maintenance as a starting point. From this point additional ME intake (*d*ME) provides for energy retention (RE) in the form of **growth**, fattening and the production of milk, eggs, etc. All these processes also involve additional heat production (*d*HP) as a sort of tax on the additional ME. Thus:

RE=dME−dHP.

The ratio *d*RE/*d*ME (which is the same as RE/*d*ME, because the starting point is that of zero RE) is known as the efficiency of utilization of metabolizable energy (k). Its converse (1 – k), which is equal to *d*HP/*d*ME, is the heat increment of the additional feed. Efficiency is different for different functions (maintenance, fattening, **lactation**, etc.) and is also dependent on the quality (metabolizability) of the diet. Animal rations are often quantified in energy terms as multiples of the ME for maintenance.

The concepts just defined for animal rations (GE, ME and RE) are also applicable to different types of food and to individual food components and this is the basis of the ME feeding system for predicting the **energy requirement**s of animals. The values quoted in food tables are those of the ME of the different foods or food constituents. These values are not the same for all species,

because of differences in their **digestive system**s (e.g. **carnivore**s, omnivores, ruminants). The values may not be completely additive when feeds are combined to form diets, because of **associative effects**. (JAMcL)

See also: Calorific factors; Energy costs

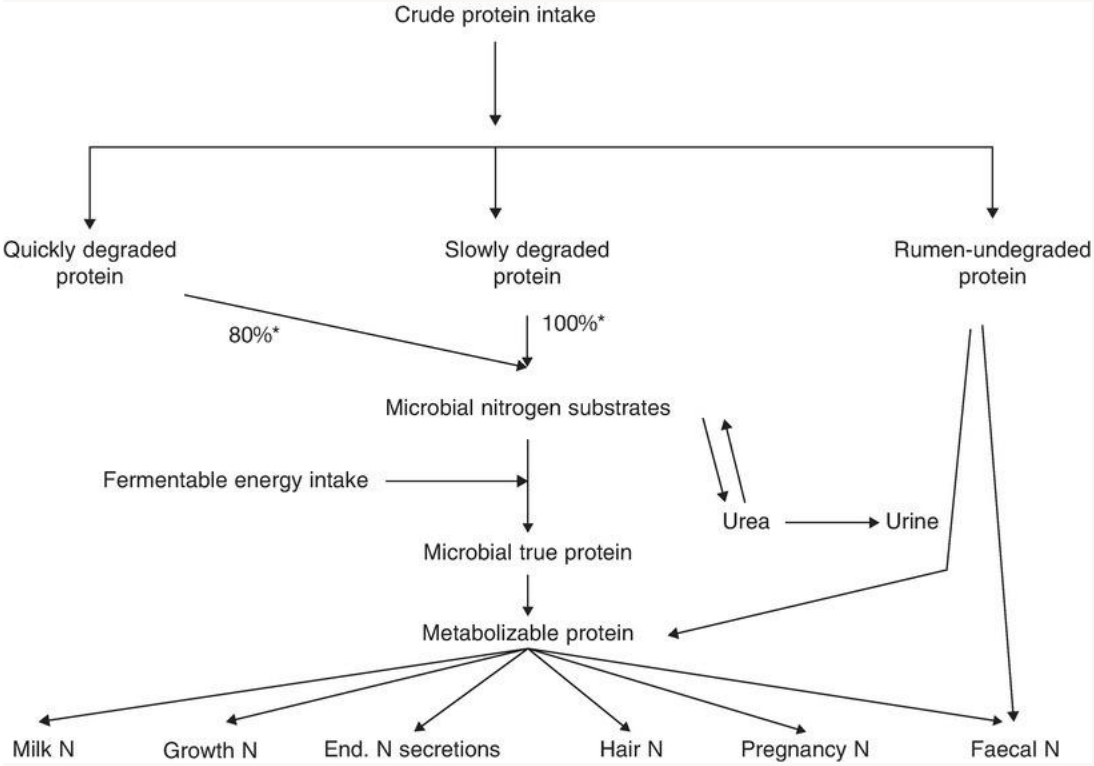
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Metabolizable protein (MP)

Protein that is usable by an animal, usually in the context of feeding ruminants. Metabolizable protein (MP) has two components: microbial **true protein** derived from the growth of bacteria and **protozoa** in the **rumen** and **reticulum** (*see* Microbial protein); and digestible undegraded **feed** protein that has passed intact through the rumen and can be digested in the **abomasum** and **small intestine**. The rate of production of **microbial protein** in the rumen depends on the supply of degradable feed protein, the supply of fermentable **energy** to the rumen microbes and the rate of flow of **digesta** out of the rumen. The supply of undegraded feed protein is also affected by the rate of flow through the rumen, which increases with the **animal production level** (APL). The animal's requirement for MP depends on its level of productivity. The major requirement for MP in adult female ruminants is for the production of milk during **lactation**, but MP is also needed for **maintenance** and **growth**, including the growth of the fetus during pregnancy, and for the production of **wool**. If the MP

absorbed is inadequate to meet maintenance requirements, MP is released from the breakdown of body tissues (mainly muscle), with a consequent loss of body weight. MP from body tissue breakdown is presumed to be utilized with an efficiency that varies with the use: for maintenance 1.0, for pregnancy 0.85, for lactation 0.68, for body growth 0.6 and for wool growth 0.26. (JMW)



The metabolizable protein system for cattle. (*The proportion of the protein that is utilized to form the microbial nitrogen substrates.)

Metabolizability

The proportion of food **energy** that can be metabolized by the animal. The concept is similar to **digestibility**. Metabolizability (q) can be calculated in several different ways:

$q=ME/GE$ $q=0.81 \times$ (energy digestibility) $q=ME/18.4$

where ME is the **metabolizable energy** content of the feed (MJ kg^{-1} DM), and GE is the total or **gross energy** content of the

feed (MJ kg^{-1} DM). (GMcLD)

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Metabolomics and metabonomics

The use of metabolic profiles is well established in humans and methods have been widely researched and developed in dairy cows (Payne *et al*., 1970), but they have not entered widespread use in the livestock industries. Their value is predicated on a relationship between metabolic constituents of **blood** or **milk** and the health and productivity of the animals. Dairy cows are the logical contender for the development of metabolic profiling, because samples are taken daily that could be used for such purposes. Initial research on metabolic profiles used blood samples and was almost universally conducted with low-yielding dairy cows (Kumar and Pachhauri, 2000), whereas it is high-yielding cows that are increasingly used in intensive systems of production which are more likely to be challenged physiologically. Standard protocols for collecting samples for metabolic profiling have been developed using blood (Bertoni and Trevisi, 2013), paying particular attention to sources of variation, such as methods of blood collection and its timing in relation to feeding practices, which is particularly important in relation to indicators of nutritional status. Reference values are proposed for cows in various stages of **lactation**, but further detail is needed from clinically healthy cows. This will help to improve the comparability of metabolic profiling techniques

between studies.

A new science of metabonomics is emerging for the quantitative measurement of the dynamic multiparametric metabolic response of living systems to pathophysiological stimuli or genetic modification (Nicholson, 2006). This offers diagnostic capabilities to veterinarians using the metabolic profiles of high-yielding cows, which have been genetically modified to select for high yields. The bovine **mammary gland** is capable of extracting nutrients from large volumes of blood, with more than 500 l processed to produce l l of milk (Linzell, 1974). However, intake restrictions in early lactation and excessive nutrient demands render **adipose tissue** loss inevitable. This places the cow at high risk of **metabolic disorder**s and it is therefore beneficial to understand the **metabolism** of high-yielding Holstein dairy cows in relation to the correlations between milk yield, blood (Nozad *et al*., 2013) and milk components (Nozad *et al*., 2012). The risk of metabolic challenges is particularly high in the newly developing intensive dairies, using primarily high-yielding Holstein cows imported from Canada and Germany. The metabolic profile test can assist such developing dairy industries by better quantifying dairy metabolic parameters (Bashtani *et al*., 2009; Hossein-Zadeh and Ardalan, 2011) to prevent disease and improve milk yield, using key indices in blood, milk and **feed** (Sakhaee *et al*., 2011, Mokhber Dezfouli *et al*., 2011). (CJCP)

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Metal

Element that tends to form positive ions in solution. In water, metal oxides tend to form hydroxides. Most conduct electricity and can be formed into a variety of shapes. In pure form they have a high **specific gravity** and high physical strength. About three-quarters of the elements are classified as metals. (NJB)

Metalloenzymes

These are enzymes that, when purified by conventional means, have a repeatable molar quantity of a functional **metal** associated with them. These differ from metal-activated enzymes which require an added metal to function. The distinction between metalloenzymes and metal-activated enzymes lies in the affinity of the metal for the enzyme. (NJB)

Metallothioneins

A group of proteins (molecular weight 6500) containing about 60 **amino acid**s, one-third of which are **cysteine**. These proteins are

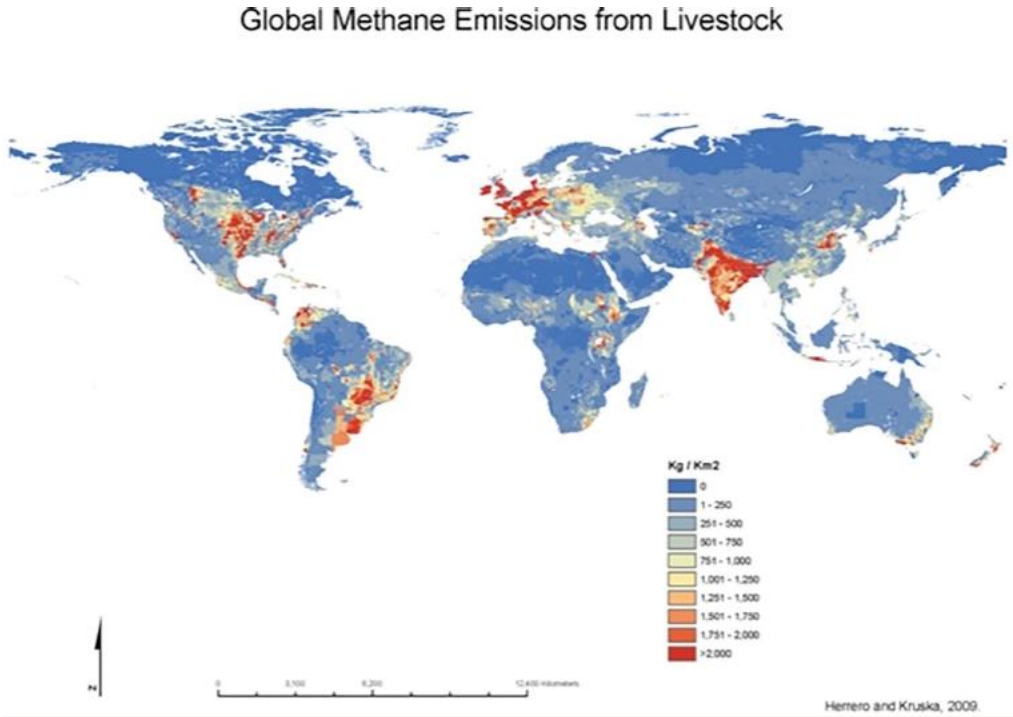
found mainly in the cytoplasm of kidney, **liver** and intestine. The cysteine residues of these proteins are involved in the binding of **copper**, **zinc**, **cadmium** and **mercury**. Metallothioneins bind these metals with high affinity and participate in their storage and sequestration. In the case of copper, these proteins have the effect of decreasing the amount of free copper which participates in generation of **free radical**s that cause tissue damage. (NJB)

Methaemoglobin

Haemoglobin in which the **iron** is in the ferric (Fe^{3+}) rather than the ferrous (Fe^{2+}) state. Also called ferrihaemoglobin, methaemoglobin is brown rather than the bright red of oxyhaemoglobin. Methaemoglobin cannot carry **oxygen** or carbon monoxide and thus is of little value in support of oxidative **metabolism**. One to two per cent of **haemoglobin** in **blood** is in the methaemoglobin form. It can be reconverted to haemoglobin in a reaction in which reduced **glutathione** participates. (NJB)

Methane

An organic gas, CH_4. It is colourless, tasteless and less dense than air. Biogenic sources, including lake sediments, marshes, **rice** paddies, sanitary landfills and intestinal contents of animals, involve methanogenic bacteria, while abiogenic sources are coal mining, natural gas emissions and biomass burning. Methane is an important greenhouse gas and features strongly in considerations of the effects of ruminant farming on **climate** change. (DMS)



Methane is a by-product of livestock digestion that makes a major contribution to global climate change. This map shows the intensity of emissions around the world. Photo courtesy of the International Livestock Research Institute/Mario Herrero and Russ Kruska. Licensed under CC BY-NC-SA 2.0. Available at: https://www.flickr.com/photos/ilri/8269560876 (accessed 5 September, 2023).

Methane cost of animal products

CO_2, methane and nitrous oxides are the main biogenic (produced by animals) greenhouse gases (GHGs) produced in the production of **meat**, fibre and **milk**. These gases are produced as a result of the **fermentation** of food by **rumen microorganisms** and the degradation of manure and **urine**. Each of these gases has a global warming potential. The expected global warming potentials over 100 years (GWP_{100}) of these gases are 1 for CO_2, 28 for methane and 298 for nitrous oxide. Because each gas has a different GWP, it is convenient to calculate the CO_2 equivalent (CO_2e) of each gas,

and to sum these to get the CO_2e cost of animal products. The CO_2e for each gas is its GWP_{100} multiplied by the amount of gas emitted. Note that there are also abiogenic CO_2e costs, associated with the costs of generating electricity, using fuel for farm machinery and vehicles, etc.

When calculating the biogenic CO_2e cost of animal products (the CO_2e intensity) only the methane and nitrous oxide costs are counted, as it is assumed that CO_2 cycles between air, plant tissue, rumen gases and air. The IPCC (2006) report suggested the following equation to calculate the annual methane emissions from a single animal:

$EF = GE \times (Ym/100) \times 365 / 55.65$

or $EF = (DMI \times 18.4) \times (Ym/100) \times 365 / 55.65$

where EF = emission factor, kg CH_4 per head per year; GE = **gross energy intake**, MJ per head per day; Ym = **methane** conversion factor, percentage of **gross energy** in feed converted to methane (values for Ym vary with animal and feed types, see table); 55.65 (MJ kg^{-1}) is the **energy** content of methane; 18.4 MJ kg^{-1} DM is the assumed GE content of feed DM.

Calculation of methane emissions (adapted from IPCC, 2006)

Livestock category	DM intake (kg per day)	Ym (%)	EF (kg per head per year)

Livestock category	DM intake (kg per day)	Ym (%)	EF (kg per head per year)
Feedlot fed cattle (diets contain 90% or more concentrates; W=450 kg)	13.5	3	48.9
Buffalo cows (W=500 kg) and their young	13.75	6.5	107.9
Dairy cows (lactating, fed pasture with some concentrates; W=600 kg, MY = 20 kg day^{-1})	18.25	6.5	143.2

Livestock category	DM intake (kg per day)	Ym (%)	EF (kg per head per year)
Other cattle and buffalo (primarily fed low quality crop residues and by-products; W=500 kg)	12	6.5	94.9
Other cattle or buffalo (grazing; W=500 kg)	13.75	6.5	107.9
Lambs (< 1 year old, suckling and grazing; W=30 kg)	0.8	4.5	4.4
Mature sheep (grazing; W=55 kg)	1.5	6.5	11.6

DM, dry matter; EF, emission factor; MY, milk yield; W, liveweight; Ym, methane conversion factor (the range around these

factors is ±1%)

There are three approaches to mitigating the methane cost of animal products: (i) reduce the total amount of methane produced; (ii) improve the CO_2e intensity of **ruminant animal** products; and (iii) offset methane production by growing trees or increasing the carbon content of soils. There are several different ways in which these can be done, listed in order of ease of application from easiest to most difficult, as follows.

Use forages that yield less methane when fermented in the rumen. A practical method for extensive sheep and beef farmers is to include **tannin**-rich pasture plants in the diet. Tannins can improve protein use and control internal parasites, as well as reducing methane. Options include planting lotus, sanfoin and sulla in pasture mixes, **turnip**, **fodder beet** and **swede** bulbs, and feeding **grain legumes** and tree (**willow** and poplar) leaves.
Change, as far as is reasonable, from an all-**forage** (i.e. pasture) diet to one that has a proportion of concentrates (e.g. cereal **grain**s, **protein** meals). **Starch** is fermented in the rumen by microorganisms that use **propionic acid** as a way of dealing with excess **hydrogen**, rather than excreting it with consequent incorporation into methane.
Increase the productivity of individual animals, by breeding for animals that are more productive, for example they grow faster and use feed more efficiently, and ensure that they are kept in good health. This allows the production of the same amount of product at a lower CO_2e cost per unit (improved CO_2e intensity),

and thus a lower overall CO_2e production from ruminant industries.

Use precision feeding to optimize nutrient use. With this technique the animal's **nutrient requirement**s are closely monitored and matched by the **nutritive value** of its feed. This approach could involve local feed manufacturers and feed analysis labs.

Breed animals that inherently produce less methane. This is a developing field and results are varied. Beef+Lamb NZ introduced a methane breeding value for sheep in 2019.

Use methane inhibitors in animals' diets; these can reduce the amount of methane produced by 20–80%. Unsaturated **fat** can be included in animal feeds, although there are limits (about 6%) to the amount that can usefully be added in the diets of ruminant animals. More recently, the *Asparagopsis* **seaweed** has been shown to reduce methane production very effectively. Some **ionophore** antibiotics (e.g. monensin) will reduce methane production by allowing those bacteria that produce **propionic acid** to proliferate; but sheep are susceptible to ionophore **poisoning**. Many of the methods in this category require that grazing animals are fed a **supplement**, which they must eat in controlled amounts.

Vaccinate animals against rumen methanogens (this technique has not yet been developed for practical use).

Although there are these different options, the mitigation of the methane cost of ruminant animal products is difficult, especially with extensively grazing animals. Further, there is a cost associated

with methane control, which may not able to be recovered at point of sale. This is a case where the producer, rather than the consumer, bears the GHG cost. (GMcLD)

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IPCC (2006) *2006 IPCC Guidelines for National Greenhouse Gas Inventories* (eds Eggelston, S., Buendia, L., Miwa, K., Ngara, T. and Tanabe, K.). *Chapter 10. Emissions from livestock and manure management*. Published for IPCC (Intergovernmental Panel on Climate Change) by IGES (Institute for Global Environmental Strategies). Available at https://www.ipcc-nggip.iges.or.jp/public/2006gl/pdf/4_Volume4/V4_10_Ch10_Livestock.pdf

Jonker, A., Green, P., Waghorn, G., van der Weerden, T., Pacheco, D. and de Klein, C. (2020) A meta-analysis comparing four measurement methods to determine the relationship between methane emissions and dry-matter intake in New Zealand dairy cattle. *Animal Production Science* 60, 96–101.

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Methanogenesis

The production of **methane**. Methane is produced by the action of methanogens, a group of Archaea that oxidize **hydrogen** as a source of electrons for **carbon dioxide** reduction via the reaction

$CO_2 + 4H_2 \rightarrow CH_4 + 2H_2O$. Methanogenesis is important as a means of electron disposal from anaerobic **fermentation**s, notably those in the **rumen** and intestines. This process allows for the **oxidation** of reduced electron carriers (NADH + H^+, NADPH + H^+ and $FADH_2$) so that catabolic, oxidative degradation of **substrates** can continue. Hydrogenase enables electrons from the fermentative bacteria and **protozoa** to be released in the form of hydrogen, and oxidized electron carriers to be regenerated. If hydrogen consumption is disrupted, hydrogen accumulates, hydrogenase is inhibited, catabolic reactions are impeded, substrate degradation is impaired, and atypical reduced products such as **lactate** and **ethanol** accumulate. Additional substrates for methanogenesis in digestive tract fermentations are formate and **methylamine**. Methane production constitutes a loss of **digestible energy** which could otherwise be channelled into **volatile fatty acid** production and used by the host animal. In order to retain normal digestive attributes of gut microbes while suppressing **energy** loss as methane, an alternative means of electron disposal must be available to the fermentative microbes. Examples of alternative electron disposal pathways are reduction of **nitrate** to **ammonia**, fumarate to **succinate**, and of CO_2 to **acetate**. Methane is also produced from complete decomposition of the **organic matter** of animal excreta when held anaerobically for residence times of 4 days or longer. Under these conditions, bacteria thrive that are capable of oxidizing volatile fatty acids to acetic acid, hydrogen and CO_2. The methanogens involved have a species composition different from that of the gut. (DMS)

Methanotroph
An organism that grows on **methane**, which serves as an electron donor and sole carbon source for cell biomass synthesis. Methanotrophs are found in microaerobic environments of soil and water. A key **enzyme** in these organisms is methane monooxygenase which catalyses the introduction of **oxygen** into methane, resulting in methanol formation. (DMS)

Methionine
An essential amino acid ($H_3C{\cdot}S{\cdot}(CH_2)_2{\cdot}CH{\cdot}NH_2{\cdot}COOH$, molecular weight 149.2) found in protein. Methionine is a **sulphur**-containing amino acid that is often deficient in diets for animals, particularly poultry. Among the cereal **grain**s, only **maize** is considered a good source of **sulphur amino acids** (methionine + **cysteine**). **Soybean** meal is first-limiting in sulphur amino acids for **growth** of poultry and pigs.

Methionine reacts with ATP to form ***S*-adenosylmethionine** (SAM), the most important methylating compound in the body, facilitating the biosynthesis of up to 100 different methyl-containing body compounds such as **creatine**, phosphatidyl **choline** and **epinephrine**. The **polyamine**s, spermine and spermidine, also require SAM for their synthesis.

The main catabolic pathway for methionine involves *trans*-sulphuration of methionine to **cysteine**, but only the sulphur moiety of cysteine is derived from methionine. The carbon skeleton of cysteine is derived from **serine**.

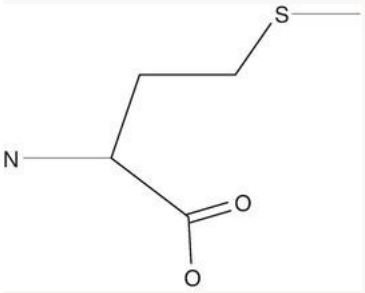
Body **protein synthesis** requires both methionine and cysteine, and each compound is required in approximately equal

portions for growth. Cysteine, however, dominates the total sulphur amino acid requirements for adult **maintenance**. Methionine can satisfy the physiological requirement for both methionine and cysteine because methionine sulphur can be converted (irreversibly) to cysteine sulphur with 100% molar efficiency. Nonetheless, diets for animals are generally formulated in practice on a weight or concentration basis rather than on a molar basis. Thus, because of the molecular weight difference between methionine and cysteine, methionine on a weight or concentration basis is about 81% efficient in yielding cysteine metabolically.

Methionine is one of the few amino acids produced commercially by chemical synthesis (as opposed to **fermentation** or chemical extraction). Chemical synthesis results in the mixed DL-**isomer** of methionine. With the exception of primates, the D-isomer of methionine is used by animals almost as efficiently as the L-isomer. The DL-hydroxy analogue of methionine is also an important commercial product. This precursor of methionine can be converted to L-methionine in a two-step metabolic process.

Conventional acid **hydrolysis** procedures used to determine the amino acid concentrations in a protein result in partial destruction of methionine and cysteine. Therefore, to obtain accurate analytical estimates of methionine and cysteine concentrations in a protein, the **sample** must be pre-oxidized using performic acid. This converts methionine to methionine sulphone and cysteine to cysteic acid. Then, HCl hydrolysis of the pre-oxidized sample allows accurate quantification of methionine

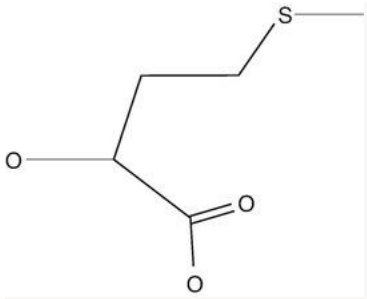
and cysteine in the protein. (DHB)



See also: Essential amino acids; Methionine hydroxy analogue

Methionine hydroxy analogue

The hydroxy analogue of methionine, 2-hydroxy-4-(methylthio) butanoic acid (hydroxymethylbutyrate) (HMB) is a chemically synthesized precursor ($H_3C{\cdot}S{\cdot}(CH_2)_2{\cdot}CH{\cdot}OH{\cdot}COOH$, molecular weight 149.2) of methionine that contains a hydroxyl radical on the α carbon rather than an amino group. It is available commercially as the liquid free acid (88% DL-OH-Met) or the **calcium salt** (86% DL-OH-Met). It is metabolized in the body to L-methionine in a two-step reaction sequence. On an isomolar basis, DL-OH-Met is thought to be somewhat lower in biological activity than L-methionine. This biological efficiency of HMB has been studied in several farmed species and when compared in efficiency to DL-Met, the latter is about 25% more efficient in poultry and fish, on an equimolar basis, probably because of increased **absorption**. (DHB; QS)



See also: Methionine

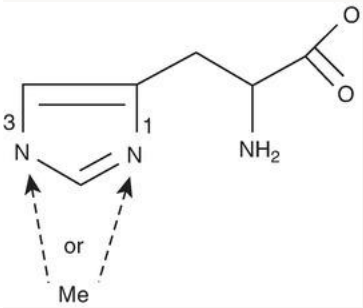
Methylamine
A gas ($CH_3 \cdot NH_2$) with a strong ammoniacal odour. (NJB)

Methylation
The process whereby a methyl group (CH_3-) is added to a recipient molecule. The methyl group donor is usually ***S*-adenosylmethionine** (AdoMet), which is the source of the methyl group for more than 50 reactions. Two other **metabolite**s are involved in single methylations and both are related to the conversion of **homocysteine** to **methionine**. **Betaine** is the methyl source when homocysteine is converted to methionine by betaine homocysteine methyltransferase. The other methyl source is *N*5-Methyltetrahydrofolate, which is also involved in the methylation of homocysteine by the enzyme *N*5-Methyltetrahydrofolate homocysteine methyltransferase. (NJB)

Methylhistidine
Histidine that is methylated in either the 1 or 3 position. 3-Methylhistidine (also referred to as N^{τ}-methylhistidine) is formed by **methylation** of **histidine** by ***S*-adenosylmethionine** after it is incorporated into **protein**. Once released from a protein it

cannot be reincorporated into protein. In those species in which it is quantitatively excreted in **urine**, it can be used as an **indicator** of protein **catabolism**. Because three-quarters of 3-methylhistidine in the body is in **muscle** (skin is also a source) it is used as an indicator of muscle breakdown. In human, rat and chicken, 3-methylhistidine is not catabolized and is quantitatively excreted in urine; it has been used as an indicator of muscle protein breakdown. However, in pigs, cattle, sheep, dairy goats, dogs and cats it is either catabolized or metabolized to **balenine** and not quantitatively recovered in urine.

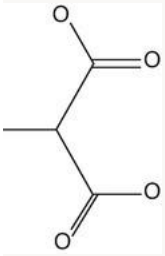
1-Methylhistidine is also found in urine. It is the result of the methylation of free histidine and is not an indicator of protein catabolism. (NJB)



Methyllysine:
see Trimethyllysine

Methylmalonic acid
Molecular structure HOOC·CH(·CH_3)·COOH (molecular weight 118.07), an intermediate in the conversion of **propionate**, via propionyl-CoA, to **succinate** (an intermediate in the TCA cycle). Propionyl-CoA is carboxylated (CO_2 is added) by the **biotin**-dependent **enzyme**, propionyl-CoA **carboxylase**, to form D-

methylmalonate, which is converted to succinyl-CoA and then to succinate, which is used for **energy**. (NJB)



5-Methyltetrahydrofolate
The major one-carbon intermediate in the folic acid one-carbon system. This intermediate is critical to **homocysteine metabolism** because **methylation** of homocysteine creates **methionine** and produces free **tetrahydrofolate**, which is required for **folate**-dependent one-carbon metabolism. Homocysteine methylation is also dependent on **vitamin** B_{12}. A deficiency of vitamin B_{12} results in a significant increase in 5-methyltetrahydrofolate because of decreased methylation of homocysteine. This leads to a measurable increase in **blood** homocysteine and a deficiency of tetrahydrofolate. This metabolic situation is described as the 'methyl trap'. (NJB)

Micro diet
Pelleted fish food with diameter of tens to hundreds of microns. Usually coated with a biodegradable polymer, such as **gelatin** or **zein**. (RHP)

Microbial ecology:
see Gastrointestinal microflora

Microbial flora, intestinal:
see Gastrointestinal microflora

Microbial protein
The protein of microbial cells, including those of archaea, bacteria, protozoa, fungi and yeasts. Microbial protein produced in the **rumen** and **reticulum** is the principal source of **amino acid**s for ruminants and it has a good balance of essential amino acids. Most classes of ruminant livestock can meet their total requirement for **metabolizable protein** from the supply of microbial **true protein** alone. The exceptions are high-yielding dairy cows and wool-producing sheep. These animals may require supplementary digestible undegraded feed protein to meet their requirement for metabolizable protein: they may also need supplementary essential amino acids such as **methionine** and **lysine**. Much of the dietary protein eaten by the animal is degraded to **ammonia** by the microbial population of the rumen and it is therefore possible to include **non-protein nitrogen** substances, such as **urea**, in diets that are deficient in degradable protein. Such deficiencies might arise when the dietary ingredients, such as **straw** or **maize silage**, are low in total protein, or where the degradability of the feed protein is relatively low, perhaps as a result of **heat treatment** during processing.

The production of microbial protein in the rumen depends on the supply of degradable protein and fermentable energy (*see* Metabolizable protein). Degraded protein is not used with complete efficiency for microbial protein synthesis, because some (the quickly degraded fraction) is converted to ammonia, which is

absorbed through the rumen wall and converted to urea in the liver. About 20% of the quickly degraded protein is lost from the rumen. The remainder is potentially available to the rumen microbial population. This is known as the effective rumen degradable protein (ERDP) and is the amount of protein (or **nitrogen**) available for microbial growth and **metabolism**. The amount of ERDP that the microbial population can utilize depends on the amount of energy available: the fermentable **metabolizable energy** (FME). Some sources of energy are considered to be of low value to the microbes, particularly those that yield low levels of ATP during their **digestion** in the rumen. In the calculation of the FME the energy of **lipids**, **organic acid**s and undegraded protein is subtracted from the total metabolizable energy. The yield of microbial **crude protein** (MCP) per **megajoule** of FME depends on the **animal production level** (APL), because at lower APL the outflow rate from the rumen is reduced and at the lower outflow rate bacteria and protozoa die before passing out of the rumen and are digested by other rumen microbes. Their protein is recycled to produce new microbial protein. However, this process requires energy and so additional FME is utilized with no net increase in yield of microbial protein. The limit to the total yield of MCP is determined either by ERDP or by FME. If set by ERDP, MCP production equals the supply of ERDP; if set by FME, MCP production equals the FME multiplied by Y (the yield of MCP MJ^{-1} FME). This quantity ranges from 8 g MCP MJ^{-1} FME at an APL of 1.0, to 11.5 at an APL of 4.0. The lesser of the two calculated values of MCP is taken. This value is

then reduced to take account of the fact that about 75% of MCP is true protein and that it is absorbed into the **blood** with an efficiency of about 85%. Thus microbial true protein supply is only about 64% of the MCP produced. (JMW; GMcLD)

Micronutrients
Nutrients required in low dietary concentrations (ng, μg or mg kg^{-1}). Nutrients that fall into this category are **vitamins** and **minerals**. Using the pig as an example, **copper**, **iron**, **manganese**, **zinc** and all of the vitamins with the exception of vitamin B_{12} are required in mg kg^{-1} diet, whereas **iodine**, **molybdenum**, **selenium** and vitamin B_{12} are required in μg kg^{-1} diet. (NJB)

Microorganisms
Small living animal or plant organisms capable of **reproduction**. They can be seen only with the aid of an optical or electron microscope. They include single cells such as **algae**, **yeast**, **fungi**, bacteria or **protozoa**. (NJB)

Microvillus
A submicroscopic finger-like projection of the apical membrane (that which faces the lumen) of the epithelial cells of the **villi**, which are themselves finger-like projections of the epithelial cell layer of the **small intestine**. A large number of closely packed microvilli create a brush-like surface, called the **brush border**, on the surface of the villus. Microvilli are also found in the renal tubules. The structure of villi and microvilli increases 100-fold the

luminal surface of the intestine. (SB)

Microwave treatment:
see Heat treatment

Middlings:
see Milling by-products

Milk
A highly nutritious liquid produced by female mammals for the sustenance of their young offspring. It is one of the few natural foods that can meet the total nutritional needs of humans. Dairy products are a major source of **calcium** and high-quality **protein** in the human diet. Although **fats** from dairy products have had a negative image since the 1980s, recent studies have shown that **fatty acid**s in milk (especially conjugated **linoleic acid**) can play a significant role in reducing the incidence of cancer, **diabetes** and **atherosclerosis**, as well as partitioning **energy** away from **body fat** towards **muscle** tissue (Bauman *et al*., 2001).

The major constituent of milk is water. Dissolved in the water are **lactose**, **albumin** and **water-soluble vitamins**, **minerals** and nitrogenous substances. Colloids of **casein**, calcium and **phosphorus** are suspended in the water, as are minute fat globules. Most of the constituents of milk are synthesized in the **mammary gland** from precursors absorbed from the **blood**.

Apart from water, the main constituents of milk are **butterfat**, protein and lactose. The proportions of these components vary between species (see table) and breeds, and are influenced by the

stage of **lactation** and type of food.

Butterfat, protein and lactose contents (%) of milk from different species.

	Butterfat	**Protein**	**Lactose**
Cattle	3.9	3.4	4.8
Goat	4.5	3.3	4.1
Sheep	7.4	5.5	4.8
Pig	8.5	5.8	4.8

Butterfat consists of triglycerides that are synthesized in the mammary gland from glycerol and a mixture of fatty acids ranging in carbon numbers from 4 to 22 in ruminants and 10 to 22 in non-ruminants. Shorter-chain fatty acids (up to 16 carbon atoms) are synthesized in the mammary gland from acetic acid (and β-hydroxy **butyrate** in ruminants); longer-chain fatty acids are absorbed from the bloodstream for direct incorporation into milk triglycerides. In non-ruminants, **acetate** is synthesized from **glucose** in the mammary gland; in ruminants, acetate is absorbed from the bloodstream.

The protein fraction of milk comprises 80% casein, which is synthesized in the mammary gland from **amino acid**s absorbed from the bloodstream. The remaining proteins are β-**lactoglobulin** and α-lactalbumin, which are synthesized in the mammary gland, and serum albumin and immune globulins, which are absorbed from the bloodstream.

Lactose, the only **carbohydrate** present in milk, is a

disaccharide made from glucose and **galactose**, both of which are derived from glucose absorbed from the bloodstream. Lactose is the major osmotic component of milk and so its concentration varies much less than those of fat and protein. If an animal has insufficient glucose for its potential lactose synthesis, it will reduce milk yield rather than produce milk with a low lactose concentration.

Annual milk yields are 4000–12,000 l in dairy cows, 600–1100 l in goats and 200–700 l in sheep. The principal determinants of annual milk yield are genetic merit of an animal and overall **plane of nutrition**. Daily milk yield is affected by genetic merit, stage of lactation, milking frequency, supply of nutrients and state of body reserves. Generally, **energy intake** is the main factor limiting milk yield; energy and **protein source**s affect milk composition. In early lactation, provided that dietary protein supply is sufficient, animals will mobilize body fat reserves in support of milk production.

Fibrous sources of energy tend to increase the butterfat content of milk because cellulolytic bacteria in the **rumen** produce mainly acetate, which is a precursor for **fatty acid synthesis** in the **mammary gland**. **Starch** increases **propionate** production in the rumen by amylolytic bacteria. Propionate is the main precursor for glucose production, which directly influences milk yield, through the requirement for glucose as a general **energy source** and as a precursor for lactose synthesis. Glucose indirectly influences milk yield through the effects on circulating plasma **insulin** levels, which control the partition of energy between body

fat and milk synthesis. Glucose also influences milk protein concentration indirectly. Essential and **non-essential amino acid**s are required for milk **protein synthesis** in the mammary gland. Amino acids are also utilized for **gluconeogenesis** if propionate supply is inadequate. Therefore, increased propionate supply can lead to higher blood glucose concentrations, sparing amino acids from gluconeogenesis and thereby increasing milk protein content.

Dietary fat is used as a concentrated energy source for milk production and also has a direct effect on the butterfat content of milk. However, if dietary fat content exceeds 60 g kg^{-1} dry matter (DM), **rumen digestion** of fibre can be disrupted through the physical and detergent effects of **long-chain fatty acid**s on fibre particles and **rumen microorganism**s, respectively. This problem can be overcome by feeding the fatty acids in a protected form as calcium **salts**, as small particles with a high melting point, or encapsulated in **formaldehyde**-treated casein. Dietary fat tends have a negative effect on milk protein concentration by increasing milk yield (thereby diluting milk protein), decreasing fermentable energy intake and increasing the **glucose** requirement for **absorption** of fatty acids from the gut (Garnsworthy, 1997).

In non-ruminants, milk yield is determined by **genotype**, age, **litter size**, body reserves and nutrition. Energy intake has a direct effect on milk yield in sows and protein supply influences milk protein content, since the diet is the only source of essential amino acids in non-ruminants. (PCG)

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Garnsworthy, P.C. (1997) Fats in dairy cow diets. In: Garnsworthy, P.C. and Wiseman, J. (eds) *Recent Advances in Animal Nutrition – 1997*. Nottingham University Press, Nottingham, pp. 87–104.

Milk fever

An acute hypocalcaemic condition of dairy cows and goats associated with the onset of **lactation**. **Blood calcium** concentration, normally maintained at 2–2.5 mM, falls below 1.5 mM, impairing nerve and **muscle** function and resulting in recumbency and inability to stand. Affected animals must be treated to increase blood calcium concentration (usually by intravenous calcium administration) to prevent death. Milk fever occurs because the homeostatic mechanisms that normally maintain blood calcium concentration fail. There are two major nutritional factors that increase the susceptibility to milk fever. Metabolic **alkalosis**, caused by diets that are high in **potassium** or **sodium**, interferes with the function of **parathyroid hormone** (which regulates calcium) in target tissues, preventing adequate calcium **homeostasis**. Addition of anions (**chloride**, **sulphate**) to the diet can counteract the alkalinizing effects of potassium and sodium and help to reduce the incidence of milk fever. **Hypomagnesaemia**, caused by inadequate dietary **magnesium** or interference with **rumen** magnesium absorption,

can also interfere with parathyroid hormone secretion and function. (JPG)

See also: Lactation disorders

Further reading

Blowey, R.W. (2016) *The Veterinary Book for Dairy Farmers*, 4th edn. 5M Publishing, Great Easton, Essex, UK.

Milk products:

see Dairy products

Milk substitute

Artificial milk, usually in powder form, that is reconstituted with water before use, designed to replace mother's milk in a young animal before **weaning**.

Many animal production systems require young animals to be artificially reared. For example, calves are removed from dairy cows within 24 h of birth so that milk can be used for human consumption; piglets may be weaned early so that the sow can be bred again; orphaned lambs often need to be reared artificially because it is very difficult to make ewes **suckle** lambs that are not their own.

The quality of a milk substitute depends on its ability to mimic natural milk, both chemically and physically. The newborn or young animal's **digestive system** is designed to digest milk and so any substantial deviation from natural milk constituents can cause digestive upsets. Of particular importance is **casein**, which has the ability to clot under the action of **rennin** and **pepsin**. Once clotted, milk is slowly digested in the **stomach** and **small**

intestine. If a suitable clot does not develop, milk passes rapidly to the hindgut, where it ferments and causes **diarrhoea**. For this reason, the best (and most expensive) milk substitutes are based on skimmed milk.

Skimmed milk is a **by-product** of cream and butter manufacture. The **butterfat** can be replaced by vegetable **oils**, which need to be dispersed throughout the milk substitute by an **emulsifier**. Milk substitutes based on **whey**, a by-product of cheese manufacture, plus vegetable oils and animal or vegetable proteins, historically led to poorer animal performance due to digestive upsets. Recently, the use of whey proteins, concentrated by ultrafiltration, has led to performances comparable with skim-based milk substitutes. This is because concentrated whey proteins have a very high immunoglobulin content, which helps to boost the immune system, as well as being highly digestible. Some milk substitutes have added **organic acid**s to improve keeping quality and allow them to be fed cold. (PCG)

Milk thistle (*Silybum marianum*)

A biennial plant with thick roots and branched stems, height 0.8–1.5 m. The flowers of this plant are pink or purple, with a wide bayonet appendage. The seeds are inside the capitulum of the flowers, brown in colour, and are the size of **wheat**. Milk thistle grows in barren lands and around agricultural lands and roads as a dominant plant in many parts of Europe and Asia. It has very low needs for water and high resistance to severe environmental stresses, such as cold and sudden heat. In the northern hemisphere, seeds can be sown in the month of August after

ploughing and discing barren lands (such as wheat) and in the month of June of the following year, without the need for irrigation. Milk thistle can be harvested by a wheat harvesting machine combine. The extracted flavonoids and the active constituents of the thistle plant are silymarin (4–6%). The extracts of milk thistle seeds contain 65–80% silymarin and 20–35% **fatty acid**s (including **linoleic acid**, **oleic acid**, **palmitic acid**), as well as plant **sterols** campesterol and stigmasterol, **amine**s, **saponin**s and **glucose sugars**. Silymarin is a combination of phenolic molecules, including seven types of **flavonolignan**s (silybin type A, silybin type B, isoslybin type A, isosilybin type B, silychristin, isosilychristin and silydianin) and a **flavonoid** called taxifolin. Milk thistle leaves contain the flavonoids apigenin, luteolin, kaempferol, **glucosides**, and beta-sitosterol (Morazzoni and Bombardelli, 1995; Scott Luper, 1998; Zaker-Esteghamati *et al*., 2020; Porwal *et al*., 2019).



Milk thistle flower. Photo courtesy of Mark Gunn. Licensed under CC BY 2.0.

Milk thistle can play a significant role in improving the **antioxidant** activity of the **blood**, protecting the liver from pollution, reducing many types of cancers caused by

malnutrition and unhealthy air, increasing blood haemoglobin concentration to supply **oxygen** to tissues, repairing damaged tissues, preventing the formation of **free radical**s in the body, reducing a variety of adverse effects of toxins such as **aflatoxin**, and potentially strengthening the immune system of humans and domestic animals (Porwal *et al*., 2019; Khazaei *et al*., 2022; Feshanghchi *et al*., 2022). (AS; BH-G; CJCP)

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Milkfish (*Chanos chanos*)

The only known species of the family Chanidae, widely distributed throughout the tropical and subtropical regions of the Indian and Pacific Oceans. Milkfish are euryhaline and survive in salinity of 0–50 parts per 1000. They are a popular cultured species in the tropics because of their fast growth, herbivorous food habits and tolerance of a wide range of environmental conditions. Milkfish have been cultured extensively in freshwater pens as well as **brackish-water** ponds. Milkfish farming is believed to have begun in Indonesia some 700 years ago and was introduced to the Philippines and Taiwan.



Milkfish cage culture in Southeast Asia. Photo courtesy of Southeast Asian Fisheries Development Centre. Licensed under CC BY-NC-SA 2.0.

Milkfish find their food mainly by vision rather than chemosensory mechanisms. In natural habitats they feed on benthic, epiphytic and planktonic organisms but in culture ponds they depend on two types of natural foods, locally known in the Philippines as *lablab* (cyanobacterial mat) and *lumut* (filamentous green **algae**). In recent years, research has been carried out to develop artificial diets for milkfish**.** The optimum dietary protein for maximum growth, feed efficiency and survival has been reported to be about 40% by dry weight. In semi-intensive pond culture systems, commercial diets with 23–27% **crude protein** are thought to be sufficient for satisfactory growth. Milkfish do not tolerate high levels of dietary **lipid** and 7–10% by dry weight has been reported to be the optimum. They benefit from multiple daily feedings and are reported to gain weight 20% faster when feeding frequency is increased from four to eight times daily. The global total production yield of milkfish was about 1.33 million tonnes in 2018. (RMG; QS).

Millets

A group of small-seeded, annual cereal **grasses**, many of which are adapted to hot, **drought**-prone arid climates. Millets are the most drought-tolerant of all **cereal**s, more so than **sorghum**. They display the lowest water requirement of all cereals, are pest resistant and grow well without the application of fertilizers or other inputs. There are 14 known species of millets. Of these, pearl

millet (*Pennisetum typhoides*), finger millet (*Eleusine coracana*), proso millet (*Panicum miliaceum*) and foxtail millet (*Setaria italica*) are most important; other types of regional significance include kodo (*Paspalum scorbiclatum*), little (*Panicum sumatrense*), barnyard (*Echinochloa crusgalli*) and fonio (*Digitaria exilis*) millets. Kernels of millets show considerable diversity in seed colour, size and shape. The most widely grown species is pearl millet, which is an important crop in India, parts of Africa and the USA. It is the tallest millet and has the largest **grain**. Pearl millet ranks sixth in the world's cereal production and the area under cultivation is on the increase. Most of the world's millet production is in India, Nigeria, Niger, Mali, Burkina Faso, Chad and China.



Millet, a valuable source of protein for human nutrition (Japanese Foxtail variety). Photo courtesy of Stronglk7. Licensed under CC BY-SA 3.0.

Cultivars that can be used for both **forage** and grain production are popular among small farmers and allow greater flexibility in choosing when to harvest in relation to grain and **fodder** value.

The grain:crop residue ratio in most millets is around 1:4 and the economic value of such multipurpose use can be observed in India, where as much as half the income may come from crop residues. In the USA, pearl millet is used as a fresh forage, **silage**, or **hay**. The **feed** value to ruminants is limited by the high proportion of cell walls in relation to other tissues. The cell walls are high in **lignin** and related **phenolic compound**s adversely influencing the utilization of cell-wall **carbohydrates**.

Like other cereals, millet seeds are predominantly **starch**. The millets generally contain less **metabolizable energy** than **maize** for poultry but more protein. In particular, the **crude protein** content of pearl millet (145 g kg^{-1}), which is high for a non-leguminous seed, is noteworthy. Another characteristic feature is that millets are relatively rich in **iron** and **phosphorus**. Finger millet has the highest **calcium** content among all cereals. The feeding value of pearl millet is superior or similar to those of **sorghum**, **wheat** and **barley**, but inferior to that of maize. However, pearl millet when used as an **energy source** in balanced poultry diets can completely replace maize.

Composition of the four main millets, in comparison with maize (g kg^{-1} dry matter basis)

Species	**CP**	**EE**	**CF**	**Ash**	**Ca**	**P**	**AME (**MJ kg^{-1})
Maize	90	40	25	15	0.2	2.5	15.0

Species	CP	EE	CF	Ash	Ca	P	AME (MJ kg^{-1})
Pearl millet	140	45	25	20	0.5	3.0	13.8
Finger millet	90	20	35	30	4.0	3.0	12.6
Proso millet	130	35	60	35	0.7	2.5	11.5
Foxtail millet	120	40	70	30	0.4	3.0	13.0

CP, crude protein; EE, ether extract; CF, crude fibre; Ca, calcium; P, phosphorus; AME, apparent metabolizable energy

The relatively high fibre content, along with the coarseness of the seeds and the presence in the hull of high level of **tannins**, detracts from the usefulness of other millet types as feed ingredients for poultry. The feeding value of finger millet is lower than that of pearl millet, owing to the presence of high levels of tannin. In general, these minor millets can replace maize at levels ranging from 200 to 400 g kg^{-1} in balanced diets. Higher inclusion levels must be avoided because of their coarseness and tannin contents. When millets are used in poultry diets, it is recommended that they be ground, pelleted and fed in combination with maize rather than alone.

Utilization of millet grains as animal feeds is currently negligible compared with other cereals. It has been estimated that less than 10% of global production is fed to animals. (VR)

Further reading

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Milling

The process of grinding, **crushing** or pressing in a mill to comminute a material into particles of various sizes. It is an important process in both feed and food manufacturing industries, extensively used in the conversion of whole cereal **grain**s and seeds to their various derivatives (e.g. **wheat** into **flour**). (ED)

Milling by-products

When **cereal**s, especially **wheat**, are milled to produce **flour**, the coarse fractions are separated and are often used for animal feeding. The composition of these materials varies according to the way the milling fractions are combined. **Bran** consists mainly of the **testa**, **pericarp** and **aleurone** layers of the **grain**. Wheat feed, also called millers' offals, middlings or pollards, consists of fine bran particles and aleurone with some **endosperm**. (MFF)

Mimosine

A toxic **amino acid** from ***Leucaena*** *leucocephala*. In non-ruminants, mimosine causes poor growth, loss of hair, **cataract**s in

the eyes and reproductive problems. Levels of *Leucaena* meal at 5–10% of the diet result in poor performance in pigs, poultry and rabbits. Ruminants grazing *Leucaena* may show poor growth, loss of hair, **lameness**, lesions in the mouth and oesophageal and reproductive problems. In continental USA and Australia, consumption of *Leucaena* by ruminants causes the problems described above, but in Hawaii and Indonesia cattle and goats can consume *Leucaena* with impunity. Transfer of **rumen fluid** from animals in Hawaii and Indonesia to Australian ruminants resulted in a complete elimination of the toxic effects and better utilization of this high-protein (25–35% **crude protein**) **forage**. The effects of mimosine on non-ruminants can be reduced by **supplementation** of the diet with ferrous **sulphate** or mineral supplements containing **zinc**. (KEP)

Mineral

Inorganic substance. A number of inorganic elements are essential nutrients. They include **calcium**, **phosphorus**, **sodium**, **chloride**, **potassium**, **iron**, **zinc**, **magnesium**, **manganese**, **sulphur**, **copper**, **iodine** and **cobalt**. All of these have known metabolic functions and requirements have been estimated for each of them, though not in all species. Other mineral elements are also known to have metabolic roles but no requirement has been established. These include **selenium**, **molybdenum** and **chromium**. For some other minerals – **nickel**, **boron**, **lithium**, **fluorine** and **vanadium** – there is no known metabolic function but there is some evidence of their beneficial role. Of those mineral elements considered essential nutrients, those for which the

requirement is > 1 mg kg^{-1} diet are called macrominerals and those for which the requirement is < 1 mg kg^{-1} are called **trace element**s. Those for which no requirement is known, but which are thought to be required in very small amounts, are called **ultra-trace element**s. (PGR)

Mineral and vitamin supplements

All farm animals need a wide range of minerals and vitamins to maintain health and productivity. Mineral and vitamin supplements are formulated for inclusion in the concentrate feed so that the mineral and vitamin requirements of the particular species will be met when the animal consumes normal amounts of the feed. (KJMcC)

Mineral deficiencies

Certain minerals (macrominerals) are required in large amounts (g kg^{-1} diet). Others (trace minerals) are required in minor amounts (mg kg^{-1} diet). While not comprehensive, the clinical signs associated with dietary deficiency of these minerals are outlined in the table. (JPG)

Clinical signs of mineral deficiencies

Mineral	Dietary deficiency symptoms
Macrominerals	

Mineral	Dietary deficiency symptoms
Calcium	Bone disease – osteoporosis (adult), rickets (young); hypocalcaemia – tetany, paresis, abnormal blood clotting, reduced eggshell thickness
Phosphorus	Bone disease – osteomalacia (adults), rickets (young); impaired growth and feed intake, appetite for unusual items (pica)
Magnesium	Impaired neuromuscular activity, tetany, impaired growth, low milk production, urinary calculi; reduced eggshell thickness and hatchability
Sodium	Depressed growth, depressed milk or egg production, pica, reduced milk fat concentration in ruminants
Chloride	Depressed growth, depressed milk or egg production, pica, decreased plasma volume

Mineral	Dietary deficiency symptoms
Potassium	Reduced feed and water intake, impaired growth, muscle weakness; rapid decline in milk production; sudden death in poultry
Sulphur (ruminants only)	Reduced production of microbial protein within rumen, leading to impaired growth or milk production
Trace minerals	
Chromium	Impairment of glucose tolerance, reproduction and immune response
Cobalt (ruminants only)	(Used by rumen microbes to produce vitamin B_{12} vital for efficient use of propionate.) Reduced growth and productivity

Mineral	Dietary deficiency symptoms
Copper	Anaemia, rough hair coat with fading colours due to inability to make melanin, impaired immune responses; defective collagen synthesis leading to impaired bone growth, osteochondrosis, stillbirths, neonatal ataxia and swayback and, in birds, aortic rupture
Iodine	Inability to make thyroid hormones; goitre; reduced growth, reproduction, milk production and cold tolerance
Iron	Anaemia, reduced growth, intolerance of exercise, reduced immune response
Manganese	Reduced reproductive efficiency, anoestrus; skeletal abnormalities and reduced growth in length of bones, perosis and slipped tendons in birds

Mineral	Dietary deficiency symptoms
Selenium	Degeneration of skeletal muscle, ‘white muscle disease’ and cardiac muscle ‘mulberry heart disease’, leading to muscle weakness and heart failure; impaired immune responses; retained placenta in cattle; infertility in many species
Zinc	Impaired keratin production resulting in rough hair coat, dermatitis (parakeratosis in swine), weak hooves, poor feathering; impaired immune response (lack of thymus development); impaired wound healing; reduced growth; short, thick bones; testicular hypoplasia

Mineral supplements

All farm animals need a wide range of minerals in the feed to provide a balanced diet and these are not normally available in adequate quantities in the ingredients used to formulate diets. Mineral supplements are formulated to meet the shortfall by

mixing together appropriate proportions of mineral **salts**. These may be provided as 'licks' to which the animals (usually ruminants) have free access. More often they are added to the concentrate feed during mixing, thus ensuring uniform intake by the animals. (KJMcC)

Minimal metabolism

There is no standard condition at which a minimal **metabolic rate** can be both defined and accurately measured for animals. Discounting exceptional conditions, such as hibernation and prolonged **starvation**, minimal metabolic rates are attained only after complete **digestion** of the last meal (and this takes longer than 24 h in ruminants) and whilst the animal is lying down. The conditions cannot be enforced on animals for long enough for measurement of **fasting metabolism**. What is usually measured is the resting **metabolism** of an animal provided with a **maintenance** diet. When this measurement is made continuously over a long period combined with observation of the animal's behaviour, it is possible to select periods when the animal is lying down and determine its least observable metabolic rate. All of the above have been used from time to time as estimates of basal metabolic rate, which is used as the reference level for interspecies comparisons and from which to assess metabolic increases caused by activity, feeding, **thermoregulation**, etc. (JAMcL)

See also: Basal metabolism

Mobile nylon bag technique:

see Digestion; *In sacco*

Models:
see Growth models; Simulation models

Moisture:
see Dry matter

Moisture content, determination:
see Dry matter

Molasses
A thick treacly liquid, a **by-product** of **sugar** production from both **sugarcane** and **sugarbeet**. (MFF)

Mollusc
Molluscs have been used as food in subsistence economies since before recorded history and are extensively fished by traditional **harvesting** methods. They are also cultivated by a variety of technologies ranging from simple capture of juveniles for on-growing in ponds or lagoons, to elaborate procedures involving hatcheries, nurseries and complex grow-out and harvesting systems.

They have a wide diversity of life forms ranging from the free-ranging and sometimes migratory squids and cuttlefishes, with their internal shells, through the filter-feeding double-shelled bivalves, to the single-shelled snail-like gastropods. Others, such as the nudibranchs, have internal shells and external gills. They occupy all the oceans from polar seas to the tropics and are also common in **fresh water**. Some of the gastropods are wholly terrestrial. Their feeding habits range from filter feeding,

browsing on marine **algae** and epiphytes, to aggressive predation.

Total recorded landings of molluscs from all sources, wild and cultivated, in 2018 were 17.7 million tonnes (FAO, 2020), most of which were cultivated. The majority of these cultivated **shellfish** were oysters (principally the Pacific oyster, *Crassostrea gigas*), with much smaller amounts of clams, cockles, mussels and **scallops**. Many of these groups were also harvested in capture fisheries but by far the majority were cultivated. The most important group in the capture fisheries are cephalopods (squids, octopus, cuttlefish) with 3.6 million tonnes landed in 2018. Very few of this group are cultivated. By far the majority of molluscs are grown or fished in marine waters. Freshwater landings account for barely 450,000 tonnes and few of these are cultivated.

Some molluscs may be eaten alive and raw; oysters particularly are considered a delicacy and support a valuable 'half-shell' trade, but mussels, clams and scallops may also be eaten this way. This practice requires careful attention to the cleanliness of the water in which they are grown to ensure that the shellfish are wholesome, and also to their storage and transport to ensure that quality remains high and there is no spoilage. Some may be cooked and dried; others are canned. Where distribution systems allow, many species are simply sold raw for preparation in traditional dishes.

Besides being used directly as human food, some species (e.g. the squids) are used as bait in other capture fisheries and so contribute to the fisheries economy in a different way. Some are rendered as meal. An interesting and profitable non-food use is the

culture of pearl oysters for both pearls and mother-of-pearl. (DJS; CJCP)

Reference

FAO (2020) *The State of World Fisheries and Aquaculture 2020. Sustainability in Action*. Food and Agriculture Organization, Rome. doi: 10.4060/ca9229en

Mollusc culture

Molluscs are arguably the most important animal phylum for **aquaculture** production from marine and **brackish water**s. Over 80% of marine aquaculture production is accounted for by filter-feeding **shellfish**, the majority of which are bivalve molluscs such as oysters, mussels, clams and cockles. Their culture extends back several thousand years and it is difficult with some species to know whether they are in fact wild or cultivated. Bivalves in particular have a wide range of human intervention in their culture. Mussels, for example, may be grown by setting out lines or posts in the water for the spat (young bivalve) to settle upon, or harvested directly from wild spat that sets on cultivated oysters.

A wide range of technologies has been developed to facilitate the capture of the spat and the harvesting of the final product. Oyster culture may rely on the capture of free-living spat spawned from either wild or cultivated stocks, or upon seed produced from selected brood stock in a hatchery. The collected seed may be grown to a marketable size in racks or trays, or in suspension, or simply scattered back on to the bottom. The advantages of off-bottom culture are that there is better control over losses due to predation, survival is usually better and harvesting is more

efficient, but the costs, both for capital and labour, are considerably higher.



Oyster farm in the Trieux estuary, France. Photo courtesy of Jeanne Menjoulet. Licensed under CC BY 2.0.

A recent worldwide trend in **scallop** fisheries is the use of enhancement techniques. Scallop seeds are captured by setting out collectors at an appropriate time of the year, and the small scallops are grown for a period in small-mesh nets suspended in the water. When they have grown past the size where they are vulnerable to predation, they are released back on to the scallop grounds for harvesting by traditional methods. By careful selection of the areas seeded and scheduling of the areas harvested, it is expected that growth rates and survival will be maximized and overall harvest will increase.

Filter-feeding shellfish have the capacity to consume and become contaminated by bacteria and also by toxin-producing **phytoplankton**. Accordingly, technologies have been developed,

and agreed upon internationally, for the testing and inspection of shellfish to ensure that they are safe to eat. In some circumstances shellfish that are marginally contaminated may be depurated (cleansed) or otherwise processed to ensure that they meet appropriate health standards and pose no risk to consumers.

Increasing **harvesting** pressure, and reduction of available habitat for wild marine stocks and for terrestrial species such as escargots (snails), is stimulating the rapid development of technologies for species not hitherto grown in controlled conditions, or for species introduced from other parts of the world. Examples of the former are **abalone** and geoducks, now being cultivated in Canada. Worldwide the most important oyster grown (3.4 million tonnes in 1998) is now the Pacific oyster, *Crassostrea gigas*, which has supplanted native oysters in many countries. Examples of other species that are successfully cultivated outside their normal range are the bay scallop, *Argopecten irradians*, into China, and the Manila clam, *Tapes philippinarum*, into western North America and western Europe. (DJS)

See also: Mussel culture; Shellfish culture

Molybdenum (Mo)

A mineral element with an atomic mass of 95.94. It exists in biological systems in a number of **oxidation** states, but the most common are +4, +5 and +6. Molybdenum is generally found in nature as compounds with **sulphur** and **oxygen**. It is readily absorbed from the diet via the intestinal cells; the transport mechanism seems to be passive. The mineral, at approximately 5 nmol l^{-1} plasma, is transported in the **blood** bound to proteins.

Erythrocytes may contain 10 times the amount in plasma. Both concentrations can vary depending on the amount consumed.

Molybdenum is an essential component of at least three mammalian **enzymes**: xanthine **dehydrogenase**, **aldehyde** oxidase and sulphite oxidase. These enzymes catalyse redox reactions that pass electrons to **cytochrome** *c*, molecular oxygen, or NAD^+. Sulphite oxidase is an important Mo-containing enzyme that catalyses the final steps in the degradation of sulphur **amino acid**s. Recent evidence suggests that each of these enzymes contains a Mo-containing co-factor called molybdopterin. The co-factor is apparently essential for full activity, because in human genetic disorders expressing Mo co-factor deficiency the activities of all enzymes are reduced. Although Mo is essential for the activity of these important enzymes, it has been rather difficult to produce Mo deficiency signs in animals. While Mo is probably essential for farm animals, no requirement levels have been set for any of the species except sheep (0.5 mg kg^{-1} diet).

Of the farm animal species, ruminants seem to be the most sensitive to Mo toxicosis, and in many cases the amount that produces toxicosis depends on the **sulphate** concentration in the diet. Mo and sulphur combine to bind **copper** and cause a copper deficiency. A dietary concentration of 100 mg Mo kg^{-1} diet can produce signs of toxicity, but with 0.3% sulphate present the effective Mo concentration is lowered to 40 mg kg^{-1} diet. The US National Research Council (NRC) recommends a maximum of 5 mg Mo kg^{-1} diet for cattle and 10 mg kg^{-1} for sheep. Poultry have decreased growth rates while consuming diets with 500 mg Mo

kg^{-1} but pigs have shown no adverse effects at 1000 mg Mo kg^{-1} diet. (PGR)

See also: Thiomolybdate

Further reading

Johnson, J.L. (1997) Molybdenum. In: O'Dell, B.L. and Sunde, R.A. (eds) *Handbook of Nutritionally Essential Mineral Elements*. Marcel Dekker, New York, pp. 413–438.

Monoacylglycerol

Glycerol in which one hydroxyl group is esterified with a **fatty acid**. Also called monoglycerides, monoacylglycerols rarely occur naturally in plant or **animal fats** but are formed during the **digestion** of **triacylglycerol**s in the **small intestine**. (JAM)

See also: Lipids

Monoenoic fatty acid

A **fatty acid** containing one double bond written C=C or Δ. The double bond can support either the *cis* (the usual case) or the *trans* configuration. Also called monounsaturated fatty acid. Examples include palmitoleic (*cis*-9-hexadecenoic, 16:1 n-9 (Δ^9)), oleic (*cis*-9-octadecenoic, 18:1 n-9 (Δ^9)), elaidic (*trans*-9-octadecenoic, 18:1 n-9 (Δ^9)), gadoleic (*cis*-9-eicosenoic, 20:1 n-11 (Δ^9)), erucic (*cis*-13-docosenoic, 22:1 n-9 (Δ^{13})) and nervonic (*cis*-15-tetracosenoic 24:1 n-9 (Δ^{15})). (NJB)

Monogastric

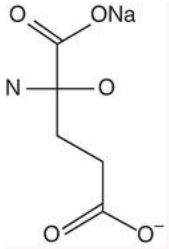
Term used in some publications to describe the structure and function of the **digestive system** of poultry, pigs and fish. It

attempts to distinguish the simpler digestive system of these species with that of cattle, sheep and other ruminant (crosslink) species, which is modified to allow the intake, microbial **digestion** and regurgitation of large quantities of **forage** prior to digestion by the animal. An essential feature of the digestive system of non-ruminant species is the possession of a single, HCl- and **enzyme**-secreting **stomach**. Despite this, the term 'monogastric' cannot be considered to have a precise meaning and the term 'non-ruminant' has greater scientific validity.

Monoglyceride:
see Monoacylglycerol

Monosaccharides
Usually unbranched molecules of three to seven carbons, all of which bear a hydroxyl group except for one that exists as a carbonyl group. If this is on a terminal carbon it gives an **aldehyde**; if on an internal carbon it gives a **ketone**. Three-carbon aldo-monosaccharides are called trioses; those with four to seven carbons are called tetroses, **pentoses**, hexoses and heptoses, respectively. (JAM)
See also: Carbohydrates

Monosodium glutamate (MSG)
$COOH{\cdot}(CH_2)_2{\cdot}CH(NH_2){\cdot}COONa$, the **sodium** salt of L-glutamic acid. It is used as a flavour enhancer. Adverse reactions to it have been reported. (NJB)



Monounsaturated fatty acid:
see Monoenoic fatty acid

Motilin
A polypeptide **hormone** produced in the **duodenum** and **jejunum** under the stimulus of **acetylcholine**. Its function is probably to regulate the **motility** of the gut in the period between meals. (SB)
See also: Gastric emptying

Motility
Movement of the gut wall, which can be of a propulsive, retentive or mixing nature. Changes in motility affect the **retention time** of the **digesta** and may result in **diarrhoea** or, conversely, constipation. (SB)
See also: Gastrointestinal tract

Moulds:
see Fungi

Moulting
An organized loss of feathers that occurs naturally. A juvenile moult occurs during the growing period at about 3 months of age in pullets, when the growth of new feather papillae pushes the old feathers out. An adult moult, which occurs spontaneously at the

end of an individual bird's laying cycle, is caused by a complex interaction of **hormone**s. It is accompanied by a cessation of **egg production**, regression of the reproductive organs and typically a 20–30% loss in body weight.



Moulting in chickens is a natural process at the end of a laying cycle, which is necessary before commencing a second laying cycle. Photo courtesy of Tamsin Cooper. Licensed under CC BY-SA 2.0.

Moulting of **laying hen**s may be induced by manipulations of management when economic circumstances suggest that two shorter laying cycles are more profitable than one longer one. This is usually induced between 50 and 60 weeks of age (prior to the age-related decline in shell quality). Various methods are used in commercial production to induce a moult, including feed reduction or withdrawal and the *ad libitum* use of diets containing low **sodium**, low **calcium** or high **zinc** designed to cause feed refusal. In addition, an accompanying drastic reduction in **photoperiod** and illuminance is used commonly, the result being a rapid cessation of egg-laying. A week before the moult, insoluble grit (5 g per bird) can be provided to minimize the incidence of crop impaction caused by birds ingesting feathers. For the first 10 days of the moult, the bird only receives a small quantity (15 g per day)

of grain such as **oats** or **barley**, which is increased to 30–60 g per day by 3 weeks. The bird is then returned to *ad libitum* feeding of a layer diet and exposed to a stimulatory photoperiod to result in a rapid increase in egg production. After the moult, egg production rate usually peaks slightly lower than the previous peak, but egg quality is improved.

The main advantage of induced moulting is that it allows a return to production faster than growing a new flock of layers from the day-old stage. It is also more profitable, by allowing a reduction in resources required and waste generated in growing more birds for egg production. In addition, it results in fewer culled hens and fewer male chicks that need to be culled at hatcheries. A further benefit is that it allows egg producers to respond quickly to disease outbreaks such as avian influenza.

A main disadvantage of induced moulting is a **welfare** concern, the result being that the practice is banned in some countries (e.g. the EU) and is being discouraged in others. Health is another issue. Forced moulting alters the pattern of **hormone** production in the birds, resulting in an increase in plasma corticosterone which, along with related hormones, causes a decrease in the levels of circulating lymphocytes and other leukocytes. The effect is a weakened immune response and the birds becoming susceptible to disease. Induced moulting of hens has been associated with an increased incidence of *Salmonella enteritidis*, a public health concern. Feed withdrawal has also been shown to reduce skeletal strength in the birds and to be associated with an increase in **pecking** behaviour. (RB; PDL)

Mucin
A class of large glycoproteins consisting of linear or branched **oligosaccharide** chains attached to a **protein** core, much like the bristles on a bottle brush. Mucins are secreted by epithelia of the respiratory, intestinal and urogenital tracts and, in some amphibians, the skin. Gastrointestinal mucins have 60–85% of their weight as **carbohydrate**, consisting of five **sugars**, **fucose**, **galactose**, *N*-acetylglucosamine, *N*-acetylgalactosamine and sialic acid. The protein core has a distinct amino acid composition, with **serine** and threonine comprising 25–60%. The hydroxyl groups on the side-chains of these amino acids link to the oligosaccharides. **Prolactin** accounts for about 15% of the total amino acid residues and is thought to inhibit α-helix formation, which would prevent protein folding and limit **glycosylation**. Average molecular weight 2×10^6. (JAM)
See also: Galactosamine

Mucopolysaccharides:
see Mucin

Mucoproteins:
see Mucin

Mucosa
The layer of mucosal cells covering the inner surface of the digestive tract and other body cavities. The mucosa includes several different types of specialized cells, for example those for the secretion of mucus (mucopolysaccharides and mucoproteins),

which protects the mucosa from attack by proteolytic **enzymes**. In the **stomach**, the mucus forms a flexible gel that coats the mucosa. The cells in the surface secrete HCO_3^- which, together with the mucus, forms an unstirred layer with a pH of about 7.0. (SB)
See also: Gastrointestinal tract; Intestinal mucosa

Mud crab (*Scylla paramamosain*)
Crustacean (Crustacea: Decapoda: Portunidae: Scylla De Han) exhibiting high abundance, rapid growth rates, high nutritional values and strong adaptability. The mud crab is regarded as a crucial species for **aquaculture** in China. It is naturally distributed from the continental coast of the East China Sea to the Java Sea. Given its high economic value, this crab is widely cultivated in many Asian countries (Djunaidah *et al*., 2003; Ut *et al*., 2007; Ye *et al*., 2011). In China (Wang *et al*., 2016), the aquaculture yield of *Scylla* spp. (more than 90% of them are *S. paramamosain*) reached 160,616 t in 2019, accounting for 54.70% of the total aquaculture production of marine crabs in that year (Fisheries Bureau of MARA, 2020). A few studies have been performed on the nutritional requirements of *S. paramamosain*, such as **lipid** levels (Zhao *et al*., 2015; Xu *et al*., 2020) and sources (Zhao *et al*., 2016), **cholesterol** levels (Zheng *et al*., 2018), **phospholipid** (PL) levels (Xu *et al*., 2019), **protein** levels (Zheng *et al*., 2020), **carbohydrate** levels (Zhan *et al*., 2020), n-3 long-chain **polyunsaturated fatty acid**s (LC-PUFA) levels (Wang *et al*., 2020) and **docosahexaenoic acid** and **eicosapentaenoic acid** (DHA/EPA) ratio (Wang *et al*., 2021). The aquaculture of *S. paramamosain* still mainly relies on fresh **feed** at present (Zhao *et*

al., 2015; Zheng *et al*., 2020). Compared with commercial diets, fresh feed has many disadvantages, such as incomplete nutrition, faster spoilage and wasting a lot of fishery resources. It is necessary to carry out more research on the nutritional requirement of *S. paramamosain* to provide a theoretical basis for the development of a high-quality commercial diet (Liu *et al*., 2021). (QS)

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Mulberry (*Morus* spp.)

Tree native to Korea and China. It has been cultivated for over 5000 years, being used for sericulture and, less commonly, for feeding to livestock. It is resistant to **drought** and **temperature** stress by virtue of its deep roots. It can produce 20–30 t per annum when cut at 10-week intervals. It has low requirements for fertilizer and can make an important contribution to **carbon sequestration**. It has a high **crude protein** content, as high as 34%, a balanced **amino acid** composition and relatively low fibre content. It is rich in flavonoids, **sterols**, **polysaccharide**s and **alkaloid**s. Fresh mulberry leaves have low dry matter content and

conservation is difficult. Drying has significant loss of nutrients and ensiling is hindered by the high water-soluble **carbohydrate**, which encourages clostridial activity. Additives such as **cellulase** and lactobacilli are necessary to produce a palatable product. (CJCP)

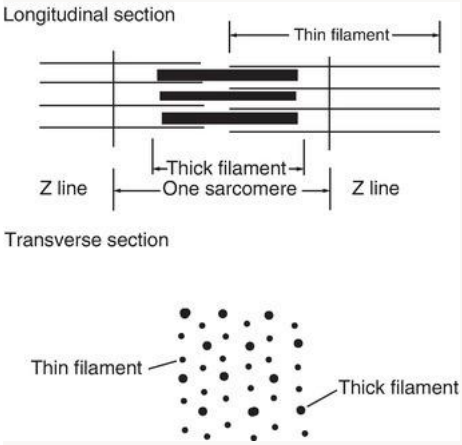


Mulberry trees offer a more efficient use of land for producing fodder for livestock than maize. Less fertilizer is needed, and the crop has a high protein content. Photo courtesy of Ichihashi Takahisa, JIRCAS. Licensed under CC BY 2.0.

Muscle

In the live animal, muscle is a contractile tissue capable of generating force. This property therefore allows locomotion, maintenance and control of posture and regulation of the function of the heart and vascular system, respiratory, gastrointestinal, renal and reproductive tracts and other systems. There are thus three fundamental classes of muscle: skeletal, smooth and cardiac. The **growth** and development of muscle tissue may be understood

through examination of the structure and cellular characteristics. **Skeletal muscle** is a syncytium formed from single nucleated mesodermal cells. During terminal differentiation these form myoblasts, which fuse to form myotubes and then give rise to the multinucleated muscle fibres. These, in turn, produce myofibrils made up of two types of contractile **protein** filaments: thick and thin (see figure). In skeletal and cardiac muscle the filaments are arranged in units called sarcomeres, consisting of one set of thick filaments (**myosin**) and two sets of thin filaments (**actin**). During contraction the thin filaments are pulled over the thick filaments by cross-bridge formation so that the sarcomere shortens and generates the force of contraction.



Arrangement of the thick and thin filaments.

The numbers of muscle fibres present, formed from the fusion of differentiated myoblasts to yield myotubes in the developing embryo, become fixed before or shortly after hatching or birth. During the postnatal growth of the animal the growth of muscle occurs only by hypertrophy (increase in cell size), not by hyperplasia (increase in cell number). Muscle cell hypertrophy occurs by two mechanisms: increase in cell circumference or ‘girth’

and increase in length. Myofibrillar content of growing muscle fibres increases as each myofibril reaches a critical size and then splits or divides into two or more daughter myofibrils. During growth the number of nuclei in the muscle also increases, due to the incorporation of satellite cells into the fibres. Satellite cells are undifferentiated precursor muscle cells or myoblasts with high nucleus:cytoplasm ratios, and these are located between the membrane and basal lamina of the muscle fibre. These cells fuse mainly with the growth regions towards the ends of the fibres. Increases in muscle fibre length during growth are a consequence of the addition of new sarcomeres at the ends of existing myofibrils. The growth region is thus at the myo-tendon junction. During long bone growth and muscle stretching, the insertion of additional sarcomeres allows adjustment of sarcomere length to that which is optimal for muscle contractile function.

The growth potential of a muscle may be determined by two factors. The first is the number of myoblasts present before fusion during embryonic development. Increased myoblast formation during the proliferative phase of development will increase the final number of muscle fibres and thus muscle mass. Secondly, as satellite cells contribute many nuclei during secondary generation of myofibres, it may be proposed that the abundance of these cells determines the ultimate size to which a muscle can grow. Research into the regulation of myoblast proliferation and satellite cell function may provide the basis for further improvements in muscle growth in meat animals. (MMit)

See also: Body composition; Growth factors; Meat composition

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Muscular diseases

Nutritionally related disorders of the muscular tissue fall into two major categories: those associated with muscle cell degeneration and those affecting the ability of the muscle to function without altering muscle architecture. Deficiencies of **selenium** or **vitamin E** result in destruction of muscle cell membranes and proteins. This is due to an accumulation of **free radical**s and **peroxides** that are normally scavenged by the selenium-containing protein, **glutathione peroxidase**, and by vitamin E. Both skeletal and cardiac muscle are affected, though in ruminants **skeletal muscle** changes are more prominent, while in pigs cardiac muscle changes are more prevalent. Toxic principles from plants (e.g. **gossypol** in pig feed) can also induce necrosis of muscle cells. Muscle dysfunction diseases are often secondary to **electrolyte** imbalances that interfere with nerve transmission, resting membrane potential or action potential conduction within the muscle. Nutritionally related disorders, resulting in low **blood** concentrations of **calcium**, **magnesium**, or **potassium**, are generally characterized by **muscle** weakness or tetanic contraction of muscle. (JPG)

Mushrooms

The fleshy fruiting bodies of **fungi**. In North America alone, 10,000 species of mushroom exist, of which 250 are edible and 250 are poisonous while the nature of the remainder is uncertain. Most of the edible species are gathered from the wild but some are cultivated. Mushrooms can be fed to ruminants at low inclusion rates (5–10%) but large quantities are unlikely to be available for animal feeding. The nutrient composition (g kg^{-1}) of mushrooms is **crude protein** 201, **crude fibre** 135, **ether extract** 101, **salt** 31 and total free **amino acid**s 32.96–109.69 (mg g^{-1}), and they are rich in B **vitamins**. (JKM)

Mussel culture

Mussels grow almost everywhere on hard surfaces in shallow marine and **brackish water**s. They can be a nuisance to mariners and in the cooling systems of boats and coastal generating stations. Mussels are fast growing and have been harvested and cultivated as food for centuries.

Typically a mussel farmer will moor a series of lines suspended just below the surface of the water in anticipation of newly metamorphosed mussel larvae settling on them. These small mussels adhere to the ropes by their byssus threads and begin to grow, filtering **phytoplankton** from the water. Depending on location and species, the mussels may be stripped off the collecting ropes when they have grown to 10–20 mm long, and transferred to other systems for grow-out. This usually requires that the mussels be wrapped, along with another rope, in a cotton gauze material that will rot and fall away after the mussels have re-fastened

themselves to the rope. Alternatively the mussels may be stuffed into a plastic mesh tube of such a size that individual mussels can just crawl through the mesh. These 'socks' or 'sleeves' of mussels are suspended just below the surface of the water, while the mussels grow to marketable size. The suspension technology varies from place to place. In western France, mussel ropes are wrapped around posts (*buchots*) set in the mud. Elsewhere they may be suspended from 'tables' set into the bottom, from floating rafts, or from anchored long lines, buoyed at the surface to keep the mussels clear of the bottom. Several species of blue and green mussels are cultivated worldwide. Landings exceed 1.4 million tonnes.



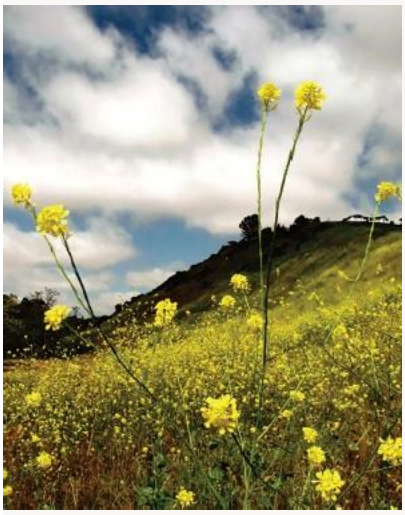
Typically, mussels are cultured on lines, from which they are harvested when they reach market weight. Photo courtesy of Steve Bittenger. Licensed under CC BY 2.0.

There has been rapid technological development to aid farmers in setting their gear, collecting and socking spat, and in mechanical

harvesting. Artisanal techniques are still effective and profitable in some areas. (DJS)

Mustard

The common name of a group of related **brassica**s. White mustard (*Brassica hirta* Moench or *Sinapis alba* L.), black mustard (*B. nigra* Koch) and Indian or leaf mustard (*B. juncea* Coss) are cultivated primarily for their oily seeds and as a condiment.



Mustard grass. Photo courtesy of Moojazz. Licensed under Public Domain Mark 1.0.

Mustard can be grown as a cover crop, which may be fed green, and **forage** mustard has a **metabolizable energy** content of 9.0 MJ kg^{-1} dry matter. Mustard **oil** cake or meal, which is a **by-product** of mustard oil production, is fed to animals. For animal feeding the toxic **glucosides**, which can affect the thyroid gland, must be removed. This can be achieved by steaming for 2 h and extraction of the ground seed with water. This causes a reaction between the enzyme **myrosinase** and the glucoside. In black mustard, myrosinase reacts with the glucoside sinigrin to produce a

volatile irritating oil but in white mustard it reacts with the glucoside sinalbin and the oil produced is less irritating. The extracted meal can be fed to adult ruminants (< 1.5 kg per day or 7.5% of the diet in adult cattle) but must be given with more palatable feeds to prevent reduced **feed intake**. In diets for calves, solvent-extracted meal can completely replace **soybean** or **groundnut** meal but mustard expeller meal should not replace more than half. In poultry diets, low-glucoside mustard seed *B. juncea*, *B. napus* and *B. rapa* can be used as a 1:1 replacement of canola meal, but high-glucoside meals should not exceed 10% of the diet. (JKM)

Typical composition of mustard products.

	Nutrients (g kg^{-1} DM)						
	Dry matter (g kg^{-1})	**Crude protein**	**Crude fibre**	**Ash**	**Ether extract**	**NFE**	**NDF**	**Glucoside** (µmol g^{-1})
For age mustard								
Oilcake	150	193	–	–	–	–	–	–

	Nutrients (g kg^{-1} DM)							
	Dry matter (g kg^{-1})	**Crude protein**	**Crude fibre**	**Ash**	**Ether extract**	**NFE**	**NDF**	**Glucoside** (µmol g^{-1})
Mechanically extracted	898	385	35	99	107	374	–	–
Solvent extracted	880	260	182	76	23	459	–	–
Low glucoside								
B. juncea	–	459	–	–	–	–	297	34

	Nutrients (g kg^{-1} DM)						
	Dry matter (g kg^{-1})	**Crude protein**	**Crude fibre**	**Ash**	**Ether extract**	**NFE**	**NDF**	**Glucoside** (μmol g^{-1})
B. napus	–	446	–	–	–	–	132	22
B. rapa	–	431	–	–	–	–	196	25
High-glucoside meal	–	300–320	120–130	–	190–220	–	–	–
Wild mustard meal	48	260	134	44	335	–	–	92

	Nutrients (g kg^{-1} DM)						
Dry matter (g kg^{-1})	**Crude protein**	**Crude fibre**	**Ash**	**Ether extract**	**NFE**	**NDF**	**Glucoside** (μmol g^{-1})
Dehulled and defatted meal	–	480	38	70	–	–	–	230

NDF, neutral-detergent fibre; NFE, nitrogen-free extract.

Mycotoxins

Harmful **metabolite**s produced by some moulds (**fungi**). Those of concern are produced by fungi that grow on **grain** crops in the

field or during grain storage. Major fungal genera producing mycotoxins include *Aspergillus*, *Penicillium* and *Fusarium*. *Aspergillus flavus* and *A. parasiticus* produce **aflatoxin**s (AF). Aflatoxin, produced by *Aspergillus flavus* and *A. parasiticus*, is the most investigated mycotoxin and **contamination** levels in feedstuffs are regulated in many countries, because aflatoxin is a potent **carcinogen**ic hepatotoxin. **Ochratoxin**, produced by *Aspergillus* and *Penicillium* fungi, is also often regulated, as it is a carcinogenic renal toxin. The mycotoxin citrinin (CT) is a nephrotoxin, produced by several species of the genus *Penicillium* and three species of *Aspergillus*. The principal CT-producing fungus in feeds is *P. viridicatum*. Ochratoxins (OA) are produced by several *Aspergillus* and *Penicillium* species. OA is a potent nephrotoxin. Other mycotoxins produced by *Aspergillus* and *Penicillium* include cyclopiazonic acid (CPA), kojic acid and rubratoxins. *Fusarium* mycotoxins include zearalenones (Z), **fumonisin**s (F), moniliforme, fusarochromanone, fusaric acid and various **trichothecene**s such as T-2 toxin, diacetoxyscirpenol (DAS) and **deoxynivalenol** (DON). Major pathologies induced by mycotoxins include liver damage (AF, F), kidney lesions (AF, CT, OA), hyperoestrogenism (Z), **vomiting** and feed refusal (**trichothecene**s) and neurological degeneration (F). Mycotoxins associated with forages include **ergot alkaloid**s (endophyte-infected tall fescue) and lolitrems (perennial ryegrass staggers).



Assessing chilies and peanuts for mycotoxin risk in Nepal. Photo courtesy of Jagger Harvey. Licensed under CC BY 2.0.

Contamination can occur in the field pre-harvest or during inadequate storage, such as under high moisture conditions, or following insect or **drought** damage. Recent global surveys of mycotoxin contamination of feedstuffs have indicated that *Fusarium* mycotoxins are the most common, including fumonisins (which inhibit membrane **lipid** synthesis), **deoxynivalenol** (DON) (**vomitoxin**, triggers vomiting and loss of **appetite**) and zearalenone (impairs **reproduction**). The most frequently contaminated feedstuffs are grains, including **corn**, **wheat** and **barley**. **Silages** can also be a significant source of contamination in ruminant diets. Advances in mycotoxin analysis, including LC/MS/MS (liquid **chromatography** coupled with tandem mass

spectrometers), now make it possible to quantify up to several hundred mycotoxins and metabolites simultaneously. This has led to the conclusion that multiple mycotoxin contamination is normal and quantification of 'emerging' mycotoxins is now possible (Gruber-Dorninger *et al*., 2017). These include enniatins, fusaproliferin, fusaric acid, culmorin, aurofusarin and many others. With multiple mycotoxin contamination, additive immunosuppressive effects can be seen resulting in increased frequency of disease. It is also possible to have synergistic effects where the presence of one mycotoxin can increase the toxicity of another. If the feeding of contaminated materials cannot be avoided, a common and effective strategy is dietary inclusion of mycotoxin adsorbents. These are non-nutritive, high-molecular-weight polymers, often **silica**-based, which bind mycotoxins in the intestinal lumen, thereby minimizing adsorption. This approach has been shown to reduce *Fusarium* mycotoxicoses in poultry (Girish *et al*., 2008) and other species. (PC; TKS)

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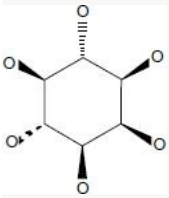
Myelin

Composed of plasma membrane from Schwann cells in the peripheral nervous system and oligodendrocytes in the central nervous system of vertebrate animals. The so-called myelin sheath is composed of multiple layers of specialized membranes that are rich in **glycolipid**s and act as insulation to promote high conduction velocities in small-diameter nerve fibres. (GG)

Myo-inositol

cis-1, 2, 3, 5, *trans*-4, 6-Hexahydroxycyclohexane, $C_6H_{12}O_6$, one of the two optically active forms of **inositol**. In animals, inositol is found in cell membranes as **phosphatidylinositol** and phosphatidylinositol 4,5-bisphosphate. Phosphatidylinositol 4,5-bisphosphate is the connection between a cell membrane **hormone** receptor and rapid changes in cellular concentrations of **calcium**.

Inositol is biologically active and a structural part of biological membranes. Deficiency causes **appetite** suppression, fin erosion, poor **growth**, slow **gastric emptying** and decreased cholinesterase and **lipid metabolism** disorders in fish species. An exogenous source is required in some fish species, such as the **common carp**, because insufficient is synthesized, but not in others, such as striped bass, **tilapia** and **Atlantic salmon**. When needed it is added in a multivitamin **premix**. (NJB; QS; CJCP)



Myopathy

Any degenerative disease of cardiac or **skeletal muscle**. Most common of the nutritional myopathies are those caused by **vitamin E** or **selenium** deficiency. Vitamin E is important for protection of cell membranes, as it is the only **antioxidant** capable of quenching free-radical **peroxides** generated within cell membranes during the course of muscle **metabolism**. Vitamin E is found in fresh green forages and vegetables. It is one of the **fat-soluble vitamins**, which allows it to act within the **lipid** bilayer of cell membranes. Selenium is an essential component of the enzyme, **glutathione peroxidase**, which converts highly reactive forms of **oxygen** such as **hydrogen peroxide** and **superoxide** anion **free radical**s to harmless compounds such as water by donating **hydrogen** ions. Glutathione peroxidase protects the cytosol of the cell from free radical damage. In areas where the soil is deficient in selenium, plants may not provide enough selenium to meet the dietary requirement of the animals fed those plants. A deficiency of either vitamin E or selenium can allow free radicals to accumulate, resulting in degeneration of muscle fibres.

Selenium deficiency is most common in ruminants, particularly young calves and lambs, and causes the syndrome known as white muscle disease. The muscles of affected animals are pale and have white streaks running across them. Histologically, muscle degeneration begins at the Z lines with loss of myofibre structure and swelling of sarcoplasmic membranes. In lambs, this syndrome primarily affects skeletal muscle; in calves, the cardiac muscle is also affected. Vitamin E deficiency exacerbates the selenium

deficiency but is rarely the sole cause of white muscle disease in ruminants. In pigs, selenium or vitamin E deficiency primarily affects cardiac muscle but other organ systems may also be involved. In poultry, the breast muscles are most commonly affected.

Toxic plant substances (e.g. **gossypol** in pig diets) can also cause degeneration of muscle. Common infectious diseases that can also cause muscle degeneration include the clostridial diseases, such as black leg and malignant oedema. (JPG)
See also: Muscular diseases

Myosin
A **protein** found in **muscle** and tissues with motile function. It is the major protein component of the thick filament (about twice the diameter of **actin**) backbone that combines with actin to produce muscle contraction in which **adenosine triphosphate** (ATP) provides the **energy**. Myosin accounts for 55% of total muscle protein. (NJB)

Myristic acid
Tetradecanoic acid, a saturated **long-chain fatty acid**, $CH_3{\cdot}(CH_2)_{12}{\cdot}COOH$, shorthand designation 14:0; molecular weight 228, with melting point of 53.9°C. A major component of **coconut** and palm **oils**; also present in human **milk**, dairy **fat** (for example, 10–15% of the **fatty acid**s in butter), poultry fat, nutmeg and myrtles. (NJB; JAM)

Myrosinase

Beta-thioglucoside glucohydrolase (EC 3.2.3.1). The only known natural *S*-**glycosidase** plant **enzyme**, its principal activity is the **hydrolysis** of **glucosinolate**s to isothiocyanates. It is activated by L-**ascorbic acid** and competitively inhibited by **sulphate** reaction products. It is a dimer with an apparent molecular mass of 120 kDa, and is isolated from *Raphanus sativus* (daikon). It is stabilized by a Zn ion and is heavily glycosylated. It has a hydrophobic pocket, ideally situated for the binding of the hydrophobic side-chain of glucosinolates with two **arginine** residues positioned for interaction with the sulphate group of the **substrate**. The complete structure of a plant-specific heptasaccharide is observed at one **glycosylation** site. (JDO)

N

N*-nitroso compounds*Nitrosamine**s are formed by nitrosation of secondary, tertiary and some primary **amine**s and of quaternary ammonium compounds. They can also be formed by reaction of amines with **nitrate** and thus may be formed within foods or feeds that are preserved with nitrates or nitrites. They are of concern because many are carcinogenic. Fish preserved with high levels of

nitrite may be highly carcinogenic. **Methylamine**s are abundant in fish tissue and readily react with nitrate to form nitrosamines. Nitrosamides are also powerful carcinogens. (PC)

Naphthoquinones

A class of aromatic diketones in which the carbonyl groups are part of the ring structure. One of the three possible **quinone**s derived from naphthalene, $C_{10}H_{18}$, a double unsaturated ring structure, is 1,4-naphthoquinone, the ring structure of **menadione**, **phylloquinone** and **menaquinone**-7, all biologically active forms of **vitamin K**. Others are 1,2- and 2,6-naphthoquinones. (NJB)

NAS-NRC (USA)

The US National Academy of Sciences (NAS) with its operating arm, the National Research Council (NRC) Board on Agriculture and Natural Resources (BANR), is the global leader in the production of reports relating to animal nutrition. Its most important reports for application in animal feeding are its series on Nutrient Requirements of Domestic Animals, started in the 1950s.

The NAS was established in 1863 by an Act of Congress, signed by President Abraham Lincoln, as a private, non-governmental institution to advise the nation on issues related to science and technology. In 1916, NAS formed the NRC in response to a request from President Woodrow Wilson to provide government with broader scientific research services to assist in military preparedness of the country. The NRC included the role of animal nutrition in this effort, forming the Animal Nutrition Subcommittee

of Committee on Food and Nutrition in 1917 and a Division of Biology and Agriculture in 1919.

The first publications included the following in 1921: *Cooperative Experiments upon Protein Requirements for the Growth of Cattle*; *On Formulation of Methods of Experimentation in Animal Production*; and *The Determination of the Protein Requirements of Animals and of the Protein Values of Farm Feeds and Rations*.

During the Great Depression, the NRC produced reports to meet challenges in animal agriculture presented by that crisis and was able to make a significant contribution to the World War II effort with the following publications in 1942–1943: *The Fluorine Problem of Livestock Feeding*; *Iodine – Its Necessity and Stabilization*; *The Nutrition of Swine during the War Emergency*; *Nutrition and Reproduction of Farm Animals*; *Suggestions for Meeting the War-Time Poultry Feed Situation*; *War Emergency Plans for Raising Calves and Heifers*; *The Effect of Storage of Grains on Their Nutritive Value*; *Is Animal Protein an Essential Constituent of Swine and Poultry Rations*; *Suggestions for Meeting the Poultry Feed Situation during 1943*; and *Use of Phosphorus-Containing Substitutes for Bone Meal in Livestock Feeding with Particular Reference to the Fluorine Hazard*.

In 1944, recognizing a need for authoritative references on animal nutrition, the Board reorganized as the Board on Agriculture and Natural Resources (BANR). BANR brought together the nation's most talented scientists and practitioners to advise policymakers and engage the public on the crucial,

contemporary issues affecting food, agriculture and the nation's natural resources. It produced the first **nutrient requirement** reports as an educational tool for industry, the research community and students, and to serve as a central component of outreach programmes to improve care of research, farm and companion animals.

Initially (in the 1940s) the reports were published as Recommended Nutrient Allowances to improve the production and profitability on farms and included: *Poultry* (1944); *Swine* (1944); *Beef Cattle* (1945); *Dairy Cattle* (1945); *Sheep* (1945); and *Horses* (1949).

In the 1950s the focus of the publications changed to nutrient requirements and included: *Nutrient Requirements of Dogs*; *Nutrient Requirements of Trout, Salmon, and Catfish*; *Nutrient Requirements of Foxes and Minks*; *Nutrient Requirements of Rabbits*; *Nutrient Requirements of Cats*; and *Nutrient Requirements of Laboratory Animals*. Subsequent to their initial publication these reports were updated periodically and other reports were added, i.e.: *Nutrient Requirements of Nonhuman Primates* (1978); *Nutrient Requirements of Dogs and Cats* (2006); *Nutrient Requirements of Small Ruminants: Sheep, Goats, Cervids, and New World Camelids* (2007); *Nutrient Requirements of Fish and Shrimp* (2011); *Nutrient Requirements of Dairy Cattle*, 7th Revised Edition (2001); *Nutrient Requirements of Swine*, 11th Revised Edition (2012); and *Nutrient Requirements of Beef Cattle*, 8th Revised Edition (2016).

In addition to reviewing research findings and presenting

estimates of nutrient requirements in relation to stage of life, production and reproduction, these publications typically cover **digestion**, biochemistry and physiological aspects of nutrients; **nutrient deficiency** and animal **welfare** aspects; environmental aspects of nutrients; nutrient model evaluation and prediction equations; and nutrient composition of feeds.

Other related publications have included: *The Effect of Genetic Variance on Nutritional Requirements of Animals* (1975); *Nutritional Energetics of Domestic Animals* (1981); *Taurine Requirement of the Cat* (1981); *United States–Canadian Tables of Feed Composition* (1982); *Underutilized Resources as Animal Feedstuffs* (1983); *Selenium in Nutrition* (1983); *Ruminant Nitrogen Usage* (1985); *Vitamin Tolerance of Animals* (1987); *Metabolic Modifiers: Effects on the Nutrient Requirements of Food-Producing Animals* (1994); *The Role of Chromium in Animal Nutrition* (1997); *Air Emissions from Animal Feeding Operations* (2003); *Mineral Tolerance of Animals* (2005); and *Safety of Dietary Supplements in the Diets for Horses, Dogs, and Cats* (2009). Several of these publications have been translated into other languages.

Currently BANR continues to operate as a principal agency in providing the latest animal nutrition information to the academic community, feed regulators, the feed industry, producers, consultants and related industries. The *Nutrient Requirements* series has expanded its focus to include: sustainable animal agriculture; food safety and quality; animal care and well-being; environmental impacts; greenhouse gas emissions; and nutritional

quality of animal products. It continues to be a platform for engagement with, and outreach to, the US food and agricultural sciences community, positioning the work of the National Academies and the Board as an extension of research into science policy. (BM)

Natural feeding behaviour

The public often assume that an animal's **welfare** is good if it is engaging in natural behaviour and, as such, it behoves us to consider the relevance of natural feeding behaviour. Typically animals that are husbanded by humans are fed an artificial diet, often highly processed for ease of storage and feeding. However, this is frequently to the detriment of the animal's welfare, which becomes evident as the animal develops stereotyped **feeding behaviour** when it is able to consume its feed in a small fraction of the time it would take in the wild. For example, livestock at pasture may **forage** for 15 h per day, but when they are brought into a building and fed a concentrated diet they can consume their daily ration in just a few hours. This applies to all the major domesticated livestock species and they redirect their feeding behaviour to surrogate behaviours, such as bar-**biting** in pigs, **feather pecking** in chickens, **tongue rolling** in cattle and **wool biting** in sheep. (CJCP)



The natural feeding behaviour of wild *Bos gaurus* cattle in Malaysia is browsing in the forest and grazing in forest clearings. Photo courtesy of Clive Phillips. Unlicensed.

Near-infrared (NIR) spectroscopy

An analytical technique involving absorbance processes associated with overtones and combination bands of vibrational transitions in molecules that occur in the region of 730–2500 nm. The spectra observed involve mainly **hydrogen**-bearing groups, e.g. C-H, OH, N-H bands.

NIR spectra of foods can provide a basis for instant multiple analyses of their composition using correlation transform spectroscopy. **Sugars**, **starch** and **cellulose** ($C_x(H_2O)_y$) are all polyhydroxy **aldehyde**s and **ketone**s rearranged as hemi-acetal ring monomers: thus, **carbohydrate** is characterized by -O-H stretching overtones of the hydroxymethylene group. **Lipids**, being long hydrocarbon chains, are characterized by predominant hydrocarbon -CH_2- bands, mainly associated with the methylene group. **Protein** is characterized by -CONH- linkages between constituent **amino acid**s and so the characteristic feature of protein molecules is the **nitrogen** in the **peptide** bond adjacent to

a carbonyl group C=O. Spectra of an intact food are a summation of all its components.

NIR is used for the routine quantitative determination of water, proteins, low-molecular-weight hydrocarbons and **fat** in the agricultural, food, petroleum and chemical industries. In NIR spectroscopy, NIR **light** is applied to the specimen and the reflected or transmitted spectra are used in multivariate calibration models to predict the **chemical composition** or attributes, such as **digestibility** of forages. NIR spectroscopy is an important tool for the routine quantitative determination of constituents in ground solids. This includes the analysis of agricultural products such as **oilseed** and **grain**s for the determination of protein, moisture, starch, **oil**, lipids and **cellulose**.

NIR is calibrated by scanning large sets of typical samples of one kind having a wide range in composition. The resulting spectra are used to select a representative subset of samples for reference analyses using traditional **analytical methods**. The reference values obtained are then used to construct a calibration model that maps spectra onto chemical composition, using internal cross-validation to gauge performance. Multivariate statistical methods such as multiple linear regression or partial least squares are used in the modelling process. The composition or quality of any subsequent unknown **sample** is then predicted from its spectrum by using the calibration model. Analysis by NIR is different from separation methods such as **chromatography** in that the intact sample matrix is examined and contributes to the analysis. On the grounds of speed and precision, NIR is often the only cost-effective

quality control method for routinely testing food commodities.

NIR faecal spectra can be used to predict the diet composition (**legumes** versus **grasses**), protein content and digestibility, and the probable performance of **grazing** animals. It has also been used to identify pregnancy and tick burdens. Faecal NIR spectra have been used to identify different animal species. (JEM; IM; GMcLD)

Further reading

Dryden, G. McL. (2003) *Near Infrared Reflectance Spectroscopy: Applications in Deer Nutrition*. RIRDC Publication No. W03/007. Rural Industries Research and Development Corporation, Canberra, Australia.

Neem (*Azadirachta indica* A. Juss)

An evergreen tree, found widely in Asia and the tropics, with many medicinal uses. Leaves can be used as an emergency famine feed. Neem seed cake is the residue left after the extraction of **oil** from seeds; it can be used for fertilizer or feed. Approximately 100,000 t of neem seed cake is available annually in India alone. The cake contains around 15% **crude protein** (see tables) but is not very palatable, having a bitter **taste** due to the presence of nimbidin. Treatment with 1% NaOH, followed by washing with water, will reduce the level of nimbidin. Levels of the cake in poultry concentrate should be limited to 5%, but higher levels can be used in rations for growing cattle. The optimum level of inclusion for sheep is 25%. (LR)

Typical composition of neem products (% dry matter).

	DM (%)	**CP**	**CF**	**Ash**	**EE**	**NFE**	**Ca**	**P**
Fresh leaves	35.8	14.4	13.7	10.8	5.2	56.0	2.29	0.20
Neem seed cake		15.4	22.2	15.0	6.0	42.0		

CF, crude fibre; CP, crude protein; DM, dry matter; EE, ether extract; NFE, nitrogen-free extract.

Typical ME content and digestibility (%) of major constituents (abbreviated as above) in neem leaves fed to ruminants.

	CP	**CF**	**EE**	**NFE**	**ME** (MJ kg^{-1})
Leaves	52.0	23.0	58.0	68.0	8.51



The neem tree, a native of the Indian subcontinent, has many agricultural and medicinal uses. Photo courtesy of ABHiriksh. Licensed under CC BY-SA 3.0.

Nervonic acid

A 24-carbon monounsaturated fatty acid, *cis*-15-tetracosenoic, 24:1 n-9 (Δ^{15}). It is found in nervous tissue. (NJB)

Net energy

That part of the **gross energy** that is used for the animal's **maintenance**, retained as product or used for work. It is equal to the **metabolizable energy** minus the **heat increment of feeding**. The net energy system of assessing total **feed** requirements for cattle has now been largely replaced by the metabolizable **energy system**. (JAMcL)

Net protein ratio (NPR)

A measure of **protein quality**. In the assay, growing animals (usually rats or chicks) are given a diet containing the test protein (or mixture of proteins) for a set period (commonly 10 days to 4 weeks). NPR is calculated from the weight gain of the test group (T), the weight loss of a similar group of animals given a protein-free diet (C) and the amount of **crude protein** consumed by the test animals (P) as:

NPR=(T+C)/P

Unlike **protein efficiency ratio** (PER), the assay takes account of the use of the protein in meeting the animal's **maintenance** requirements. (NJB)

Net protein utilization (NPU)

One of the systems used to evaluate the quality of protein(s) for use in human and animal diets. It is defined as the percentage of the dietary protein retained. The value of dietary protein (therefore, not a single protein) is estimated by use of an animal growth trial. This method involves measuring total body **nitrogen** in a group of experimental animals (groups of four or more rats) which have consumed a protein-free diet and another group fed a similar diet containing the test protein. After the animals have consumed the diets for the desired time (10 or more days) the value of the protein is estimated using the formula for NPU:

NPU = 100 × [(Body N of test group) – (Body N of protein–free

(NJB)

Neurotransmitter

A chemical that functions at the junctions (synapses) between two

nerve cells (axon to dendrite) or between a nerve cell and a cell of another type such as **muscle** (neuromuscular junction) or a gland. The presynaptic neuron has at its termination synaptic vesicles containing neurotransmitters (e.g. **acetylcholine**, **serotonin**). In response to an impulse the synaptic vesicles release the neurotransmitter into the synaptic cleft, where it migrates 20–40 nm across the junction to affect the nerve or muscle, etc. The term neurotransmitter applies to individual chemicals such as acetylcholine or to classes of chemicals such as **amine**s, excitatory or inhibitory **amino acid**s, polypeptides, **purines**, gases or **lipids**. (NJB)

Neutral detergent fibre (NDF)
An insoluble matrix prepared by the extraction of food plants and mixed feeds in a solution of **sodium** dodecyl **sulphate** (SDS) and ethylene-diamine tetraacetic acid (EDTA) in a phosphate **buffer** at pH 7. NDF is an estimate of the cell wall fraction of forages and mixed feeds. Cell wall **polysaccharide**s (with the exception of pectin), **lignin** and cutin are the major components of NDF from forages. Proteins, **lipids**, non-structural polysaccharides and other cytoplasmic constituents are removed by the extraction. NDF is used to measure the amount of cell wall in foods and to determine fibre **digestibility**. Within the context of the detergent system of **forage** analysis, NDF separates completely available food components that are nutritionally uniform from those **feed** components that are only partially available or completely unavailable for **digestion**. The detergent system of forage analysis was developed by P.J. Van Soest to replace the fibre analysis of the

Weende system with a more rational and easily applied system. Digestibility of a forage is estimated by analysis of NDF and an estimate of the degradability of NDF by lignin analysis, *in vitro* degradability of NDF or enzymatic degradability with fungal cellulases. (JDR)
See also: Feed composition table and analysis

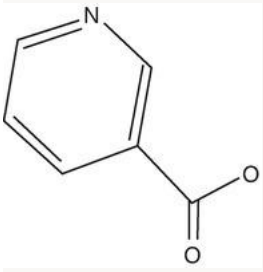
Neutron activation analysis (NAA)
An extremely sensitive, non-destructive technique used for the determination of about 69 elements. The technique involves the bombardment of the **sample** with neutrons to convert stable elements to radionuclides, which are subsequently measured by the radioactivity they emit as they decay. The method allows trace multi-element analyses with minimal sample preparation in various matrices such as food, fuel, drugs, fertilizers, minerals and water. (JEM)

Newborn animals
The first needs of newborn animals are for food and warmth. Because they have a high ratio of surface area to body weight, and because they are wet, newborn mammals and newly hatched birds are susceptible to **hypothermia**, which then limits their ability to find shelter and food. The first nutritional need of newborn mammals is for **colostrum** to provide passive **immunity** against infections, particularly of the **gastrointestinal tract**. The capacity to absorb immunoglobulins intact is short-lived and animals should receive adequate amounts of colostrum immediately after birth. Recommended amounts and maximal

permitted delays after birth are: foal 12 h; calf 6% of body weight within 6 h; lamb 20% body weight over the first 18 h; piglet 40 ml in two feeds within 4–6 h of birth. As well as providing **antibodies**, colostrum of all species is rich in **vitamins** A, D and B_{12}, which do not cross the placenta easily, and also **growth factor**s such as **insulin-like growth factor**s I and II, which stimulate early development.



The first needs of newborn animals are for food and warmth. Photo courtesy of Graham and Sheila. Licensed under CC BY 2.0.



Newborn animals have great **growth** potential and need sufficient dietary **energy** to make full use of this. For example, piglets will consume food equal to four times their basal **metabolic rate** for the first few weeks. A high **energy intake** also helps to prevent **hypothermia**. **Iron supplementation** is

necessary for housed pigs.

Milk replacers should closely resemble the natural product, with well-dispersed **fat**, and cautious use of unnatural **sugars** such as **sucrose**, which are not well digested by the newborn.
For chicks early **feed intake** is critical, as residual yolk is quickly absorbed. Transportation may delay feed intake and **starvation** of chicks at this critical point can compromise long-term growth and immune function. (JKM)
See also: Calf; Colostrum; Piglets; Weaning

Niacin
One of the B-vitamins, known as the anti-pellagra **vitamin**. The vitamin activity is possessed by niacin (nicotinic acid; pyridine-3-carboxylic acid; $C_5H_4{\cdot}COOH$) and its **amide**, niacinamide (nicotinamide; $C_5H_4{\cdot}CO{\cdot}NH_2$). **Pellagra**, a disease of humans, was once prevalent in populations who were dependent on **maize** as their main food. Rapid progress in the solution of the pellagra problem was made after it was realized that 'black-tongue', a condition in dogs fed a pellagra-producing diet, could be cured by nicotinic acid.

The niacin-containing **coenzyme**s NAD^+ (**nicotinamide adenine dinucleotide**) and $NADP^+$ (nicotinamide adenine dinucleotide phosphate) are produced by all the tissues in the body. In **metabolism**, niacin functions in **oxidation**–reduction reactions as an essential component of the co-factors NAD^+ or $NADP^+$. NAD^+ or $NADP^+$ participates as a co-factor in many

dehydrogenase reactions. Generally, NAD^+ is linked to dehydrogenases that catalyse oxidation–reduction reactions in catabolic (oxidative) pathways involving **enzymes** such as **lactate dehydrogenase** in the cytoplasm or **malate dehydrogenase** in mitochondria. $NADP^+$-linked dehydrogenases or reductases are often connected with systems involved with reductive synthesis, such as the **pentose** cycle, providing reducing equivalents for the biosynthesis of **fatty acid**s from two carbon acetyl-CoA units.

Niacin is widely distributed in plant and animal tissues. Foods such as **fish**, **meat**, **milk**, **cereal**s, **legumes** and green leafy vegetables are good sources. NAD^+ and $NADP^+$, as the vitamin co-factors in which niacin is incorporated, are found in food and are absorbed as nicotinamide after the vitamin co-factors have been hydrolysed by enzymes in the **intestinal mucosa**. At low concentrations they are absorbed in the stomach and intestine by a **sodium**-dependent facilitative **diffusion** process. At high concentrations they are absorbed by diffusion. Niacin can be synthesized from L-**tryptophan**, but not in quantities that meet the requirement. Conversion efficiency of tryptophan to niacin is affected by the vitamin B_6, vitamin B_2 and **iron** status of an individual. In the laboratory rat, ~40 mg of L-tryptophan is required to produce 1 mg of niacin.

Niacin is excreted in the **urine** as a methylated derivative, N^1-methylnicotinamide, and as N^1-methyl-2-pyridone-5-carboxamide and N^1-methyl-4-pyridone-5-carboxamide along with minor amounts of niacin, niacin oxide and the hydroxyl form of niacin.

Urinary excretion of N^1-methylnicotinamide and N^1methyl-2-pyridone-5-carboxamide have been used to assess niacin status. The requirements of non-ruminant animals are in the range 10–30 mg kg^{-1} diet. (NJB)

See also: History of nutritional sciences

Key reference

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Geisler, C.E., Miller, K.E., Ghimire, S. and Renquist, B.J. (2021) The role of GPR109a signaling in niacin induced effects on fed and fasted hepatic metabolism. *International Journal of Molecular Science,* 22, 4001.

Niacinamide:

see Niacin

Nickel (Ni)

A transition element with an atomic mass of 58.693. It exists in six **oxidation** states, but Ni^{2+} is the principal form in biological systems. Nickel is found in the earth's crust at about 100 mg kg^{-1}; however, Ni concentrations in animal feedstuffs are low, ranging from 0 to 3 mg kg^{-1}. The **absorption** of Ni from the intestinal tract is very low relative to some other trace metals; it ranges from 1% to 10% of intake. The rate of absorption can be elevated by low

iron in the diet, and various physiological states such as pregnancy and **lactation** can increase Ni absorption as well. As a result of the low absorption rate, tissue concentrations of Ni are relatively low, with kidney, liver, bone and hair containing the highest concentrations (0.1–0.25 mg kg^{-1} fresh tissue).

Ni is an essential component of a number of **enzymes** in plants and bacteria, the most notable enzyme being **urease** found in **soybean**s, **rice** and the **jackbean**. Whether Ni is an essential nutrient for biochemical processes in animals is still debated. If there is an essential requirement for Ni, it is very, very small and contamination from the air and immediate environment is enough to satisfy requirements.

Because of the low absorption rate of Ni, dietary Ni is relatively non-toxic. Dietary Ni at 250 mg kg^{-1} in the form of nickel carbonate had no adverse effects on cattle but 500 mg kg^{-1} caused a reduction in **feed intake**. Similarly, poultry were only affected when dietary concentrations were 500 mg kg^{-1} or more. (PGR)

Further reading

Eder, K. and Kirchgessner, M. (1997) Nickel. In: O'Dell, B.L. and Sunde, R.A. (eds) *Handbook of Nutritionally Essential Mineral Elements*. Marcel Dekker, New York, pp. 439–451.

Nicotinamide:

see Niacin

Nicotinamide adenine dinucleotide (NAD)

Molecular structure

$C_6H_6N_2O{\cdot}C_5H_8O_3{\cdot}PO_3{\cdot}O{\cdot}HPO_3{\cdot}C_5H_8O_3{\cdot}C_5H_4N_5$, molecular

weight 663.44 (previously called diphosphopyridine **nucleotide**; DPN; **coenzyme** I; CoI codehydrogenase I). NAD is involved as a co-factor in **oxidation**–reduction reactions in both anaerobic and aerobic cellular **metabolism**. For example, in anaerobic **glycolysis** NADH + H^+ is produced and later used to reduce **pyruvate** to L-**lactate** ($CH_3{\cdot}CO{\cdot}COO^-$ + NADH + H^+ → $CH_3{\cdot}CHOH{\cdot}COO^-$ + NAD^+). In aerobic metabolism, in the oxidation of **substrates**, NAD^+ is converted to NADH + H^+ (lactate + NAD^+ → pyruvate + NADH + H^+). The **energy** so acquired is utilized by the electron transport system in the mitochondrion to produce ATP from ADP and P_i. (NJB)

Nicotinic acid:
see Niacin

Night blindness
A condition (nyctalopia) in which the animal is unable to see in dim **light** and takes a long time to adjust when moved from a bright light, though able to see normally in full light. It occurs in all species of farm animals and is caused by deficiency in **vitamin A**, most commonly in animals deprived of green **forage** for long periods. Night blindness may be observed when an animal is driven through obstacles in dim light. Night blindness has also been described as an inherited condition in horses. (WRW)

Nile tilapia (*Oreochromis niloticus*):*see* Tilapia

Nipple drinker:

see Drinker

Nitrate

The anion (NO_3^-) produced when nitric acid (HNO_3) disassociates into the cation H^+ and NO_3^- . Nitrate is a normal **metabolite** produced in the **catabolism** of L-**arginine**. **Nitrogen** from ammonium **acetate** is also excreted as nitrate in the rat. In plants, nitrate is taken up and reduced to NH_4^+ for use in *de novo* **amino acid** biosynthesis. (NJB)

Nitric oxide (NO)

The nitric oxide radical (NO·) is a gas and is a potent vasodilator produced by endothelial cells. NO· has a half-life of 3–4 s in cellular systems. The **enzyme** nitric oxide synthase, a cytoplasmic enzyme, produces NO· from L-**arginine**. In the reaction, L-arginine is converted into NO· and L-**citrulline**. NO· plays a role in maintenance of **blood** pressure, as a **neurotransmitter** in the brain and may have a role in **skeletal muscle** relaxation, inhibits adhesion, activation and aggregation of platelets. **Nitrite** can also be converted to NO· in the process of denitrification where the end-product is dinitrogen gas. (NJB; GW)

Nitrite

An anion (NO_2^-) produced from **nitrate** by nitrate reductase. Nitrite can be further reduced to NO· (**nitric oxide** radical). It is an intermediate in the process of denitrification by which dinitrogen gas is produced. (NJB)

Nitrogen (N)

An element (atomic mass 14) contained in the body in the form of proteins, **amino acid**s, **nucleic acid**s, **purines**, **pyrimidine**s, **vitamins**, **hormone**s, **antibodies**, **enzymes**, **urea**, **ammonia** and several other compounds. In nutrition, total nitrogen (N) in feedstuffs and body components is estimated by either the **Kjeldahl** or the **Dumas method**. In the **Weende** system of **proximate analysis**, '**crude protein**' is estimated as N × 6.25 on the assumption that the average N concentration in protein-bound amino acids is 16% (100 ÷ 16 = 6.25). However, because the N concentration in amino acids actually varies from 7.7% (**tyrosine**) to 32.2% (**arginine**), other factors may be more appropriate for certain proteins (e.g. for milk and cereal proteins), depending on their amino acid composition. Nitrogen in the body is excreted primarily as undigested dietary protein and **microbial protein** in the faeces as well as urea in urine, which is produced primarily in the liver from **catabolism** of excess dietary amino acids and amino acids released by body protein breakdown.

Some urea produced in the liver enters the gut via **diffusion** but most goes to the kidney, where it is excreted in the urine. Not all of the urea entering the gut of mammals is excreted in the faeces, because bacterial **urease** breaks down some of the gut urea to ammonia, CO_2 and H_2O. Most of this ammonia is reabsorbed and then re-metabolized in the liver to carbamoyl phosphate, and ultimately to urea again. Avian species excrete **uric acid** rather than urea as an end-product of N **metabolism**. The urethra of avians enters the **colon** such that urine and faeces are voided

together.

Ruminant animals can use urea or ammonia to make bacterial protein in the **rumen**. Also, some of the urea produced in the liver can recycle back to the rumen, where it is catabolized to ammonia and then to bacterial protein. Thus, bacterial protein produced in the rumen together with unfermented (bypass) dietary protein are the main N sources presented to the **abomasum**

(the true stomach) and **small intestine** of ruminants for **digestion** and **absorption** of amino acids. (DHB)

Nitrogen balance

A term used to describe a calculated total body balance of nitrogen ($N_{balance} = N_{in} - N_{out}$) in animal and human experiments. The concept of balance is dependent on the premise that nitrogen cannot be stored in a unique **protein** in the manner that hydrogen is stored in fat. No storage form of protein is known. Nitrogen consumed in excess of needs is expected to be converted to **urea** and excreted. Thus, **amino acid** and ammonium nitrogen consumed should be a source of nitrogen for accretion of new body substance and for replacement of endogenous nitrogen that is lost from the body as skin and **hair** and in faeces (for example intestinal excretions such as **enzymes**, cells, etc.) and in **urine**. Nitrogen balance should be positive in animals gaining weight and negative in animals losing weight. In adult animals at **maintenance**, N balance should be close to zero; this is called N equilibrium.

N balance can be used as the criterion of adequacy in

experiments designed to estimate an animal's protein (N × 6.25) or amino acid requirements for **growth** or maintenance. In these experiments the concentration of the amino acid or **crude protein** in the diet is varied and the nitrogen balance is estimated from the amount of dietary nitrogen consumed and the total amount of nitrogen excreted in urine and faeces by each of the animals fed the various diets. The maximum nitrogen balance is used as the estimate of the amount of amino acid required to maximize growth. Similar approaches are taken to estimate maintenance requirements where the balance should be zero.

Experiments designed to determine N balance require considerable effort. A number of animals must be fed the specified diets for some period of time to obtain a new steady state; then total intake and total faecal and urinary nitrogen excretion must be measured on a daily basis over a specified period of time (usually in multiples of days). The amount of time devoted to a balance experiment is critical to the repeatability of the estimate. A short time (< 1 day) would result in unacceptable error, since the nitrogen excreted may vary with time of day: faecal and urinary excretions are periodic, not continuous events. Daily variation can be 'smoothed' by carrying out the experiment for a longer period of time so that one void or defecation more or less has a small effect on the calculated answer. In experiments with humans where all apparent N consumed and N lost has been carefully assessed, calculated N balance has been positive (1.6 g N per day) in experiments over 50–220 days. In direct experiments with pigs, N balance was 16% higher than in comparative slaughters.

Experimental errors in N balance experiments tend to give a positive bias, i.e. N balance tends to be overestimated. Thus, estimates of body protein accretion from N balance experiments must be treated with caution. (NJB)

Nitrogen metabolism

The gaseous element, nitrogen, has an atomic number of 7. It is a member of group VA of the periodic system. It is a diatomic gas (N_2) that makes up 78.084 ± 0.004% volume per cent of dry air. It has a molecular (atomic) weight of 14.0067 and **oxidation** states that vary from NH_3 to N_2 to NO_3^-. Atmospheric N_2 is reduced to **ammonia** by a process called nitrogen fixation done only by bacteria in root nodules of leguminous plants. The other source of nitrogen for use by plants is **nitrate**-N (NO_3^-). Plants use these sources of nitrogen in the biosynthesis of **amino acid**s and other **nitrogenous compound**s (**nucleic acid**s, **phospholipid**s, **vitamins**, etc.) necessary for cellular structure and **metabolism**. When plants are consumed by animals or die, their nitrogenous components become available for use by other organisms. Bacteria in the soil reduce nitrate-N (NO_3^-) to dinitrogen gas N_2 in a process known as denitrification.

In animals, the majority of nitrogen is associated with the amino acids in proteins but nitrogen is also found in phospholipids, nucleic acids and a large number of other molecules. Nitrogen metabolism in animals focuses on amino acids and ammonia. Nitrogen in the form of ammonium **salts** can be used by animals as a source of nitrogen for the biosynthesis of dispensable amino

acids. The ammonium-N is incorporated into **glutamate** by the **enzyme** L-glutamate **dehydrogenase**. Dispensable amino acids can be synthesized by transferring the nitrogen from glutamate to the **keto acid** of the amino acid in question (e.g. **pyruvate** + L-glutamate → L-**alanine** + α-ketoglutarate). Glutamate-N can also be used as a nitrogen source for conversion of the keto acids of the indispensable amino acids to their respective amino acids (e.g. α-ketoisocaproate + L-glutamate → L-**leucine** + α-ketoglutarate). The indispensable amino acids L-**lysine** and L-threonine cannot be formed in this way as their keto acids are either not produced or do not participate is such reactions.

The stable isotope of nitrogen, ^{15}N, is widely used as a tracer in research dealing with nitrogen metabolism. This includes the rate and extent of **digestion** and **absorption** of nitrogenous compounds, rates of synthesis and degradation of specific proteins and the metabolic transformations of amino acids to other nitrogenous constituents and the quantitative significance of these processes in relation to an animal's overall metabolism. An important dynamic aspect of nitrogen metabolism in animals involves the processes of **protein synthesis** and protein breakdown, processes that, together, are known as **protein turnover**. They can be measured using stable (^{2}H, ^{15}N, ^{13}C) or radioactive (^{3}H, ^{35}S, ^{14}C) isotopes. All the proteins in the animal body are involved in these processes. The half-life of proteins (a measurement with units of time^{-1}) varies from 6 min to as long as 6 months or more. The process of protein turnover allows animals to modify their metabolic potential continuously, to meet new

nutritional and environmental demands. In addition to protein turnover, amino acid nitrogen is incorporated into protein that is lost from the body as milk, fetuses, skin or hair. Nitrogen derived from amino acid **catabolism** is directed towards the production of ammonia-N and aspartate-N used in the synthesis of **urea** ($H_2N{\cdot}CO{\cdot}NH_2$). The main nitrogen excretory product in mammalian urine is urea but up to 5% of urinary N may be in the form of ammonium-N. Ammonium-N as a percentage of total urinary nitrogen can vary because of alterations in acid–base balance, since $NH_4^+$is used as a counter ion for anions such as Cl^- that must be excreted. The main nitrogen excretion product in birds is **uric acid**, while that in fish can be urea if the fish lives in **salt water** or ammonium if it lives in **fresh water**. (NJB)

Nitrogen recycling

The cyclical movement of nitrogen between the gut and the rest of the body, particularly important in ruminants. Nitrogen from **amino acid**s catabolized in the tissues is incorporated into **urea**. A portion of **blood** urea is secreted into the **gastrointestinal tract**, where bacteria use it as a source of nitrogen for their **growth**. In ruminants, the **saliva** is a major route of urea entry into the **rumen**. The bacteria from the rumen are digested in the **small intestine** and the resulting amino acids are absorbed. These may in turn be catabolized, giving rise to urea which again can be secreted into the rumen, continuing the cycle. The same process occurs in non-ruminants but to a lesser degree. Similar cycling has been described for **sulphur**. (NJB)

Nitrogen retention

An increase in the nitrogen content of the body, synonymous with positive **nitrogen balance**. It may be measured in a nitrogen balance experiment as the difference between the nitrogen consumed and the nitrogen excreted in **faeces** and **urine**. It may also be measured in a comparative slaughter experiment as the gain in total body nitrogen over the course of the experiment and can have units of g per day or mol per day. (NJB)

Nitrogen utilization efficiency

The utilization efficiency of nitrogen refers to the percentage of dietary nitrogen (proteins, **amino acid**s, and non-amino acid nitrogen such as **ammonia** and **urea**) being converted into proteins, peptides, and amino acids in body tissues, **milk**, **eggs**, **wool**, and other useful products in animals. Biological efficiency is a major determinant of economic efficiency to minimize costs for livestock and poultry production as well as **aquaculture**. Levels of economic efficiency are usually set by practitioners and there is not a gold standard or a universally established minimum above which the biological efficiency of animal production would be considered adequate. A major goal of animal agriculture is to fully realize the genetic potential of farm animals for their **reproduction**, **lactation**, **growth** (including accretion of **protein** in **skeletal muscle**), and resistance to infectious and metabolic diseases, while preventing excessive accumulation of white **adipose tissue** in the body.

Because dietary protein has no **nutritive value** until it is digested by the **gastrointestinal tract**, **digestion** is a key factor

affecting the efficiency of nitrogen utilization by animals. About 97% of nitrogen in the body exists as proteins. Due to differences in the **digestive system**s and nutrient **metabolism**, there are species differences in the efficiency of the utilization of dietary nitrogen for body or product protein gain (see table). Because **insulin** sensitivity in skeletal muscle and the rate of whole-body **protein synthesis** are decreased with age, young animals have a greater nitrogen utilization efficiency than older ones. Nutritional strategies to improve the retention of dietary nitrogen as protein in animals include: (i) supplementing functional amino acids (e.g. **arginine**, **branched-chain amino acid**s, **glutamine**, **glutamate**, **glycine** and **tryptophan**) to plant protein-based diets to reduce intestinal amino acid **catabolism**, increase the entry of dietary amino acids into the portal circulation, and activate cell signalling pathways (such as the mechanistic target of rapamycin pathway (MTOR)); (ii) optimizing the proportion and amounts of all proteinogenic amino acids in diets through use of synthetic amino acids, including those that can be synthesized in the body; (iii) creating and augmenting pathways for the endogenous synthesis of amino acids (e.g. arginine, glutamine, **proline** and threonine) through genetic or metabolic engineering; and (iv) alleviating adverse impacts of the environment (e.g. **heat stress** and air pollution) on animal metabolism and health. In strict **carnivore**s, dietary **taurine** is essential as a non-proteinogenic amino acid for the optimum efficiency of nitrogen utilization. (GW)

Efficiencies of the utilization of dietary protein for the production of animal protein in the current agricultural system[a]

Species	Weeks of production	Efficiency for body or product protein gain (%)	Efficiency for edible protein gain (%)
Broiler chickens	6	39.9	33.3
Pigs	25	37.6	29.6
Laying hens[b]	55	34.0	31.3
Hybrid-striped bass[c]	26	34.2	15.4
'Cereal' sheep	13	28.6	18.3
Grazing sheep	13	11.8	7.6
Sheep (Merino; wool)	52	15.8	22.5
Cows (milk)	44	17.9	17.9
'Cereal' beef cattle	54	18.9	12.1
Grazing beef cattle	76	10.5	6.7

[a] The efficiency for protein gain was calculated as edible protein in product (e.g. tissue, eggs, or milk) ÷ protein intake from diet × 100%. The

values for land animals were obtained from Cao *et al.* (2021), Williamson (2011) and Wu (2018).

[b] A laying hen produces 17.7 kg edible eggs (295 eggs × 60 g per egg) in 55 weeks. The edible egg does not include its shell.

[c] Hybrid-striped bass growing from 120 g to 610 g over a 6-month period (Rawles *et al.*, 2018). The efficiency for protein gain was calculated as edible protein based on the assumption that fish-processing industries generate 45% of edible protein from hybrid-striped bass.

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Nitrogen-free extract (NFE)

This is an estimate of the soluble **carbohydrate** (i.e. **sugars**, **starch** and **hemicellulose**) present in a feed or other material. NFE is determined by difference: it is the substance remaining after the weights of all other assayed components (moisture, **crude**

protein, **crude fibre**, **ether extract** and **ash**) have been subtracted from the weight of starting material. The accuracy of NFE measurement is questionable in that, being determined by difference, it includes the accumulated errors of other assays. It is not, in itself, an assay, but simply 'what's left'. (CBC)

Nitrogenous compounds
Organic or inorganic compounds that contain the element **nitrogen**. In animal nutrition, those of concern include **ammonia** (NH_3) and oxides of nitrogen (nitrogen dioxide, NO_2; nitrous oxide, N_2O; **nitric oxide**, NO), water-soluble inorganic forms such as hydroxylamine (NH_2OH), **nitrite** (NO_2^-) and **nitrate** (NO_3^-) and a host of organic forms critical to the structure and function of living organisms, such as **amine**s, **amide**s, imines, **amino acid**s and related compounds, **nucleic acid**s, **phospholipid**s, **carnitine**, **creatine** and **vitamins**, as well as waste products such as **urea** and uric acid. (NJB)
See also: Non-protein nitrogen

Nitrosamines
Formed by the reaction of nitrites with **amine**s during preservation or curing of **meat**, cooking or in the warm acidic conditions of mammalian stomachs. Although nitrosamines are potent hepatotoxins and **carcinogen**s, only a few **poisoning**s have been reported when sheep and mink were fed **nitrate**-treated fish meal. **Nitrite** and nitrate were formerly widely used as preservatives in cured **meat product**s. Currently, **sodium** erythrobate and **ascorbic acid** are added to nitrite-preserved

meats to limit nitrosamine production. (LFJ)

Nivalenol:
see **Deoxynivalenol**

Non-essential amino acids
The amino acids that are synthesized by animal cells were historically considered to be dispensable in diets and were classified as nutritionally non-essential amino acids (NEAAs). This concept was first proposed in 1912 on the basis of **nitrogen balance** studies with dogs. In most mammals (e.g. humans, rats and pigs), the traditionally classified NEAAs are **alanine**, **arginine**, **asparagine**, aspartate, **cysteine**, **glutamate**, **glutamine**, **glycine**, **proline**, **serine** and **tyrosine**. Rates of NEAA synthesis depend on the availability of **substrate** and **energy**, as well as species, breed, age, physiological status and disease state. The *de novo* synthesis of arginine in animal cells is species-specific, as most mammals (e.g. humans, pigs, cattle, sheep, mice and rats) synthesize this **amino acid** from glutamate, glutamine and proline, but birds, some mammals (e.g. cats, ferrets, mink and tigers) and perhaps many species of carnivorous fish cannot. In contrast to mammals, the *de novo* synthesis of proline in birds and certain fish is limited, whereas rates of glycine synthesis are much lower than rates of glycine utilization in poultry, young pigs and some fish. In ruminants, physiological amounts of **ammonia** are utilized by their ruminal bacteria to form all proteinogenic (**protein**-creating) amino acids in the presence of adequate **carbohydrates** and **sulphur**. Of note, there are species

differences in the *de novo* synthesis of **taurine** (a non-proteinogenic amino acid that is highly abundant in animal tissues), as the conversion of cysteine into taurine is active in livestock and poultry but is limited in cats, human infants and some carnivorous fish.

NEAAs have many physiological functions that cannot be fulfilled by the so-called nutritionally essential amino acids (EAAs). These functions include: neurotransmission; renal regulation of acid-base balance; conjugation with **bile** acids; antioxidative reactions in retinal cells, heart, and **skeletal muscle**; conversion of **folate** to **tetrahydrofolate** in one-carbon **metabolism**; synthesis of bioactive molecules, including amino **sugars**, **nucleotides**, **glutathione**, haem, **nitric oxide**, carbon monoxide, **hydrogen sulphide**, **polyamine**s, **serotonin**, **choline**, **carnitine**, **creatine**, γ-aminobutyrate, **dopamine**, melanin, **melatonin**, thyroid **hormone**s, D-**serine** and D-aspartate. Additionally, some NEAAs (e.g. arginine, glutamate, glutamine, glycine and proline) can activate cell signalling pathways, such as the mammalian target of rapamycin and mitogen-activated protein kinase.

NEAAs are about 50% more abundant than EAAs in the bodies of animals. Results of extensive studies over the past 30 years have shown that: (i) animals cannot adequately synthesize NEAAs to meet their optimal metabolic and functional needs under either normal or stress conditions; and (ii) animals have dietary requirements for NEAAs in order to fulfil their genetic potential for maximum **growth**, **reproduction**, **lactation** and production

performance, as well as optimal health and well-being. The concept of 'NEAAs' has now been recognized as a misnomer in nutritional science and should be replaced by amino acids that are synthesizable *de novo* in animal cells (AASAs). This new concept in nutrition is now transforming the practices of feeding farm animals (including pigs, poultry, fish and crustaceans) worldwide. (GW)
See also: Essential amino acids

Further reading

Hou, Y.Q. and Wu, G. (2018) Nutritionally essential amino acids. *Advances in Nutrition* 9, 849–851.

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Non-protein amino acids

Amino acids found in feedstuffs or in the body that are not components of protein. (DHB)

Non-protein nitrogen

Although this is not a strictly defined term, it usually refers to **nitrogenous compound**s other than proteins and polypeptides. These include **ammonia**, **amide**s, nitrogenous **glucosides**, **urea**, **amino acid**s and the amino acid derivatives **creatine**, **creatinine** and uric acid. These compounds can provide **nitrogen** which can be incorporated into amino acids and thus become part of a **protein**. Peptides such as glutathione (γ-glutamylcysteinylglycine) are not considered as non-protein nitrogen even though they are not proteins. (NJB)

Non-shivering thermogenesis
The normal response to a **cold environment** is to increase metabolic **heat production**, either voluntarily by exercising or by eating more, or reflexly by shivering or increasing muscular tension. Non-shivering **thermogenesis** is the name given to increased heat production observable in some species, especially in the very young of those species, when there is no obvious cause for its occurrence. It tends to be seen in species that have a particular form of **fat** deposit, called **brown adipose tissue**. (JAMcL)

Non-starch polysaccharides
The polymeric fraction of **dietary fibre** that includes all **polysaccharide**s except **lignin** and **starch**. It is typically a mixture of **cellulose**, **hemicellulose**s, pectins and **gums**. (JAM)
See also: Carbohydrates; Pectin substances

Norepinephrine
A **hormone**, also called noradrenaline, synthesized by the chromaffin cells of the **adrenal** medulla. It is derived from L-**tyrosine**, which is hydroxylated to become DOPA (dihydroxyphenylalanine), then decarboxylated to become **dopamine** and finally hydroxylated to become norepinephrine. It is classified as a catecholamine and is part of the sympatho-adrenal system. The preganglionic nerve fibres of the splanchnic nerve terminate in the adrenal medulla where they innervate the chromaffin cells that produce the **catecholamines**. This system is required for adaptation to acute and chronic stress. (NJB)

Nuclear magnetic resonance (NMR)

NMR spectroscopy is used to characterize the structure of organic and inorganic compounds. Certain atomic nuclei produce a magnetic moment that can be aligned by an external magnetic field producing **energy** levels that provide the basis for the NRM spectrum. The spectrum of a nucleus in a molecule is made up of radio frequencies that are characteristic of the position of that nucleus in the molecule. There are over 100 nuclei that give observable NMR spectra, the more common ones being ^{1}H, ^{13}C, ^{19}F, ^{31}P and ^{15}N.

Nuclear **magnetic resonance imaging** (MRI) uses the same principle to produce images of body organs and tissues. It is widely used in medical diagnosis and can also be used to assess **body composition**. (JEM)

Nucleic acidsRibonucleic acid

(RNA) and **deoxyribonucleic acid** (DNA) are made up of three components: a **purine** (**adenine** or **guanine**) base or **pyrimidine** (**cytosine**, **uracil** or thymine) base, a 5-carbon **sugar** (D-2-deoxyribose or D-ribose) and phosphoric acid. DNA contains only deoxyribose and RNA contains only ribose. Both DNA and RNA contain adenine, guanine and cytosine; thymine is found only in DNA while uracil is found only in RNA. (DMS)

Nucleotides

Nucleotides are derived from nucleosides, which are the combination of a **purine** or **pyrimidine** base with a **pentose sugar**. The **nucleic acid**, **adenine**, linked to ribose, is called

adenosine; and **cytosine** linked to ribose is called cytidine. Nucleotides are called ribonucleotides or deoxyribonucleotides based on whether the **sugar** is ribose or 2-deoxyribose. When the ribose or deoxyribose sugars of the nucleosides are phosphorylated in the 5′ position, they are designated as nucleotides. The five nucleotides are adenosine monophosphate (AMP), guanosine monophosphate (GMP), cytidine monophosphate (CMP), uridine monophosphate (UMP) and thymidine monophosphate (TMP). (NJB)

Nutraceutical
A substance, contained in a food, that benefits health in addition to any role it may have in meeting established **nutrient requirement**s. Nutraceuticals may include isolated nutrients, dietary **supplement**s, diets, foodstuffs and herbal products. (MFF)
See also: Functional food; Pharmafood

Nutrient
A substance in the diet that is physiologically useful in cellular, animal and plant **metabolism**. Essential nutrients (e.g. indispensable **amino acid**s, **minerals**, **vitamins**) are those that can only be acquired from the diet or medium. Many nutrients (e.g. dispensable amino acids, glucose, most **fatty acid**s) can also be derived from other nutrients or synthesized *de novo* from simpler substances by the organism. Nutrients are usually considered to be simple components of food, such as amino acids, rather than the more complex proteins, because it is the indispensable amino acids

that are required rather than **protein** per se. Nutrients participate in metabolism by providing **substrates** and precursors but do not control metabolism, which is the role of the more complex substances made from them (e.g. DNA, **enzymes**, co-factors, **coenzyme**s and **hormone**s). Nutrients include amino acids, **carbohydrates**, **fats**, vitamins, macrominerals, trace minerals and ultra-trace minerals. **Energy** is also sometimes considered as a nutrient, although it is really the summation of the heats of combustion of all the components (mainly the fats, proteins and carbohydrates) in the diet. (NJB)

Nutrient balance

The difference between the supply (intake + endogenous production) of a nutrient and its loss from the body. 'Balance' sometimes means equilibrium but sometimes gain (positive balance) or loss (negative balance). The concept can most easily be applied to nutrients that are not produced or destroyed in **metabolism**. Thus, one can measure the balance of elements such as **sodium**, carbon or **nitrogen** by deducting from intake the sum of the losses in faeces, urine, **sweat**, expired air, etc. For nutrients such as **glucose** or water, some estimate has to be made of the amounts produced or broken down in metabolism of the animal. The concept can be extended to non-nutrient balances such as **energy balance**, which encompasses the energy content of fat, protein and carbohydrate energy stored. (NJB)

Nutrient deficiency

The supply of a nutrient at a rate below an animal's requirement,

leading to clinical symptoms of deficiency. These symptoms vary widely between nutrients and between species. Primary nutrient deficiencies derive from a restricted intake of a nutrient. Secondary nutrient deficiencies may occur as result of an excess of another nutrient; for example, excess iron in the diet may sometimes cause a deficiency of **copper** and vice versa. A deficiency of even one essential nutrient in the diet can result in **inappetence**, and thence to general **undernutrition**. (JMF)
See also: Mineral deficiencies; Protein deficiency; Starvation; Vitamin deficiencies; individual nutrients

Nutrient requirement
The amount of a nutrient needed for a specified purpose which, in farm animals, may be maximum weight gain, milk yield, etc. Because an animal's requirement for a nutrient is conditioned by many factors, nutrient requirements are no longer regarded as fixed quantities that must be supplied in all circumstances; instead, changes in animal performance with alterations in nutrient intake are now seen as dynamic responses that can be used to derive estimates of requirements that are appropriate to the particular animal and circumstances. (MFF)
See also: Response to dietary energy and nutrients

Nutrient uptake:
see **Absorption**

Nutrigenomics
The scientific study of the relationships between nutrients and

genetic expression, with application in improvements to animal productivity and the prevention or treatment of diseases in animals and humans. This emerging science recognizes that the animal phenotype responds to environmental influences (especially nutrition) as well as genetic influences, and that the relationships need to be modelled and quantified. Key nutrients involved include **vitamins** D, E, C, **folate**, B_{12} and **choline**. (RB)

See also: Simulation modelling

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Nutrition

The biochemical and physiological process by which an organism uses food to support its life. It includes ingestion, **absorption**, assimilation, biosynthesis, **catabolism** and excretion. (DB)

Nutritional disorder

Any malfunction of the body caused by deficiency or excess of one or more nutrients, or imbalance between nutrients. In severe disturbances, the disorder will be accompanied by clinical symptoms, in which case there is a state of disease. (JMF)

Nutritional wisdom

The theory that animals can detect and consume **feeds** with the

optimum **nutrient** concentration for their wellbeing. There is evidence from livestock selection of diets varying in **protein** and some **mineral** elements, especially **calcium** and **sodium**, that they will select an optimum **diet**, when offered a choice of feeds. This may involve regular sampling of the different feeds, which will help the animal to survive in the case of one feed suddenly becoming unavailable. It is unclear if this ability to select an optimum diet when given a choice is a learnt characteristic, genetically programmed or both. (CJCP)
See also: Optimal foraging

Nutritive value
A non-specific term for the value of the feed as a source of **energy** or specific **nutrients** for a class of livestock. In **forage** evaluation, it has a special meaning related to characteristics that influence nutrition independent of intake – for example, **chemical composition** and **digestibility** of the forage and the nature of the digested products. (IM)

Nut
A **fruit** that consists of a hard or leathery (indehiscent) shell enclosing an edible kernel; or the kernel itself. Many types of nut are made into **oil** cakes and meals, which can be fed to all livestock classes. **Groundnut** is one of the most common cakes. All may contain **aflatoxins** and legally require **detoxification** prior to use in feeds. (JKM)

Nylon bags:

see In sacco

O

Oat unit (OU)
The oat unit system is very similar to the **starch equivalent**, and expresses the efficiency of feed for **lipid** deposition relative to the value of 1 kg of oats. The system has mainly been employed in Eastern European countries. (JvanM)
See also: Energy systems

Oats
Several members of the **Gramineae** (**grass**) family. The best known are *Avena sativa*, *A. sterilis* and *A. strigosa*. Generally 'oats' refers to *A. sativa*, which has long been established as a feed for ruminants and horses. It is mainly cultivated in the cool, moist regions of North America and northern Europe and the leading oat-producing countries include the USA, Russia, Kazakhstan, Canada, France, Poland, Finland, Germany and Australia. More recently, the demand for oats has been somewhat reduced due to competition from hybrid **maize** varieties and **lucerne** (also known as alfalfa). Among **cereal**s, oats are second only to **rye** in

their ability to survive in poor soils. With sufficient moisture, oats will grow in sandy soils or in soils of poor fertility or highly acidic soils, but the crop is particularly prone to **drought**.



The common oat, *Avena sativa*, is a cereal grown for feeding to humans, horses and cattle. It grows well in poor quality soils. Photo courtesy of Leonora Enking. Licensed under CC BY-SA 2.0.

Oat **grain** (kernel) comprises the seed, the **pericarp** (or seed coat) and the hull (or husk), the latter consisting of the palea and lemma and collectively referred to as 'glumes'. As the oat grain develops, the glumes adhere to the grain – unlike **barley**, in which the glumes fuse with the outer surface of the developing grain. In oats, the hull and the **endosperm** account for approximately 25% and 63% of the total seed weight, respectively.

Oats are cultivated mainly as a livestock feed and may be harvested unripe and fed either fresh or as **silage**. Oat grains are most commonly fed to livestock and may be physically processed by **crushing** or rolling. Relatively small quantities are used for human food purposes, since the hull is not easily removed from the grain. The contribution of the hull to the overall seed weight is

affected by variety, environment and season and can vary from 23% to 35% of the seed weight. An increase in the proportion of hull results in an increased fibre content and a concomitant decrease in overall **energy value**. A variant called naked oats (*Avena nuda*) has a hull that can be easily removed during threshing, leaving the kernel.

The **crude protein** (CP) content of oat grains, at 79–149 g kg^{-1} dry matter (DM), is influenced by the level of **nitrogen** fertilizer application, a higher protein content resulting from increased nitrogen use (see table). However, oat proteins are generally of poor quality since they are low in the essential amino acids **lysine**, **methionine**, **histidine** and **tryptophan** (4.9, 2.7, 3.1 and 2.0 g kg^{-1} DM, respectively). Glutamic acid is the most abundant **amino acid** in oat protein, with a mean content of 23.4 g kg^{-1} DM (19.5–30.0 g kg^{-1} DM). The **oil** content of oats, at 29–80 g acid **ether extract** (AEE) kg^{-1} DM, is higher than in other cereal seeds and is predominantly (60%) concentrated in the endosperm. The oil fraction comprises mainly **unsaturated fatty acid**s, particularly oleic and **linoleic acid**s (39% and 42% of total acids, respectively). **Starch** is in the range 420–530 g kg^{-1} DM. Oats are rich in **phosphorus**, micromineral elements, **thiamine**, nicotinamide and **pantothenic acid**. In naked oats the contents of CP (range 103–164 g kg^{-1} DM), oil (range 65–113 g AEE kg^{-1} DM) and starch (range 537–637 g kg^{-1} DM) are higher and these levels largely reflect the lower fibre content of the grains, at 310 and 123 g **neutral detergent fibre** (NDF) kg^{-1} DM for oats and naked oats,

respectively.

Chemical composition of oat grains and oat by-products (as g kg^{-1} DM unless specified). (Source: MAFF, 1990, UK Tables of Nutritive Value and Chemical Composition of Feedingstuffs.)

Feed type	**DM** (g kg^{-1})	**CP**	**EE**	**Starch**	**NDF**	**GE** (MJ kg^{-1} DM)
Oat grain (all seasons)	858	108	41.1	471	310	19.6
Naked oats (all seasons)	860	123	91.7	581	123	20.1
Oat husks[a]		14.4	4.4	10.0		
Oat dust[a]		111	50.0	111		
Oat feed meal[a]		37.8	16.7	63.3		

[a] Assuming an average DM content of 900 g kg^{-1}. Source: Givens, D.I., Clarke, P., Jacklin, D., Moss, A.R. and Savery, C.R. (1993) *Nutritional Aspects of Cereals, Cereal Grain By-products and Cereal Straws for Ruminants*. HGCA Research Review No. 24. HGCA, London, 180 pp.
CP, crude protein; DM, dry matter; EE, ether extract; GE, gross energy; NDF, neutral-detergent fibre.

While oats are largely cultivated for livestock feeding, they are also used in the manufacture of oatmeal for human consumption. Dehulled kernels are also used in breakfast cereal manufacture. Although oat **flour** is not generally considered suitable for bread making, it is used to make biscuits.

The processing of oats for human food gives rise to a number of **by-product**s, which are available for livestock feeding. These include oat hulls, oat dust and meal seeds, with oat hulls representing the main by-product (about 0.7 of total). Oat hulls (or husks), comprising the hull and variable quantities (maximum of 10% of total) of oat kernels from the processing of screened oats into oat groats, consist mainly of oat **bran** and **endosperm**. The hulls contain high levels of fibre (350–380 g kg^{-1} DM) and are of very low **energy value**. **Protein** content is also extremely low (about 30 g kg^{-1} DM) and is poorly digested. Oat hulls are generally unsuitable for feeding to pigs and poultry and are mainly fed to ruminants. Oat dust comprises mainly fractions of the kernel, particularly the fine hairs, which are removed from the hulls in the final stages of processing the oat grain. This product

contains modest amounts of protein (about 100 g kg^{-1} DM). A product known as oat feed is sold commercially for livestock feeding and comprises a mixture of oat dust and oat hulls (approximate ratio of 1:4) and also quantities of oat flour. It contains high levels of fibre (790 g NDF kg^{-1} DM) and the overall composition of the by-product is affected by the proportions of oat dust, hulls and flour used, especially of oat hulls. Although generally of low **nutritive value**, it is suited to **ruminant feeding**.

The dehulled kernels (also called groats) are of high nutritive value. They are mainly used for human consumption but small quantities are used in the diets of early-weaned pigs.

During further processing the tips of the kernels, containing a high proportion of germ, are removed and these, together with any other residues removed during processing, are combined and referred to as flowmeal. This is a high-quality feed and is generally used by the **compound feed** industry.

A further by-product arising following the harvest of oat grain is oat **straw**. This makes a minor contribution to the overall amount of straw available in the UK and contains comparable protein content to barley and **wheat** straws. Oats may also contribute an important source of forage for ruminants. In North America and Continental Europe, oats sown in the autumn and harvested in the spring are used as a **forage crop** for dairy cows and beef cattle. (ED)

Further reading

Mathews, R., Kamil, A. and Chu, Y. (2020) Global review of heart health

claims for oat beta-glucan products. *Nutrition Reviews,* 78 (Suppl. 1), 78–97.

Obesity

A disease condition characterized by excessive fat accumulation on the body that presents a risk to health, **welfare** and quality of life. It results from an imbalance between nutrient consumption and expenditure, in particular **energy**. The associated **eating disorder** is regulated by the **hypothalamus**. The most common association is with a high-fat diet. It affects the ability to exercise and is associated with many diseases, including **diabetes**, high **blood** pressure, osteoarthritis, heart disease, respiratory distress and cancer. Obese animals are less heat tolerant. It is common in humans, companion and **zoo animals**, typically diagnosed when animals are more than 20% heavier than their ideal weight.

According to the World Health Organization (WHO, 2022), people with a body mass index (BMI) (body weight (kg)/height $(m)^2$) of ≥ 30.0 are generally classified as obese, and those with a BMI of 25.0–29.9 are defined as overweight. There are three classes of human obesity based on BMIs: class I (30.0–34.9), class II (35.0–39.9) and class III (≥ 40.0). For comparison, individuals with BMIs of 18.5–24.9 or < 18.5 are considered to have a normal body weight or be underweight, respectively. However, these BMIs may not apply to certain populations, such as persons in Asian countries (who have relatively high proportions of **body fat**) and well-trained athletes (who have relatively high proportions of lean tissue mass). For example, Asian women with BMIs of 23.0–27.5 or > 27.5 are considered overweight or obese, respectively. Muscular

men and women, such as bodybuilders, can have a BMI above a range for the general population but may not be obese. For farm, laboratory, companion and zoo animals, body weight may serve as a criterion for overweight or obesity classification: overweight if they weigh 10–20% above their ideal body weight; obese if they weigh ≥ 20% above their ideal body weight. Both genetic and environmental (including high fat intake and sedentary lifestyle) factors contribute to the development of obesity.

Obesity in humans and companion animals is a growing health problem in many regions of the world, including developed and developing nations. The WHO reported that, in 2016, globally 39% of adults (≥ 18 years of age, about 1.9 billion people) were overweight, with 13% of them being obese (i.e. about 650 million); and the prevalence of overweight or obese children and adolescents aged 5–19 years worldwide increased 3.5 times from 4% in 1975 to 18% in 2016 (340 million). According to the US Centers for Disease Control and Prevention (CDC, 2022), 41.9% of adults (≥ 20 years of age) and 19.7% of children and adolescents (2–19 years of age) were obese in March 2020, with the obesity rate for the whole population nearly tripling over the past 50 years.

In North America, about 50% of domestic cats aged 5–11 years have a body weight greater than their ideal weight and about 30–35% of domestic cats are obese. In humans as well as farm, laboratory, companion and zoo animals, obesity increases risks of hyperglycaemia, type 2 diabetes, cardiovascular diseases (e.g. **hypertension** and stroke), many cancers (e.g. pancreatic and colon cancers), fatty **liver disease**, neurological disorders (e.g.

dementia), **kidney disease**, gout, joint problems, physical weakness, infertility and polycystic ovary syndrome, erectile dysfunction and pregnancy complications. Currently, human obesity costs the US healthcare system US$147 billion a year. Corrective activity includes regular weighing and assessing fat covering at certain key places, which vary between animals but typically include the ribs, pin bones of the pelvis and behind the shoulder blades. Improving nutrition (particularly nutrient and **energy intake**s) and increasing **energy expenditure** through regular physical exercise are key to preventing and treating obesity. (GW; CJCP)

References

CDC (Centers for Disease Control and Prevention of the United States) (2022) Overweight and obesity. Available at https://www.cdc.gov/obesity (accessed 3 September, 2022)

WHO (World Health Organization) (2022). Obesity. Available at https://www.who.int/health-topics/obesity#tab=tab_1 (accessed 3 September, 2022)

Ochratoxins

A family of isocoumarin derivatives of **phenylalanine**. Nine ochratoxins (OAs) have been identified but only ochratoxins A and B are significant. They are nephrotoxins produced by several *Aspergillus* and *Penicillium* fungi and are produced in moist **grain** stored at cool temperatures. **Ammonia** treatment of grains eliminates ochratoxin. (PC)

Octadecanoic acid

An 18-carbon **saturated fatty acid** with the common name **stearic acid**. It is found in animal and plant fats. (NJB)

Odd-chain fatty acids
Fatty acids with an odd number of carbon atoms (i.e. 3, 5, 7, 9, 11, 13). They are usually saturated. In animal **metabolism** they are catabolized by the same system as the even-chain fatty acids and this may be an advantage, because the terminal three-carbon unit derived from β-**oxidation** is propionyl-CoA, from which the carbon can be converted quantitatively to **glucose**. Odd-chain fatty acids are found in **milk** fat. In fatty acid biosynthesis two carbon units are added, yielding even-chain fatty acids when a two-carbon unit is the starting point and odd-chain fatty acids when **propionate** is the starting point. (NJB)

Oesophageal groove:
see Ruminoreticular groove

Oestrogens
Female steroid sex hormones. Oestrogens also occur in plants such as *Trifolium* spp. and include genistein, formononetin and coumestrol. These phytooestrogens interfere with animal **reproduction**. (TA)

Oestrous cycle
The hormonally controlled cycle of activity of the reproductive organs of post-pubertal, non-pregnant female animals. Most non-primate mammalian species have oestrous cycles. Ovulation occurs at regular intervals in synchrony with sexual receptivity (oestrus).

Appetite tends to be depressed on the day of oestrus. (PJHB)

Offal:
see Fish products; Meat products; Milling by-products

Oil palm (*Elaeis guineensis* Jacq.)
Tree indigenous to West Africa and grown in plantations in Asia. Indigenous trees reach 20 m in height but cultivated varieties are shorter, allowing the bunches of fruit to be picked more easily. The fruit is reddish orange when ripe and consists of a fibrous layer covering a small **nut**. Palm **oil** is extracted from both the nut and the outer covering. The fruit itself accounts for around 45% by weight of the fruit bunch. The remaining 55% can be used as fuel in the oil extraction plant.



Fruits of the oil palm tree. Photo courtesy of Theo Crazzolara. Licensed under CC BY 2.0.

Palm oil pressed from the fibrous layer constitutes 20% of the fresh bunch weight, while a further 12% is pressed fibre. Palm oil sludge is the waste from purification of palm oil. Nuts that can be

separated from the pressed fibre are 13% by weight, of which the nut kernel accounts for 4%. The kernel provides approximately equal amounts of palm kernel oil and kernel cake. Palm pressed fibre and palm oil sludge can be safely included up to 40% in ruminant rations. A mixture of palm pressed fibre and palm oil sludge in equal proportions can constitute up to 50% of the ruminant ration. However, the **palatability** of mixed rations containing palm oil sludge declines rapidly, and fresh feed mixes need to be prepared each day. Palm oil residue should be limited to 10–15% for non-ruminants. Palm oil sludge has a variable **nutrient** level, characterized by a high **ash** content (up to 24%), which interferes with the **mineral** balance.

Typical composition of oil palm products (% dry matter).

	DM (%)	**CP**	**CF**	**Ash**	**EE**	**NFE**	**Ca**	**P**
Palm pressed fibre	86.2	4.0	36.4	9.0	21.0	29.6	0.31	0.13
Palm oil sludge		9.6	11.5	11.1	21.3	46.5	0.28	0.26

	DM (%)	CP	CF	Ash	EE	NFE	Ca	P
Palm kernel cake, solvent extracted	90.8	18.6	37.0	4.5	1.7	38.2	0.31	0.85
Palm kernel cake, mechanically extracted	88.2	15.8	29.7	3.7	23.0	27.8	0.21	0.47

CF, crude fibre; CP, crude protein; DM, dry matter; EE, ether extract; NFE, nitrogen-free extract.

Typical ME content and digestibility (%) of major constituents (abbreviated as above) in mechanically-extracted palm kernal cake fed to ruminants and pigs.

	CP	CF	EE	NFE	ME (MJ kg^{-1})
Ruminant					
Palm kernel cake, mechanically extracted	84.9	60.0	96.1	85.3	13.87
Pigs					
Palm kernel cake mechanically extracted	60.0	36.3	25.0	76.7	9.43

Palm kernel cake has a high oil content but is of poor palatability on its own. Solvent extracted meal is reported to be less palatable than meal from mechanical extraction. Palatability improves when it is included in the diet of dairy cattle, raising the **butterfat** content of milk. Up to 30% palm kernel meal can be included in pig rations but high levels of inclusion cause scouring.

Palatability is higher for older pigs than with young animals. Rations with palm kernel meal results in the production of **pork** with firm fat. (LR)

Oilmeals:
see Oilseed; Oilseed cake

OilsTriacylglycerols, usually of vegetable origin (the main exceptions are **marine oils**), that are liquid at room **temperature**. Oils commonly used as animal and human foodstuffs are **maize** oil, **olive** oil, **rape**seed oil, **soybean** oil and **sunflower** oil. These have high concentrations of **unsaturated fatty acid**s, mainly oleic (18:1) and linoleic (18:2) acids. **Linseed** oil has a high content (50–60%) of **linolenic acid** (18:3). Other vegetable oils, such as **coconut** and palm kernel oils, have high concentrations of shorter-chain **saturated fatty acid**s (12:0 and 14:0). (JRS)
See also: Fats

Oilseed
The seed of plants such as **soybean**, **rape**, palm, **sunflower** and **groundnut** which contain a relatively high concentration of **lipid**. (JMW)

Oilseed cake
The residue remaining after the extraction or expression of **oil** from **oilseed**s. Major oilseeds are **soybean**, **rape**seed, **oil palm** kernel, **sunflower** and **groundnut**. (JMW)

Okinawa Longevity Diet:
see Competition for grain between humans and animals

Oleic acid
An 18-carbon **unsaturated fatty acid**, *cis*-9-octadecenoic acid, 18:1 n-9 (Δ^9). It is found in vegetable **oils**. (NJB)

Oligopeptide
A **peptide** made up of no more than eight **amino acid**s. Peptides with more than eight amino acids are called polypeptides. (NJB)

Oligosaccharides
Compounds containing two to ten **monosaccharide**s linked in a linear or branched chain. The division between oligosaccharides and **polysaccharide**s is somewhat arbitrary, varying from seven to 15 **sugar** residues. Oligosaccharides may be produced during the **metabolism** of certain polysaccharides of plant or animal origin; they are **carbohydrate** components of glycoproteins and proteoglycans, in which they may have signalling and immunological functions and they are carbohydrate constituents of **glycolipid**s. (JAM)
See also: Dietary fibre; Fructans; Galactolipids; Mucin; Peptidoglycans; Raffinose; Stachyose; Verbascose

Olive
The fruit of the olive tree (*Olea europeae* L.), grown most commonly in the Mediterranean region of Europe, North Africa, Australia and parts of America. Extraction of olive **oil** leaves a pulp, which can be dried and pelleted to produce expressed olive

cake containing over 10% oil (see table) (which can quickly become rancid), and solvent-extracted oil cake.



The olive (*Olea europaea*, meaning 'oil from/of Europe') is a species of small tree in the family Oleaceae. The species is cultivated in many places and considered naturalized in France, Corsica, Crimea, Egypt, Iran, Iraq, Syria, Java, Norfolk Island, California and Bermuda. Photo courtesy of Olive trees. Licensed under CC BY 2.0.

Typical composition of olive products.

		Nutrient composition (g kg^{-1} DM)					
	Dry matter (g kg^{-1})	**Crude protein**	**Crude fibre**	**Ash**	**Ether extract**	**NFE**	**ME** (MJ kg^{-1})
Fresh leaves	579	131	177	61	73	558	–

		Nutrient composition (g kg^{-1} DM)					
	Dry matter (g kg^{-1})	**Crude protein**	**Crude fibre**	**Ash**	**Ether extract**	**NFE**	**ME** (MJ kg^{-1})
Dry leaves	921	106	229	87	82	496	–
Twigs	868	89	289	85	61	476	–
Leaf silage	770	122	202	84	79	506	–
Olive cake	852	63–105	300–400	42–68	119–145	357–376	–
Olive pulp	600–937	84–110	200	47–88	280–330	472–592	5.1

DM, dry matter; ME, metabolizable energy; NFE, nitrogen-free extract.

The feeding quality of these is low, especially when the pits (stones) are not removed. Dried olive cake can be fed to cattle at < 10% of the diet and to grower and finishing pigs at < 5%. **Urea**-treated (50 g urea kg^{-1}) olive cake has been fed to Awassi lambs as a replacement for < 30% of dietary **cereal**s but **feed intake** was reduced. Olive leaves and twigs provide cattle **fodder**, especially when the trees are pruned. The leaves should be fed fresh but can be left on the branches and stripped later for feeding or can be ensiled. Mature drier leaves require soaking in 2.5 volume water

with 0.2% **salt** for 12 h prior to feeding. Sheep and cattle can be fed leaves fresh at 1–1.5 kg per day or dried at 0.8–1 kg per day per 100 kg liveweight. Olive oil is high in **oleic acid** and can be included in **rabbit** diets at < 30 g kg^{-1} and, with **vitamin E**, in **chicken** diets at < 100 g kg^{-1} to reduce muscle **lipid** oxidation. It can be fed to ruminants at < 30 g kg^{-1} but higher levels will reduce feed intake, due to low **palatability**. **Solid-state fermentation** has been used to increase the **protein** content of olive pomace from 59 g to 403 g kg^{-1} for inclusion in poultry diets. (JKM)

Omasum

The third compartment of the ruminant **stomach**. It communicates anteriorly with the **reticulum** through the reticulo-omasal orifice, and posteriorly with the **abomasum** through the omaso-abomasal opening. Many leaves (omasal laminae) project inwards from its greater curvature, largely filling its lumen and greatly increasing the absorptive surface area. It is lined by a stratified squamous epithelium through which water, **volatile fatty acid**s and **sodium** are absorbed. **Digesta** entering intermittently through the reticulo-omasal orifice may pass between the leaves or flow along the omasal canal into the abomasum. (RNBK)

See also: Forestomach

One-carbon metabolism in animals

One-carbon metabolism involves **folate**, **histidine**, **methionine**, **glycine** and **serine** to provide the methyl donors required for cells to synthesize thymidine and **purines** for synthesis of RNA

and DNA, **polyamine**s and **creatine** (Fig. 1). In addition, ***S*-adenosylmethionine** (SAM, a **metabolite** of methionine) is used for **methylation** of DNA, associated proteins, and RNA responsible for epigenetic gene regulation. Within mitochondria, **catabolism** of glycine, serine and **choline** (dimethylglycine sarcosine) generates 5,10-methyl-THF, 10-formyl-THF, and then folate by mitochondrial monofunctional formyl–tetrahydrofolate (THF) synthase (MTHFD1L) (Fig. 2). Then, 5,10-methylene-THF **dehydrogenase** activity interconverts the resulting 5,10-methenyl-THF with 10-formyl-THF in both the mitochondrial and cytosolic compartments. Formate–THF ligase activity can either release or reassimilate formate in an ATP-dependent manner. In the cytosol, these activities depend on MTHFD1, whereas mitochondria have both MTHFD2 (bifunctional methylene-THF dehydrogenase/methenyl-THF cyclohydrolase) and MTHFD2L (mitochondrial **isozyme** of MTHFD2 in adult tissues). The metabolic cycle that catabolizes serine in mitochondria and synthesizes serine in the cytosol is thermodynamically induced in response to differences in electrochemical potential between mitochondrial nicotinamide adenine dinucleotide + hydrogen (NADH) or nicotinamide adenine dinucleotide phosphate (NADPH) and cytosolic NADPH. MTHFD1 uses NADPH and MTHFD2/L uses NADH, whereas MTHFD2L may use both NADH and NADPH. The high NADPH/$NADP^+$ ratio in the cytosol favours the flux from formate toward serine in the cytosol. Folate is exported from mitochondria into the cytosol of cells.

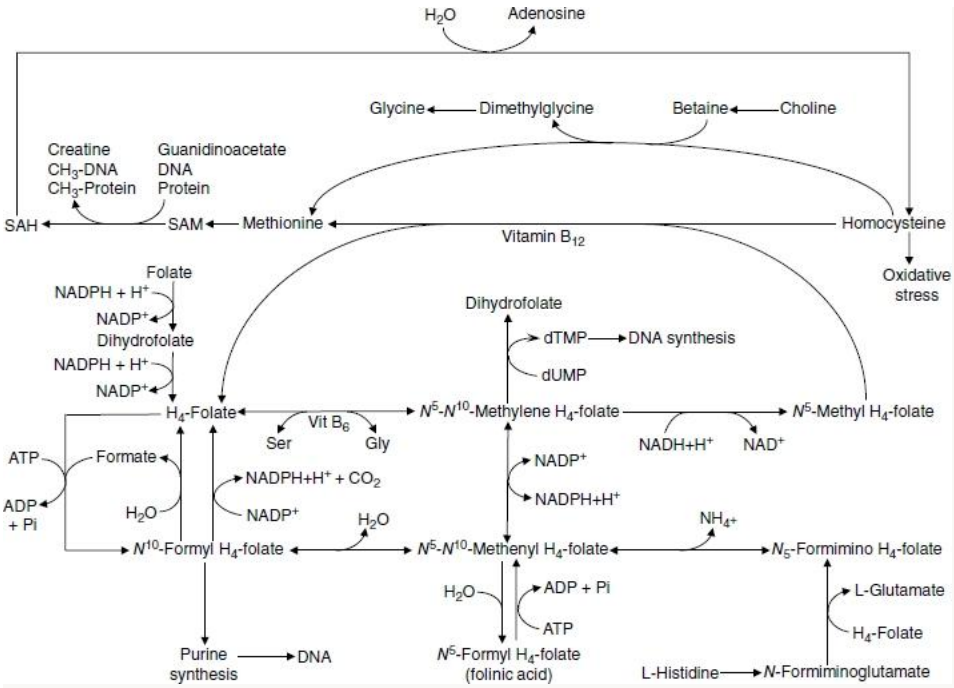


Fig. 1. Formation of formate from serine in animal cells. ALDH1L1, 10-formyl-THF dehydrogenase; ALDH1L2, 10-formyl-THF dehydrogenase; dTMP, 2′-deoxythymidylate; dUMP, 2′-deoxyuridylate; Gly, glycine; GCS, glycine cleavage system; Ser, serine; THF, tetrahydrofolate; Vit B_6, vitamin B_6.

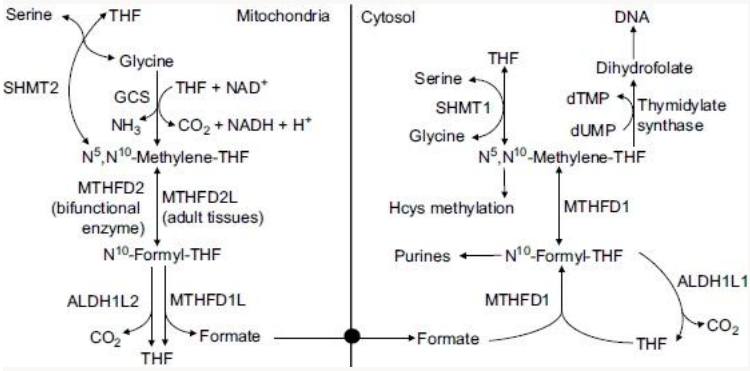


Fig. 2. One-carbon metabolism in cells. dTMP, deoxythymidine 5'-monophosphate; dUMP, deoxyuridine 5'-monophosphate; Gly, glycine; H_4-folate, tetrahydrofolate; Hcys, homocysteine; MTHFD1, methylene-THF dehydrogenase (cytosolic); MTHFD1L, mitochondrial monofunctional *N*10-formyl-THF synthetase; MTHFD2, mitochondrial bifunctional methylene-THF dehydrogenase/methenyl-THF cyclohydrolase; MTHFD2L, mitochondrial **isozyme** of MTHFD2 in adult tissues; SHMT1, serine hydroxymethyltransferase-1 (cytosolic); SHMT2,

serine hydroxymethyltransferase-2 (mitochondrial); SAH, *S*-adenosylhomocysteine; SAM, *S*-adenosylmethionine; Ser, serine; THF, tetrahydrofolate; Vit, vitamin. Reproduced from Wu, G. (2022) *Amino Acids: Biochemistry and Nutrition*. CRC Press, Boca Raton, Florida.

Serine hydroxymethyltransferase 2 (SHMT2) initiates one-carbon metabolism as this **enzyme** converts serine to glycine for **nucleic acid** synthesis, but serine from dietary **protein** intake can directly increase the cytosolic one-carbon pool via SHMT1. In rapidly proliferating cells, catabolism of serine, glycine and choline is the primary source of cytosolic one-carbon units released from their mitochondria. Increased rates of biosynthesis of serine from **glucose** and **fructose**, as well as **glutamate** (the amino group donor), is one of the characteristics of proliferating cells such as those of placentae and tumours. Within mitochondria, SHMT2 catalyses the reversible reaction of serine and THF to glycine and 5,10-methylene-THF. 5,10-methylene-THF is required for synthesis of formate within mitochondria. Formate then moves into the cytosol for synthesis of thymidine for synthesis of purines.

Quantitatively, choline, methionine, serine, glycine and histidine are the most important dietary sources of one-carbon units. Folate in animal diets is absorbed in the intestine and enters the vascular circulation. Dietary deficiencies in folate result in anaemia, neural tube defects, inhibition of cellular proliferation required for growth and development and cardiovascular deficiencies. (FWB; GW)

Further reading

Bazer, F.W., Seo, H., Johnson, G.A. and Wu, G. (2020) One-carbon

metabolism and development of the conceptus during pregnancy: lessons from studies with sheep and pigs. *Advances in Experimental Medicine and Biology* 1285, 1–15.

Brosnan, M.E. and Brosnan, J.T. (2016) Formate: the neglected member of one-carbon metabolism. *Annual Review of Nutrition* 36, 369–388.

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Onion

Several species (*Allium* spp.) of bulb-bearing plants cultivated in temperate and subtropical regions. The bulb is a modified stem of fibrous material that is fed fresh or used as a flavouring in animal feed. It has diuretic qualities and stimulates the intestines.



Red and white onions. Photo courtesy of Richard North. Licensed under CC BY 2.0.

Animals fed onions have increased water intake. For ruminants, mixing chopped or crushed onions in a **total mixed ration** will prevent addictive consumption. Cattle fed onions (> 25% of total diet) exhibit elevated red blood cell numbers and **haemoglobin** concentrations, and while the packed cell volume returns to baseline values within 30 days following discontinuation of feeding, Heinz bodies will be detected in erythrocytes for longer periods at

levels proportional to the amount of onions consumed. Onions can be fed to cattle at 25% and sheep at 50% of the total dry matter (DM) intake, but they cause meat and milk **taint** and limits of 5–10% are recommended in dairy and finishing beef cattle. The DM content of onions is 113 g kg^{-1} and the nutritive composition (g kg^{-1} DM) is **crude protein** 104, **crude fibre** 159, **ether extract** 14, **starch** and **sugar** 762, and **ash** 33. (JKM; CJCP)

Ophidine:
see Balenine

Optimal foraging
It is speculated that animals will select areas of feed that allow them to optimize their intake of vital nutrients. This may require them to sample feeds regularly, visiting patches of feed to determine the **nutrient availability**. Intake rate is maximized by visiting patches of feed with different levels of nutrient availability at a frequency determined by the distance between patches and availability of nutrients in each patch. The energetic cost of foraging is offset against the nutritional benefit derived from grazing any particular patch. Optimal foraging is in essence a demonstration of **nutritional wisdom**.

Optimal foraging theory determines that the composition and volume of **grass** eaten is balanced against the cost of grazing to optimize intake of the required nutrients. Herbage height determines **biting** rate and bite size, so that intake can be maintained at constant levels by increasing the biting rate when individual bites are small. However, very short pastures require

longer grazing time as bite mass declines to low levels and is unable to be compensated for by a rapid biting rate.

Herbivores typically spend much longer eating than **carnivore**s, because the derived nutrients from the pasture grass are less than from animals. Horses, for example, typically graze for 13–18 h per day, cattle for 10–12 h. (CJCP)
See also: Dispersion strategy

Orange (*Citrus sinensis*)
Globally, oranges are the largest citrus crop. They are grown mainly in the tropics and subtropics. Grass in citrus orchards can be grazed by sheep and calves. Cattle can eat approximately 40 kg of fresh oranges per day but the fruit should be fed after milking, to avoid **milk** discoloration. Sliced oranges can be fed to pigs. Citrus pulp and meal, peel, rag (internal tissue) and seeds are palatable to cattle. Fresh pulp can be ensiled to feed all year round and **fermentation** is improved when the pulp is ensiled with tropical grass. Citrus **molasses**, a thick, bitter liquid condensed from liquor discarded from the pulp, can be fed to cattle and used to substitute 10–40% of **maize** in pig rations. Dry citrus pulp is very palatable and keeps well when lime is added to remove the pectin. The **oil** from citrus seeds can be extracted but the oil cake can be fed only to ruminants, due to its limonin content. The dry matter (DM) content of oranges is 150–250 g kg^{-1} and the nutritive composition (g kg^{-1} DM) is **crude protein** 70–113, **crude fibre** 50–94, **ash** 39–66, **ether extract** 24–75 and NFE 400–780. (JKM)
See also: Citrus products

Organic acids
Acids (R·COOH) that contain carbon. Note, however, that carbonic acid (H_2CO_3) is not considered to be an organic acid. All have a dissociable **hydrogen** ion ($R{\cdot}COO \rightleftharpoons R{\cdot}COO^- + H^+$). Common examples in nutrition are acetic ($CH_3{\cdot}COOH$) and the longer straight-chain **fatty acid**s. Other organic acids can be more complex, such as **benzoic acid** ($C_5H_5{\cdot}COOH$) or the bile acid, **cholic acid** ($C_{24}H_{40}O_5$). (NJB)

Organic compounds
Compounds that contain the element carbon but excluding **carbon dioxide** (CO_2), **bicarbonate** (HCO_3^-), carbonic acid (H_2CO_3) and related compounds. Compounds can be: (i) aliphatic (straight-chained), including alcohols and esters; (ii) **carbohydrates**, simple **sugars** and complex carbohydrate compounds found in plant cell walls; (iii) cyclic (closed-ring) compounds such as naphthalene, benzene and combinations of these two in fat-soluble **vitamins**; or (iv) **amino acid**s and products derived from them. (NJB)

Organic farming and human and animal nutrition
Food to a large extent is what holds a society together and eating is closely linked to deep spiritual experiences.

[Peter Farb and George Armelagos in *Consuming Passions: The Anthropology of Eating, 1980*]

The origins of organic farming can be traced to proponents such as Rudolph Steiner (1861–1925), an Austrian philosopher; Sir

Albert Howard (1873–1947), a Cambridge-trained botanist; Lord Northbourne (1896–1982), an Oxford-trained agriculturalist; and Hans-Peter Rusch (1906–1977), a medical practitioner who collaborated with Hans Müller (1891–1988) to develop a system of biological agriculture in Switzerland. The term 'organic farming' appears to have been conceived by Lord Northbourne, derived from his concept of 'the farm as organism' in which he distinguished 'chemical farming' from 'organic farming'. His 1940 book *Look to the Land* is regarded as a manifesto of organic agriculture. Howard's concept of soil fertility was centred on building soil humus with an emphasis on a 'living bridge' between the soil and the life it contained (such as fungi, mycorrhizae and bacteria), and on how this chain of life from the soil supported the health of crops, livestock and humans. Human health in this instance may be taken to include mental health arising from satisfaction that the products were derived from a system of farming that attempted to minimize the damage to the soil, plants, animals and humans.

Steiner went on to propose 'biodynamic agriculture', a system of organic farming that has its basis in a spiritual view of the world, using approaches such as fermented herbal and mineral preparations as compost additives and field sprays and the use of an astronomical sowing and planting calendar. This farming system became popular in Australia and parts of North America.



Austrian philosopher Rudolf Steiner (1861–1925) had important ideas about farming systems that shaped our attitudes to organic farming. Photo courtesy of Stefano Lubiana. Licensed under CC BY 2.0.

Lady Eve Balfour (1898–1990) was one of the first women to study agriculture at a British university, graduating from the institution now known as the University of Reading. In 1939 she established the Haughley Experiment in England, the first study to compare organic and conventional farming methods on one farm, and in 1946 she co-founded and became the first president of the Soil Association, an international organization which promotes sustainable agriculture. She became one of the UK's main organic farming advocates, at a time when post-war Britain was seeking to increase domestic production, and hence food security, through highly mechanized, intensive agriculture (with the support of the Agriculture Act of 1947). The Experiment was taken over by the

Soil Association in 1947, which for the next 25 years directed and sponsored it. The work was not a scientific experiment in the conventional sense, because it had no replication, most probably because funding was difficult, and it needed to last for several decades to demonstrate long-term lasting effects on soil microflora and fauna. Based on the early findings, Balfour published a book *The Living Soil* in 1943, which was criticized in a review in the journal *Soil Science*: 'The author is an evangelist for organic farming. She has little understanding of scientific method. If the evidence does not favor her thesis, it is ignored' (Anonymous, 1951). Nevertheless, an article in *Nature*, acknowledging the difficulty of conducting such work, reported the study as important (Anonymous, 1957). A scientific paper was later published which used between- and within-field variation to demonstrate large increases in earthworm population and longer roots and shoots from winter wheat (Blakemore, 2000). Soil samples were not subjected to statistical analysis but, based on means and standard errors, suggested much greater concentrations of soil carbon and some other elements in the organic unit.

According to the Codex Alimentarius Commission and the Joint FAO/WHO Food Standards Programme, organic agriculture is:

> ... a holistic production management system which promotes and enhances agroecosystem health, including biodiversity, biological cycles, and soil biological activity ... emphasizes the use of management practices in preference to the use of off-farm inputs as opposed to using synthetic materials. The primary goal is to optimize the health and productivity of interdependent communities of soil life, plants, animals and people ... the systems are based on specific and precise standards of production which aim at achieving optimal agroecosystems which are socially, ecologically and economically sustainable.

Organic production also requires certification and verification

of the production system. This requires that the organic producer must maintain records sufficient to preserve the identity of all organically managed crops and stock, and all inputs of edible and non-edible organic products from the farm (Blair, 2012). Like all other foods, organic foods in most countries are subject to national food regulations to ensure their safety and (unless sold directly to the consumer) are subject to routine inspection and testing for chemical, toxicological and microbiological hazards.

The European Union has one of the most comprehensive set of regulations concerning organic farming. Organic certification is available for live and unprocessed agricultural products, animals, plants, seeds and mushrooms, processed food and feed for non-human animals. There are lists of agrifood products, aquaculture products, algae, microalgae and yeasts that can be used in organic agriculture. New concepts for organic agriculture in the EU, and its suppliers outside the EU, include biodiversity, a non-toxic environment, long-term fertility and resistance against disease in plants and animals, and longevity. New Zealand is one country that includes a detailed list of approved feed ingredients in its organic regulations, a very useful feature of their regulations. The EU has a somewhat similar list to New Zealand, but it details non-organic feedstuffs that can be used in limited quantities in organic feeds for poultry. It may be inferred from the EU list that organic sources of the named ingredients are acceptable. In addition, the New Zealand regulations stipulate that the feeds must meet the Agricultural Compounds and Veterinary Medicines (ACVM) Act and regulations, and the Hazardous Substances and New

Organisms (HSNO) Act, or are exempt, thus providing additional assurance to the consumer. The EU has certified suppliers and trade agreements with many countries that include agreement on organic certification.

As outlined above, in the organic system the farm is treated as a whole entity with an acknowledged close interrelationship of the soil, plants and animals in a closed, self-nourishing system. Organic farms are often more generalized with integrated production systems, compared with conventional farms, which tend to specialize in producing crop, pigs, eggs, milk, etc. Ideally, the organic farm is self-sufficient in terms of needs such as fertilizers, seeds, feeds, etc. and is intended to be sustainable and harmonious with the environment. It prohibits the use of chemical fertilizers and pesticides, products produced by genetic modification (GM) techniques, irradiation as a preserving process, sewage sludge as fertilizer, and synthetic processing aids and food additives.



Organic farming in the Philippines. Synthetic fertilizers are replaced by manure and weeding is usually by hand. Photo courtesy of DFAT photo library. Licensed under CC BY 2.0.

When organic herds and flocks are established, the breed or strain of animal should be selected so that the animals are adapted to their environment and resistant to certain diseases. Livestock must come from holdings that comply with the rules governing organic farming, and they must be reared in accordance with those rules throughout their lives. In the production of organic meat, the animal must be given a prescribed amount of living space (no cages), access to outdoors and be given organic feed. Only natural pesticides and medications are allowed for preventive purposes, but medications are allowed for treatment of diseased livestock, and vaccines are permitted. If an animal is diseased and is treated with medication, it no longer can be considered organic. No antibiotics or **growth hormone**s are permitted.

Organic agriculture requires that farming systems provide for the health and natural behaviour of livestock, through access to outdoors, shade and shelter, sufficient space for exercise, fresh air, clean drinking water and direct sunlight. The result is that organic food has the appeal of having been produced 'more naturally' and not by so-called 'factory farms'. It is, however, more expensive to produce than conventional food, because it is more labour intensive. Compared with intensive agriculture, crop yields from organic farms are generally lower (by on average about 20%), depending on the extent to which legumes and manure can replace chemical fertilizers. Similar reductions are reported for livestock production. However, in developing countries crop yields may be the same or greater (provided that insect damage can be controlled), as well as reducing dependency on expensive chemical

inputs and sustaining livelihoods. Contributions to **climate** change are contentious; emissions are less, but so too is productivity, and lower production requires more land to produce the same amount of food and potentially greater deforestation. Organic crop production requires more tillage than conventional production, a disadvantage in areas of low rainfall. The lower output suggests a resilience to climate change and other challenges confronting agricultural systems today. Organic farming is conducted more commonly on small farms that do not offer the economies of scale available on larger farms (Durham and Mizek, 2021). Consequently, organic food is usually more costly to the consumer, with the products selling at a premium. The EU provides subsidies representing up to 20% of farm income to encourage organic farming, which will help it to achieve carbon neutrality.

The publication of the book *Silent Spring* by Rachel Carson in 1962 was important in that it brought the issue of **pesticide**s and the environment to the attention of the public. As a result, an increasing number of consumers began to seek out organic foods since the regulations required that these had been produced without the use of chemical pesticides.

According to data presented in the publication *The World of Organic Agriculture* (Willer *et al*., 2021), organic agriculture was practised in 187 countries in 2019, and 72.3 million hectares of agricultural land were managed organically by at least 3.1 million farmers. The increase over the previous year in organic farmland in 2019 was recorded as 1.1 million hectares (1.6%). Countries with the most organic agricultural land are Australia (35.7 million

hectares), Argentina (3.7 million hectares) and Spain (2.4 million hectares). Globally, 1.5% of farmland is organic, the highest organic shares of total agricultural land being Oceania (9.6%) and the European Union (8.1%). Global sales of organic food and drink reached more than 106 billion euros in 2019.

In 2021 Sikkim, a Himalayan state in India, became the first state in the world to convert all of its farmland to organic following a phase-out of chemical fertilizers and pesticides that started in 2010. Sri Lanka attempted to follow that example in 2021 and become the first country to be 100% organic in terms of crop production, but according to press reports (e.g. the *European Scientist*) the result has been that agricultural production has decreased and rural poverty has increased (Malkanthi, 2021). A main contributory factor appears to be an inadequate supply of acceptable fertilizer. Based on the Sikkim experience, it may also be concluded that a more gradual conversion to organic agriculture is more likely to be successful.

Under the European Green Deal, the EU has set an ambitious target for 2030 (EC, 2021) with the main aims being for at least 25% of EU agricultural land to be farmed organically and a significant increase in organic **aquaculture** (fish farming). One interesting aspect of the aquaculture proposal is that it is aimed at farmed fish and not wild fish. This is because farmed fish can be fed and reared in such a way that they meet the standards for organic designation. Since fishers have no control over the rearing or feeding of wild fish, it is impossible to grant the organic designation to their catches. A related question is whether **fish**

products such as fish meal are permitted in the organic feed regulations relating to livestock. It is fortunate that they are accepted as such, since they are valuable sources of **protein** and **amino acid**s for poultry and **pig feeding**, particularly when supplementary sources of pure amino acids are restricted or not allowed. However, they have to be derived from sustainable sources and any **antioxidant** added to prevent spoilage has to be from an approved list. An example of a new feedstuff that might be acceptable in organic feeds is insect larval meal, which is being produced in several countries from **substrates** such as household and grocery-store **food waste**. Some certifying agencies take the view that the meal produced is a permissible ingredient (and a good source of protein) in organic feed, while others take the view that the insect meal is unacceptable as an organic feed ingredient since the substrate used cannot be verified as organic. Producers planning to use this type of product should, therefore, obtain approval from a local certifying agency before doing so.

As explained by Blair (2012), the attainment of organic status involves four stages:

1. application of organic principles (standards and regulations);
2. adherence to local organic regulations;
3. certification by local organic regulators; and
4. verification by local certifying agencies.

'Organic' is a production claim and not a food safety claim. According to the USDA (United States Department of Agriculture) there are four labelling categories for organic foods:

1. ‘100% organic’ foods contain only certified organic ingredients and use certified organic processing aids.
2. ‘Organic’ foods must contain at least 95% certified organic ingredients.
3. Foods ‘made with organic’ (specified ingredients) must contain at least 70% organic ingredients.
4. Foods with less than 70% organic ingredients may not display the USDA ‘organic’ seal on the package but may identify which ingredients are organic on the ingredient panel.

Other countries and organizations have derived their own standards for defining foods as organic. The organic regulations prevailing worldwide are developing a commonality. This will assist trade in organic products between countries and facilitate imports into the three large markets: Europe, North America and Japan.

Most consumers accept that any organic food offered for sale has been produced according to the prevailing regulations. However, several cases of fraud have been reported, some sellers passing off regular food and feedstuffs as the more expensive organic type. Unfortunately there is no way of proving that the food is indeed organic just by inspection. Several research groups have attempted to derive a chemical test to identify whether foods have been produced organically, but to date none have been successful and suitable for implementation. Authenticity has to be verified by records. As a result, many consumers prefer to buy organic food directly from the grower. A large range of organic foodstuffs is now

available in many countries, including vegetable produce, fruit, milk, meat and eggs.

Consumers are attracted to organic foods because the way in which they have been produced is considered more environmentally friendly or the perception that the food is safer, more nutritious, healthier and tastier. They may have an overall feeling that the product has desirable attributes, a so-called 'halo effect'. For instance, Schutz and Lorenz (1976) and Johansson *et al.* (1999) reported that information about the way food had been produced influenced its acceptability to consumers. When compared with unlabelled foods, the same products labelled as organic generally showed increases in measures of preference. Both studies suggested that consumers have expectations regarding the superior **taste** of organic produce, based on label information. Schuldt and Schwarz (2010) tested the responses of university students to web pages displaying nutritional information on conventional cookies or similar cookies 'made with organic flour and sugar'. The participants were then asked: 'Compared to other cookie brands, do you think that 1 serving of these [organic] cookies contains fewer calories or more calories?' and 'Compared to other cookie brands, how often should these [organic] cookies be eaten?' The results showed that the students inferred that the organic cookies were lower in calories and could be eaten more often than conventional cookies. This effect was observed even when the nutrition label conveyed an identical calorie content. The effect was more pronounced among participants who were strong supporters of organic production and had strong feelings about

environmental issues.

Mondelaers *et al*. (2009) found that health-related traits were more important than environmental traits in shaping consumer preference for organic vegetables. The presence of an organic label was important in relation to buying intensity.

Food safety

In spite of public perceptions, the Food and Agriculture Organization of the United Nations (FAO, 2021) cautioned that the organic label is not a guarantee of food safety. It explained that 'organic' refers only to a product that has been produced in accordance with certain standards throughout the production, handling, processing and marketing stages; it does not refer to the characteristics and properties of the finished product. Organic labels are based on rules that prohibit or limit the use of synthetic fertilizers and agrochemicals. Some **pesticide**s that are produced physiologically by plants as a defence mechanism continue to be used in organic agriculture, but there are stringent health tests for these organic pesticides, just as there are for pesticides that are not organic. The International Agency for Research on Cancer (IARC) has determined that the carcinogenicity to humans for three pyrethroids (deltamethrin, fenvalerate, permethrin) is not classifiable. However, organic food is often (mistakenly) considered to be 'chemical-free', which is attractive to certain consumer demographics (Durham and Mizek, 2021).

Residues

The documented findings on residues of pesticides and chemicals in conventionally produced foods of North American origin

indicate that these cannot be considered a major health concern (Blair, 2012). It is true that, in general, conventionally produced food may contain higher concentrations of pesticide residues than organically produced food (e.g. Pussemier *et al.*, 2006), but the levels in question are lower than the levels that can be considered deleterious. Some of the residues were detected merely at the limit of detection. Monitoring data published by several countries show that the **contamination** rate of conventional foods in terms of pesticides and chemical residues is falling.

A systematic review of 240 studies concluded that organic produce may reduce exposure to both pesticide residues and antibiotic-resistant bacteria (Smith-Spangler *et al.*, 2012). Testing of 12,168 samples (plant and animal products) in the 2010 EU-coordinated programme (Bjørge *et al.*, 2019) showed that 47.7% had measurable pesticide residues above the limit of quantification (LOQ), but below or at the maximum residue level (MRL); 1.6% exceeded the respective (MRL) values. A comparison of pesticide levels in organic and conventional samples of fruit, vegetables and other plant products showed that 43.2% of conventional and 10.8% of organic samples had measurable residues below or at the MRL value; 4.2% of conventional and 1.0% of organic samples exceeded the MRL values. Most of the pesticide residues detected in organic samples are not permitted for use in organic farming. Conventional products were frequently found to contain several pesticides while most organic samples were found to contain few or only one type of pesticide. Although the dataset was limited in size and distribution the authors suggested that, based on their findings, organic plant

products contain fewer and substantially lower amounts of pesticide residues than conventional products. They also suggested that the general level of pesticide residues in both conventional and organic food is low, and well below what is likely to result in adverse health effects. This conclusion was based on a comparison of estimated dietary exposure with toxicological reference values, i.e. acceptable daily intake (ADI) for chronic effects, and acute reference dose (ARfD) for acute effects. The finding of pesticide residues that exceeded established regulatory limits in a minority of tested samples was not considered by the authors to represent a health risk. A comparison of pesticide levels in 18,243 conventionally grown fruit and vegetable samples in the same dataset and their reference levels suggested that a short-term acute consumer health risk could not be excluded for 79 samples which showed values exceeding the ARfD. None of these 79 samples were organic. As the authors noted, values in excess of the ARfD occurred in only 0.4% of the samples and the scenario used for acute intake assessment was conservative, suggesting that the toxicological implications were limited. This was also reflected in the chronic exposure assessment, in which none of the samples were found to exceed the toxicological reference value (ADI). Based on the comparison of estimated dietary exposure with toxicological reference values, i.e. acceptable daily intake (ADI) for chronic effects, and acute reference dose (ARfD) for acute effects, the overall conclusion of these researchers was that the general level of pesticide residues in both conventional and organic foods is low and well below what is likely to result in adverse health effects.

The finding of pesticide residues that exceeded established regulatory limits in a minority of samples tested was not considered to represent a health risk.

EFSA (2021) issued a decision on an application by the Cyprus International Institute for Environmental and Public Health, Cyprus University of Technology, which had been submitted for authorization of a health claim pursuant to Article 14 of Regulation (EC) No. 1924/2006 via the Competent Authority of Cyprus. The EFSA Panel on Nutrition, Novel Foods and Food Allergens (NDA) was asked to deliver an opinion on the scientific substantiation of a health claim related to organic foods and contribution to the protection of body cells and molecules (lipids and DNA) from oxidative damage. The scope of the application was proposed to fall under a health claim referring to children's development and health. According to the submission, the applicant claimed that organic foods are characterized by their lower level of pesticide residues compared with foods not labelled as organic. In its decision the Panel noted that, in the application and the human studies submitted, the nutritional composition and the pesticide concentration in 'organic food' were not reported. Consequently, the Panel considered that organic foods which were the subject of the health claim, and the foods that they were intended to replace, were not sufficiently characterized. Therefore, the Panel concluded that a cause-and-effect relationship could not be established between the consumption of organic foods and contribution to the protection of body cells and molecules (lipids and DNA) from oxidative damage.

A comparison of organic and conventional foods would be much clearer if organic foods were subjected to the amount of official testing applied to conventional foods. The available findings indicate that the low levels of residues reported in conventional foods rarely exceed acceptable limits (Blair, 2012) and action is taken by regulatory authorities to remove such foods from the marketplace whenever the allowable levels are discovered. Based on the documented evidence, levels of pesticides are likely to be lower in organic produce than in regular produce, but a reduced intake in our diet is probably not meaningful in terms of human health. However, consumers concerned about the possibility of eating contaminated produce could minimize the risk by purchasing the produce directly from a local grower whom they trust. **Mycotoxin** and microbiological contamination are more important and can occur both in organic and regular foods. Concerns about 'mad-cow disease' and about possible hormone, chemical and antibiotic dangers in conventionally produced **meats** are not justified. Food regulations in developed countries are now effective in addressing these issues. For example, meat and **bone meal**, believed to be the origin of bovine encephalopathy, may still be permitted in some countries as a fertilizer on both conventional and organic farms, but usually only when the product has had any specified risk material (SRM) (including the skull, brain, spinal cord and a portion of the small intestine) removed at the abattoir. Many developed countries have banned most **animal protein**s, including SRM, for use in ruminant cattle feed and subsequently SRMs were also banned from all other animal feeds, pet foods and

fertilizers. Meat and bone meal is not approved for use in organic feed for organic livestock. Incorrect handling of meat, especially poultry meat, that leads to contamination with food-**poisoning** organisms is a recognized threat to the consumer and is of greater importance than whether the meat is from animals raised conventionally or organically. Monitoring studies conducted by official agencies indicate that the meat supply in North America is not heavily contaminated by chemical and pesticide residues or **dioxin**s and similar environmental contaminants. The levels found in various surveys can be regarded as trace amounts.

A few instances of violative residue levels have been reported in meat in several countries, but none of the published comparisons of organic and conventional meats indicate any major difference in contamination rate. Residues of chlorinated-hydrocarbon and organophosphate pesticides have been reported both in organic and in conventionally raised cattle. There are insufficient data to allow an accurate comparison to be drawn. Organic meat is therefore not completely devoid of residues. **Hormone**s are not permitted in conventional or organic pig or poultry production, but there are unconfirmed reports of their use in developing countries.

In general, the concentrations of contaminants have been found to be low in both organic (farmed) and wild (conventional) **fish**. However, pesticide residues have been found in fish produced in **aquaculture** systems, most of which are conducted in developing countries, and pesticides can also leach from fields into waterways to contaminate wild fish.

In the dairy industry, the quality of conventionally produced

milk is well controlled in Western countries and is of high quality. However, there are concerns when conventional dairy farms in some countries use artificial **growth hormone**s to boost milk production (recombinant bovine somatotropin, or rBST, a genetically engineered hormone that increases milk production). rBST injection into cows has been a part of the US food supply since this hormone treatment received approval by the Food and Drug Administration (FDA) in 1993. Its use increases both BST and **insulin-like growth factor** 1 (IGF1) in milk and meat of injected cows, but BST is destroyed by pasteurization. In addition, rBST is biologically inactive in humans and is a protein hormone that is digested and destroyed by intestinal enzymes when consumed. Each company seeking approval for rBST has to demonstrate that it has no biological activity in milk when it is consumed. The impact of IGF1 consumption is not clear, with the greatest potential risk being to infants who can absorb the proteins intact. Use of rBST is not permitted in the European Union, Canada and some other countries, mainly because cows treated with rBST tend to develop more udder infections, localized reactions to the injections and foot problems. Organic farming prohibits the use of rBST or any hormone or hormone analogue, such as those used to control bovine reproduction. Although the impacts on cow and human health are not fully understood, this allows the consumer to be more confident in the safety of the product for a small additional cost.

The available evidence indicates that both regular and organic cows' milk can contain chemical and pesticide residues,

demonstrating that pesticides are sometimes used on organic farms illegally. In the USA conventional dairy production has been reported to have residues of antibiotics and pesticides, whereas these could not be detected in organic dairy production systems (Welsh *et al*., 2019). Milk safety programmes in developed countries now require that all bulk milk tankers be sampled and analysed for animal drug residues and antibiotics before the milk is processed. Any tanker found positive is rejected for human consumption. Data from several countries indicate a 100% compliance rate for domestically produced milk in terms of pesticide and chemical residues, but there are repeated reports of residues in milk of cows in developing countries. The data from official monitoring agencies in developed countries do not always distinguish between organic and conventional dairy products. Pesticide residues have also been found in human milk, due to the bioaccumulation of pesticides over time. Some of these, such as DDT, continue to appear, despite regulations banning their use. Again, residues are more common in developing than developed countries. In many countries, it has been possible to chart declining residues of the more harmful pesticides, such as DDT, in recent decades, following bans on their use late in the last century.

The **fatty acid** profile of **eggs** from organic chicken farms may be more favourable than conventional farms because of the effects of **free range** in systems such as organic systems. Antibiotic residues in eggs are no longer a concern for the consumer, but broiler production systems in developing countries may still use antibiotics, with residues detected in the meat (Berghiche *et al*.,

2019). All commercial egg-laying poultry – free-range, barn or caged – are fed diets free of antibiotics, unless administered by a veterinarian, and, if the hens are treated, the eggs are not permitted to be sent to market. Little or no contamination of regular eggs with chemical residues has been reported, although contaminated soils in some parts of Europe appear to cause residues of dioxins in the eggs of hens allowed to range outdoors. Foods grown in such areas, conventional and organic, are likely to be contaminated for some time. Hence the level of residues in eggs from intensive production systems is usually less than from backyard producers.

Residues of **heavy metals** have been reported in **fruit** juice, both organic and conventional. The **copper** level has been reported to be elevated in some organic fruit and produce but this does not appear to be a current problem, especially since copper-based fungicides have now been banned. Copper residues came under scrutiny because of the use of Bordeaux mixture (an aqueous solution of copper sulphate and other copper salts) as a fungicide in organic agriculture. It has been reported that organic growers apply more frequent treatments with copper-based fungicides on their crops than do conventional farmers (Trewavas, 2001). Despite the fact that their use was banned after 2002, copper salts remain persistent in soil and thus raise concerns over possible food contamination with this element.

Several studies have reported a reduction in urinary excretion of pesticide residues when consumers switched to an organic diet (e.g. Hylanda *et al*., 2019). This could be a sensible strategy to

adopt when foods available locally have been grown on soils that are heavily contaminated with chemicals or the food has received excessive spraying with insecticides. Hylanda *et al*. (2019) did not state whether the pesticides investigated in the food studied in their investigation were at violative levels.

Microbiological contamination

It is likely that fresh organic vegetables represent a greater risk from **food poisoning** than conventional vegetables, because of the use of animal manure as fertilizer and a greater exposure of livestock to wild animals and birds. The serious outbreak of ***Escherichia coli*** sickness in Europe in 2011 highlighted the potential for organic produce to be a source of infection, with the European Commission through its Rapid Alert System for Food and Feed notifying the 27 Member States about one of the confirmed sources responsible for the shigatoxin-producing *E. coli* (STEC) outbreak affecting primarily Germany and four other Member States. This notification followed the reporting by the German authorities that they had identified organic cucumbers from two provinces of Spain (Almeria and Malaga) as one of the sources (EC, 2011). A subsequent joint technical report, issued by the European Centre for Disease Control (ECDC) and the European Food Safety Authority (EFSA) on 10 June, 2011, announced that contaminated **bean** sprouts from an organic farm in Northern Germany were most likely the source of the outbreak (ECDC-EFSA, 2011a). By then 29 people had died and almost 3000 people had been sickened by the infection in Europe. A subsequent announcement on 29 June, 2011 by ECDC-EFSA (2011b) further

implicated the consumption of raw fenugreek sprouts as a possible source of the outbreak in France as well as Germany. The investigation included a study of the source of the seed as well as the system of sprout production. On 5 July, 2011, the European Union voted to ban imports of some seeds and beans from Egypt until 31 October, because of their probable connection with the recent *E. coli* outbreaks in Europe. The ban covered imports of Egyptian seeds and beans for sprouting, including **legumes**, fenugreek and **soybean**s. It is advisable for consumers to be aware of the facts relating to these infections, especially since it is now known that washing microbe-infected produce or meat is not effective in avoiding food poisoning. Contamination with *Salmonella* and other food-poisoning organisms is not consistently different between organic and regular eggs and may be higher in organic eggs if they are unwashed or there is a risk of faecal contamination.

Overall, there is not enough documented data to allow a determination of whether organic farms are safer, less safe or equally at risk as sources of food poisoning. To minimize the risk of contamination, several countries (such as the USA and Canada) do not allow the use of non-composted manure. As noted above, another possible risk factor for organic farms is increased contact with wildlife, rodents, insects and birds, which are potential sources of contamination with faecal pathogens. *Salmonella* and related food-poisoning organisms are best controlled in organic and conventional poultry flocks and pig herds by vaccinations, a procedure that avoids the use of medication and the possibility of

the occurrence of disease risks to consumers.

Mycotoxin (mould toxin) contamination

Mycotoxin contamination of foods such as cereal grains and dried fruit is common worldwide and can occur in both organic and conventional products. It is likely that growing and harvesting conditions have a much greater influence on the likelihood of mycotoxin contamination than the production system (organic vs. conventional) although the recorded data do suggest a higher risk with organic grains, related to a higher incidence of insect damage. An adequate quality control programme of grains and dried fruit, etc., as well as appropriate storage conditions prior to sale of the products, help to minimize any mycotoxin problems. Such a programme also minimizes any problems in animals fed these products or bedded on cereal straw, and residues in their meat or milk. There are recorded instances of risks from mycotoxins in fruit juices, unless precautionary steps are taken. One of these mycotoxins is patulin. More frequent and higher concentrations of patulin have been reported in organic fruit juices and purees than in conventional products. The problem can be avoided by ensuring that the fruit is unaffected by spoilage. In addition it is advisable to pasteurize the juice.

Other chemical risks

Potato tubers contain glycoalkaloids, which are natural green-coloured compounds produced under the skin of the potato to repel insects and other soil organisms. These compounds can be toxic to humans. Some research indicated a higher level in conventionally grown potatoes than in organically grown potatoes,

but other research indicated the opposite. In none of these reports were the glycoalkaloids present at concentrations high enough to cause problems to humans (Blair, 2012). Also, the concentrations varied from year to year.

A main effect in vegetables grown organically is a lower **nitrate** content, due to the use of manure as fertilizer. Nitrate is generally considered a water pollutant and possibly an undesirable fertilizer residue in the food chain. The significance of nitrate in the human diet is somewhat controversial. High intakes of nitrate from drinking water have been shown to cause methaemoglobinaemia in infants and it has been suggested that high nitrate intakes may form carcinogenic **nitrosamine**s in the stomach. However, dietary nitrate may also exert a protective effect on the circulatory system. Therefore, it is not certain whether high nitrate concentrations in vegetables should be considered detrimental to adults. Several scientists have, in fact, suggested that nitrate be classified as a nutrient for humans. Research in the 1970s suggested that, by reducing nitrate to **nitrite**, commensal bacteria might be involved in the pathogenesis of gastric cancers and other malignancies, as nitrite can enhance the generation of **carcinogen**ic *N*-**nitrosamine**s. More recent studies (e.g. Lundberg *et al*., 2004) indicate that the bacterial metabolism of nitrate to nitrite and the subsequent formation of biologically active nitrogen oxides could be beneficial. Hord *et al*. (2009), in a paper published in the *American Journal of Clinical Nutrition*, quantified the nitrate and nitrite concentrations in foods and then incorporated the values into two hypothetical dietary patterns that emphasized high-nitrate

or low-nitrate vegetable and fruit choices based on the Dietary Approaches to Stop **Hypertension** (DASH) diet. They found that nitrate concentrations in these two patterns varied from 174 to 1222 mg, indicating that the hypothetical high-nitrate DASH diet pattern exceeds the World Health Organization's acceptable daily intake (ADI) for nitrate by 550% for a 60 kg adult. On this basis these researchers suggested that the data call into question the rationale for recommendations to limit nitrate and nitrite consumption from plant foods, and that a comprehensive re-evaluation of the health effects of food sources of nitrates and nitrites is appropriate. On the basis of their findings they also suggested that the strength of the evidence linking the consumption of nitrate- and nitrite-containing plant foods to beneficial health effects supports the consideration of these compounds as nutrients. A study conducted in Japan provided more information on this topic (Sobko *et al*., 2010). The 25 participants of the study were physically active, healthy volunteers (10 men and 15 women) of mean age 36 years and with a BMI < 18.5. The study had a randomized cross-over design with two dietary intervention periods during which the subjects received either a Japanese or a control (non-Japanese) diet. The participants ate common Japanese vegetables, identified as the daily source of nitrate, during the study period of 10 days. To avoid the concentration differences in nitrate/nitrite in locally produced foods, the participants were provided with fresh vegetables and staple foods from the same store twice a week during both intervention periods. During the control period, participants were instructed to avoid these vegetables. The individuals participating

in the study followed the dietary protocols without a significant weight loss or gain. Daily nitrate intake was calculated. Results showed that the nitrate provided naturally by the Japanese traditional diet was 18.8 mg kg^{-1} body weight per day, exceeding the ADI by five times (ADI, 3.7 mg kg^{-1} body weight). Plasma and salivary levels of nitrate and nitrite were higher as a result of consuming the Japanese traditional diet. Also, the diastolic **blood** pressure decreased by an average of 4.5 mm Hg during the test period compared with that with the control diet. Systolic blood pressure was not affected. The authors pointed out that the effect was obtained in normotensive subjects, similar to that seen in the recent studies. They concluded that the results further support the importance of the role of dietary nitrate in relation to blood pressure regulation and suggest it as one possible explanation for the beneficial aspects of traditional Japanese food.

Human health

The possible relationship between residues in food and resultant ill-health is of great importance and has been studied intensively because of fears that residues might build up in the human body. Some contaminants, such as heavy metals and persistent **organic compound**s (POPs), tend to be deposited in several body organs and tissues (heavy metals) and fatty tissues (POPs) and are not easily metabolized or excreted. They accumulate in living creatures, in amounts higher than background levels (for instance, in the soil). Dietary exposure is commonly by diet and increases with each step up the **food chain**, as predators consume prey contaminated with these residues. An important statement on the

possible relationship between cancer incidence and pesticide/herbicide use in food production was made by the World Cancer Research Fund/American Institute for Cancer Research in 2007 (WCRF/AICR, 2007). The fact that this report did not find any relationship between herbicide or pesticide residues in food and the incidence of cancer should be reassuring to consumers, and it is surprising that the report received very little media attention when it was presented. Its publication was the culmination of an exhaustive study, involving experts in the cancer field from a large number of countries in Africa, Asia, Australia/New Zealand, Europe and North America. The report stated (section 4.7.2) that:

> The Panel considers that the evidence is insufficient to conclude that usual intakes of industrial, agricultural, and other chemicals have an effect on the risk of human cancer

In a section (4.9.1.1) dealing with pesticides and herbicides the Panel stated:

> … the chlorinated pesticide dichloro-diphenyl-trichloroethane (DDT) has been banned from use in many countries. Other organochlorine pesticides are now largely being replaced with organophosphorus and carbamate pesticides. These newer types are less persistent in the environment and have not been found to be carcinogenic in experimental settings.

The Panel further stated that:

> The use of persistent organic pollutants (organochlorine pesticides, furans, dioxins, and polychlorinated biphenyls) will be banned by 2025 under the United Nations Environment Programme's Stockholm Convention, which entered into force in May 2004. There are theoretical grounds for concern, which are constantly reviewed by international and national regulatory bodies. However, there is no epidemiological evidence that current exposures are causes of cancers in humans, and so the Panel has made no judgements.

In a section (4.9.2) dealing with organic farming the Panel concluded that:

> Claims that foods produced by organic methods are biologically or nutritionally superior to

food produced by intensive methods are not supported by clinical or epidemiological evidence, but some food compositional data indicates higher concentrations of some constituents like vitamin C and dietary fibre.

There is evidence that organic products contain fewer residues from chemicals employed in conventional agriculture. However, the subject remains a matter of controversy. A report by Gold *et al.* (2002) analysed studies of the relationship between pesticide residues in food and human cancer development. The authors of this report concluded that there was no conclusive epidemiological evidence that pesticide residues are a significant factor for human cancer. The situation may be different in some countries that have high levels of pesticide use. As pointed out by Trewavas (2004), farmers, foresters, pesticide users and manufacturers are by occupation more likely to be exposed to higher pesticide hazards than the general public. Consequently many published studies have investigated cancer rates in these groups using comparisons with matched controls from the public, particularly in age and social status. Of 12 separate investigations on farmers involving in total about 300,000 people, 11 found that farmers had overall cancer rates substantially lower than the general public. Slightly lower numbers of investigations on pesticide users and foresters revealed a similar (8 out of 11) trend, whilst only with pesticide manufacturers were cancer rates similar to those of members of the public. These and related reports probably explain the change in advice from the cancer agencies from that given earlier. For instance, the current advice of the Cancer Research Agency in the UK (Cancer Research UK) is that eating food grown on farms that use pesticides or herbicides does not increase cancer risk, although

people who work with the highest levels of pesticides may have a small cancer risk. This agency also advises consumers to have a high intake of vegetables and fruit and to follow a healthy lifestyle that includes regular exercise. It estimates that healthier diets could prevent around one in 20 cancers.

The possible benefits of organic food over conventional produce in terms of human health have not been well researched, one reason being that dietary exposure to pesticide residues at levels typically found in and on foods being harmful to the majority of consumers is difficult to prove. For instance, if consumers are being exposed to dangerous levels of pesticides in vegetable produce, how can that be reconciled with the fact that intake of fruit and vegetables is higher now than in the past, yet age expectancy is also increasing? Consequently, any conclusion would be largely speculative. Another important fact is that there have been no obvious effects on human life expectancy or public health resulting from the introduction of pesticides about 60 years ago and their widespread usage in agriculture and horticulture since then (Coggon and Inskip, 1994).

Several bodies, in addition to the cancer agencies, have commented on the health claims for organic foods. For instance, at the Food Safety Authority of Ireland (FSAI) meeting in 2008, Dr Mary Flynn, chief specialist for Public Health Nutrition, said:

> There is a widespread belief among advocates of organic food that ecological, low input production systems result in foods of higher nutritional quality. It can be concluded that although the nutrition and health aspects of organic food have been explored in many studies, there is little evidence that organic foods confer additional health benefits to humans.

Another area of research on the topic of a possible relationship between organic food and human health is the incidence of allergies in infants. Kummeling *et al*. (2008) investigated whether organic food consumption by infants was associated with developing allergies in the first 2 years of life. Diet was defined as conventional (less than 50% organic), moderately organic (50–90% organic) and strictly organic (more than 90% organic). The records showed that of the total of 815 infants, 10% had consumed a moderately organic diet and 6% a strictly organic diet. Blood samples taken at 2 years of age were analysed for IgE (the immunoglobulin that triggers the most powerful allergic reactions). Eczema was present in 32% of infants, recurrent wheezing in 11% and prolonged wheezing in 5%. At 2 years of age, 27% of children were found to have become sensitized against at least one allergen. Consumption of organic dairy products was associated with lower eczema risk, but there was no association of organic meat, fruit, vegetables or eggs, or of the proportion of organic products within the total diet, with the development of eczema, wheezing or other signs of allergy. These results suggest that a possible relationship between consumption of organic foods and a lower incidence of allergies should be investigated further.

Although it is assumed that higher levels of **phenolic compound**s and **antioxidant**s in plant tissues are beneficial in the human diet, there is a lack of definitive information on this topic.

One of the few research groups working in this area (Olsson *et al*., 2006) studied the effects of extracts from strawberries of cv.

Honeoye, grown both organically and conventionally, on cancer cell proliferation *in vitro*. The contents of several antioxidants in the strawberry extracts were analysed and their inhibition effect on cancer cell proliferation was tested. Differences were found in the content of the antioxidants between the two cultivation methods. The content of ascorbate was 36% higher and the ratio of ascorbate to **dehydroascorbate** was eight times higher in the organic strawberries than in the conventional strawberries, whereas the contents of ellagic acid, total anthocyanidins and total phenolics were lower in the organic strawberries. No significant differences were found in the content of hydroxycinnamic acid and **flavonol**s. The strawberry extracts inhibited cell proliferation in colon cancer and breast cancer cells MCF-7 in a concentration-dependent manner. Extracts from organic strawberries inhibited cell proliferation to a higher extent than from conventional strawberries at the two highest concentrations, suggesting that the content of secondary **metabolite**s with anticancer properties were higher in the organic strawberries. It was hypothesized that the higher content of ascorbate found in the organic strawberries might have affected the higher inhibition of cancer cell proliferation by the extracts from the organic strawberries. Ascorbate is thought to act synergistically with other substances in the extracts. Briviba *et al*. (2007) studied the effect of consumption of organically and conventionally produced apples on antioxidant activity and DNA damage in human peripheral blood lymphocytes. Six healthy volunteers consumed either organically or conventionally grown apples (Golden Delicious, 1000 g) from two neighbouring

commercial farms in a double-blinded, randomized, cross-over study. The average content of total identified and quantified **polyphenol**s in the organically and conventionally produced apples was 308 and 321 mg g^{-1} fresh weight, respectively. No statistically significant differences in the total content of **phenolic compound**s or in either of the polyphenolic classes were found between the production methods. Consumption of neither organically nor conventionally grown apples caused any changes in antioxidant capacity of low-density **lipoprotein**s (lag time test), endogenous DNA strand breaks, Fpg protein-sensitive sites, or capacity to protect DNA against damage caused by **hydrogen peroxide**. However, a statistically significant decrease in the levels of endonuclease III-sensitive sites and an increased capacity to protect DNA against damage induced by **iron chloride** were determined 24 h after consumption of both types of apples, indicating a similar antigenotoxic potential in organically and conventionally grown apples. While this area of research is of great potential value in helping to improve the health and well-being of the human consumer, there are at present insufficient findings to allow a clear conclusion to be drawn.

Another approach to the question of organic food and human health is to conduct experiments on test animals. Baranska *et al.* (2008) conducted a study with rats to examine whether an organic diet affected the immune response. The diets contained lactoalbumin, casein, rapeseed oil, minerals and vitamins, and were analysed for total flavonoids, **polyphenol**s, β-carotene and lutein, pesticides, and antioxidant activity. Adult male and female Wistar

rats were kept for 3 weeks under controlled conditions with free access to water and feed. The test diets were: **grain** grown without pesticides and mineral fertilizers; grain grown without pesticides; grain grown without mineral fertilizer; grain grown with pesticides and mineral fertilizers; and control (conventional) feed. The animals were paired and bred. Twelve progeny (young males) from each experimental group were then fed each of the diets for 3 and 12 weeks. Higher lymphocyte (white blood cell) proliferation was found in rats on both diets based on feeds that had been grown without the use of mineral fertilizers. The responses correlated with the content of flavonoids and polyphenols in the diets. Proliferation was lower in rats fed diets containing organic feeds. The researchers speculated that the alteration in lymphocyte proliferation could be the result of an immunostimulatory effect of flavonoids and polyphenols in the diet or from the immunosuppressive influence of some dietary components in feedstuffs grown with mineral fertilizers. Some contrary findings on the value of plant-based antioxidants in the diet in relation to human health were provided by Hsieh *et al*. (2010), adding to the argument above that the role of antioxidants in the diet is controversial. These researchers studied quercetin, especially abundant in onions and black tea, and ferulic acid, found in corn (maize), tomatoes and rice bran. They found that diabetic laboratory rats fed either quercetin or ferulic acid developed advanced forms of kidney cancer, and they concluded that the two antioxidants appear to aggravate or possibly cause kidney cancer. These researchers concluded that health agencies such as the US

Food and Drug Administration should re-evaluate the safety of plant-based antioxidants.

The conclusions of Williams (2002) are still pertinent to the whole issue of organic food and the health of consumers:

> ... there are virtually no studies of any size that have evaluated effects of organic v. conventionally grown foods on human health. Observational studies that have been conducted to compare the health profiles of organic and conventional farmers are of questionable value because of the possibility of confounding by other lifestyle factors.

The difficulty of separating the effects of a healthy lifestyle and an organic diet on overall health can be observed in the results of a study in Europe. The German National Nutrition Survey II (NVS II) is a nationwide food consumption study providing additional information on social demographics, health and lifestyle aspects as well as anthropometric measurements (Eisinger-Watzl *et al*., 2014). Using several assessments, a comparison was conducted between buyers and non-buyers of organic food during November 2005 to November 2006 from about 500 randomly chosen sample points across Germany. The 13,074 participants aged 18–80 years were divided into groups of buyers (44.9%) and non-buyers (55.1%) of organic food. It was found that purchasers of organic food consumed 17% more fruit and 23% more vegetables as well as less meat/sausages (25%) and soft drinks (58%) than non-purchasers. These results were more pronounced for women and for more intensive buyers. Additionally, purchasers of organic food exhibited healthier lifestyle characteristics with respect to smoking behaviour, physical activity and body weight compared with non-purchasers.

Nutrient composition

One of the first comprehensive reviews of reports on the nutritional value of organic foods was by Woese *et al*. (1997). These authors reviewed data published from 1926, comprising results from more than 150 investigations which compared the quality of conventional and organic foods. The foods included cereals, potatoes, vegetables, fruits, wine, beer, bread, cakes and pastries, milk, meat, eggs and honey, as well as products made from them. Nutritional studies involving animals and humans were included. Overall conclusions were difficult to reach because of the wide variation in the various factors involved and in sampling methods. However, some differences were identified. A consistent finding was that vegetables that were grown with chemical fertilizer had a higher nitrate content than vegetables grown and fertilized organically. The effect was most noticeable in leaf, root and tuber vegetables such as spinach, lettuce and beets. A trend for this effect was also seen in potatoes. Conventionally grown wheat was found to have a higher protein content, better protein quality and better baking quality. With regard to all other nutritional components measured, it was either the case that no major differences were observed in physico-chemical analyses between the foods from conventional and organic production, or that contradictory findings did not permit any clear conclusions. The same applied to sensory tests.

Blair (2012) reviewed the available evidence and, like Woese *et al*. (1997), found that organic production affects the nutritional composition of the various food groups differently. Consequently, each food needed to be considered separately for an accurate

assessment.

Limited published data suggest that there are few differences in nutritional content between organic and conventional produce. It has been shown that the moisture concentration is usually lower in organic produce, especially vegetables and in particular leaf vegetables, in comparison with conventionally grown produce. High usage of fertilizer stimulates the yield of crops partly by increasing the moisture content, thus a measurement of total harvest yield is a useful parameter. If an organic crop shows a higher nutrient content, can this be explained by the plants producing a similar amount of nutrients to conventional plants, but depositing them in fewer fruits or grains? One research group that has reported total yield as well as nutritional content is Warman and Havard (1997), at the Nova Scotia Agricultural College in Canada. A test in question involved two treatments, organic and conventional, for **carrots** (*Daucus carota* L. cv. Cellobunch) and **cabbage**s (*Brassica oleracea* L. var. capitata cv. Lennox), in each of three years. The addition of pesticides, lime and NPK (nitrogen, phosphorus, potash) fertilizer to the conventional plots followed soil test and provincial recommendations. Lime, composted manure and insect control applications to the organic plots were according to the guidelines of the Organic Crop Improvement Association Inc. The compost was analysed for total N and applied to provide 170 kg N per hectare for carrots and 300 kg N per hectare for cabbages, which assumed 50% availability of N. In addition to marketable yields, carrot leaves and roots and cabbage sections were analysed for 12 macro- and micronutrients. Vitamins

C and E and α- and β-carotene of mature crops were determined. In two of the three years, **vitamin C** was also analysed up to 24 weeks after harvest. Analysis of the three years of data showed that the yield and vitamin content of the carrots and cabbages were similar in organic and conventional crops. The same authors (Warman and Havard, 1998) conducted a similar study on the yield, vitamin and mineral contents of organically and conventionally grown potatoes and sweetcorn (maize) and obtained results very similar to those found with carrots and cabbages. Analysis of three years of data showed that the yield and vitamin C content of the potatoes were not affected by treatment. However, the conventionally grown treatment outproduced the organically grown treatment for cv. Pride and Joy sweetcorn, but there was no difference between treatments in the yield of cv. Sunnyvee corn or in the vitamin C or E contents of the sweetcorn kernels in any year.

Some studies have shown an increased content of vitamin C, β-carotene and **phenolic compound**s in organic produce. Higher concentrations of antioxidants have been reported in **tomato**es, a food item that is a major source of phenolic compounds in the diet of some consumers. Caris-Veyrat *et al*. (2004) conducted a study to measure the content of antioxidants in three cultivars of tomatoes grown conventionally and organically and the effects of intake of the tomatoes on the antioxidant plasma status of humans. They found that organic tomatoes had a higher dry-matter content (by about 10%) than conventional tomatoes, therefore the compositional details were expressed in terms of both fresh-weight and dry-weight basis. When the results were expressed on a fresh-

weight basis, organic tomatoes had higher contents of vitamin C, **carotenoid**s and **polyphenol** (except for chlorogenic acid) than conventional tomatoes. When the results were expressed on a dry-matter basis, no significant difference was found for **lycopene** and naringenin but the concentrations of vitamin C and polyphenols remained higher in purees from organic tomatoes. In the **supplementation** study 20 young female volunteers were randomly divided into two groups and provided with a drink of 100 g of tomato puree per day. No dietary supplements of any kind were being taken during the month preceding the start of the study or during the study period. The subjects were unaware of which type of puree they received. After 3 weeks of supplementation with puree, plasma was tested, and no significant difference was found in the concentration of β-carotene, lycopene or vitamin C. All subjects showed a similar increase in plasma concentration of these compounds. Results obtained after a 3-week depletion period also showed no significant difference between the two groups. This study appears to be the first in which organic and conventional foods were compared in terms of their ability to enhance the nutritional status of consumers and the findings demonstrate the complexity in evaluating the potential benefits of organic foods. Similar findings have been obtained with respect to mineral retention between organic or conventional produce.

As noted above, there is evidence that some organic **fruit** is drier than conventionally grown fruit. When this factor and stage of ripeness are taken into account the available data indicate that organic and conventional fruits do not differ significantly in their

content of major nutrients. Fruit with a lower moisture content may have a more intense flavour due to the higher concentration of nutrients, and as a result may be preferred by the consumer. In addition, there is evidence that some organically grown fruit have a higher resistance to deterioration and better keeping quality, attributed to a lower moisture content. Higher contents of **phenolic compound**s and antioxidants have been reported in some organic fruit. Organic cereals and protein crops generally have a lower content of protein, but in other nutritional aspects are similar to conventional cereals, except for a slightly higher content of phenolic compounds (Grashorn and Ritteser, 2016). According to these researchers the contribution of **methionine** from organic feedstuffs is lower in poultry diets, an important observation since methionine is generally the first-limiting amino acid in poultry diets. These authors made the important observation that although the protein content of organic cereal grains and protein crops is lower in organic sources, the content of methionine in the major feedstuffs in relation to protein content is similar.

Organic production affects the different classes of **meat** animals in different ways; accordingly, it is not possible to generalize on the effect. However, one effect recorded in all species is a lengthening of the time taken for organically raised animals to reach market weight, so that the effect of organic production is confounded with an age effect. Thus, **beef** animals raised organically grow more slowly and produce leaner carcasses. As a result, the meat tends to have less marbling and is less tender. The altered composition of beef fat with organic production (or with

grass feeding), i.e. a higher content of PUFAs (in particular CLA), is regarded as beneficial in terms of **human nutrition**. Similar findings have been reported with pigs and poultry, the research and consumer findings suggesting that the result is a slightly tougher meat but with an enhanced flavour that is preferred by some consumers (which is probably an age effect). One study found that retail organic beef had increased contents of bioactive compounds (34% more **coenzyme** Q10 and 72% more **taurine**) than retail conventional beef (Ribas-Agustí *et al*., 2019). The main difference between organic (farm-raised) and wild fish is a higher content of fat in the organic fish. Organic dairy production, involving fresh **forage** consumption whereas conventional dairy production increasingly relies on concentrated cereal-based feed, is known to result in a higher content of PUFAs in **milk**, mainly in α-**linolenic acid**. This increase is of value in terms of human nutrition, although it has been pointed out that the important PUFAs are DHA (**docosahexaenoic acid**) and EPA (**eicosapentaenoic acid**). Another consideration is that any potential benefit will be reduced by the selection of fat-free or skimmed milk rather than whole milk.

The **fatty acid** profile of **eggs** from organic production systems may be more favourable than conventional production systems. The documented evidence indicates that organic and conventional eggs are otherwise similar in nutritional characteristics, although organic eggs may be smaller and more likely to be brown-shelled rather than white-shelled.

An important report was published by Dangour *et al*. (2009a)

which confirmed the overall assessment in this chapter on the nutritional equivalency of conventional and organic foods. As stated in the scientific report, which was endorsed by the UK Food Standards Agency:

> In an analysis that included only satisfactory-quality studies, conventionally produced crops had a significantly higher content of nitrogen, and organically produced crops had a significantly higher content of phosphorus and higher titratable acidity. No evidence of a difference was detected for the remaining 8 of 11 crop nutrient categories analyzed. Analysis of the more limited database on livestock products found no evidence of a difference in nutrient content between organically and conventionally produced livestock products. On the basis of a systematic review of studies of satisfactory quality, there is no evidence of a difference in nutrient quality between organically and conventionally produced foodstuffs. The small differences in nutrient content detected are biologically plausible and mostly relate to differences in production methods.

The report received intense media attention worldwide, which was surprising since the findings were not new. Predictably it was not received well by the organic industry, but there was little in the way of factual rebuttals.

One strong rebuttal was made by Benbrook *et al*. (2009) in the form of a letter to the editor of the American *Journal of Clinical Nutrition*. This journal had published the article by Dangour *et al*. (2009a) which was the basis of the report by the UK Food Standards Agency. The letter (in part) stated:

> Dangour et al. considered 162 articles that reported comparisons from field trials, farm surveys, or market basket studies. They excluded 54% of these studies simply because the organic certifying body wasn't stated, thus eliminating many otherwise valid comparison studies. Conversely, they apparently accepted studies with mixed cultivars and breeds because they required only identification of the cultivars or breeds not that they be identical within a study. It is well known that there can be large differences in nutrient concentrations between different cultivars of the same crop ... They also arbitrarily excluded from analysis any nutrient with < 10 valid studies.

Dangour responded to the *Journal*, stating (in part):

> Our review brought together for the first time all peer-reviewed published reports on the nutrient content of organic foods, and our conclusions are based on analysis of data presented in the studies that were categorized as satisfactory quality. Our analysis was based only on data reported in published peer-reviewed articles. We acknowledge that there is no standard way of conducting these analyses, and in response to a request we have reanalyzed the extracted data by using the log of the response ratio as our metric. We now report the results of the reanalysis that replicate our original findings. The reanalysis (Dangour *et al.*, 2009b) did not alter the basic conclusions reached initially.

Another response by these researchers was to update the number of reports analysed and to publish a subsequent paper in 2010 (Dangour *et al.*, 2010). The conclusion of this more extensive review was:

> From a systematic review of the currently available published literature, evidence is lacking for **nutrition**-related health effects that result from the consumption of organicallyproduced foodstuffs.

It is clear that a major difference in approach is that Dangour *et al.* based their analyses on peer-reviewed papers in scientific journals, whereas Benbrook *et al.* used a wider database for their analysis.

Taste

It seems clear that much of the appeal of organic food, especially when purchased at the farm or at farmers' markets, is its freshness and **taste**, justifying the decision made to concentrate the Ecropolis project on the perceived taste benefits of organic food. The Ecropolis project was established under the coordination of the Research Institute of Organic Agriculture (FiBL), Frick, Switzerland, to build a database of findings on the taste of organic food (Schmid, 2014). It may well be that freshness emerges as a more important attribute in its effect on taste than taste per se. More research needs to be conducted on this issue, since freshness

is an important attribute for many food shoppers. This aspect demonstrates the important influence the organic industry has had on the appreciation of food quality in general by the public, and no doubt will have an important influence on the conventional food industry. Freshness may explain the finding that, of the well-designed studies with fruit and vegetables that have found differences, the vast majority show a preference for organic produce.

As noted above with vegetable produce, there is evidence that some organic fruit is drier than conventionally grown fruit but is similar in nutrient content to conventional produce on a moisture-corrected basis. A slightly drier fruit is likely to have a more intense flavour and as a result may be preferred by the consumer. A drier fruit is also likely to have a higher resistance to deterioration and better keeping quality. Also, **labelling** of the samples has been shown to result in a higher rating for the produce labelled 'organic' (either correctly or falsely). Tests conducted to avoid these problems (Zhao *et al*., 2007) showed no significant differences in consumer liking or consumer-perceived sensory quality between organically and conventionally grown red loose-leaf lettuce, spinach, arugula, mustard greens, tomatoes, cucumbers and onions. The only exception was with tomatoes where the conventionally produced tomatoes were rated as having a significantly stronger flavour than the organically produced tomatoes. This was attributed to the conventionally grown tomatoes being slightly riper than the organically grown tomatoes. When the tomatoes were compared at the same stage of ripeness,

no differences in taste or flavour were recorded. Animals appear to have the ability to discriminate between organic and conventional sources of cereals. In preference tests, rats selected biscuits made from organic **wheat** over biscuits made from conventional wheat. Conversely, wild birds preferred conventional wheat seed as a winter feed, a result attributed to a lower content of protein in the organic wheat.

Animal welfare

Animals raised on organic farms must have access to pasture when weather and ground conditions permit in a system commonly known as **free range**. This gives them the opportunity to express natural behaviours, which includes searching for suitable plant material to consume or, in the case of omnivores such as pigs and chickens, searching for insects and other small animals as part of their diet. Aggression is likely to be reduced if animals are outdoors rather than at the higher stocking densities when they are indoors. Health problems of mastitis and **lameness** are reduced when livestock graze pasture rather than being fed intensive diets indoors.

In organic systems, the pasture must not have artificial fertilizers and use of pesticides is limited, hence it is likely to contain a diverse range of floral species, compared with the single species (monoculture) pursued on most conventional farms. Many organic farms rely on incorporating **legumes**, such as clovers, into a sward to fix nitrogen from the atmosphere, which has significant benefits in restricting greenhouse gas emissions. These bring risks of **bloat** in livestock consuming them, which is a serious welfare

problem when it occurs.

The diverse pastures of organic farms encourage a multitude of insects, earthworms and larger animals, which provides them with an opportunity for a life with good welfare. On conventional farms, the use of pesticides kills insects indiscriminately, usually acting on the nervous systems of the insects to overstimulate the muscles, leading to paralysis and death. Although the insects do not feel pain in the way that vertebrate animals do, we can still infer a negative impact on their welfare of using pesticides. Birds are also impacted by pesticides.



Organic farming encourages earthworms in the soil, which in turn encourages wildlife. Photo courtesy of Hedera Baltica. Licensed under CC BY-SA 2.0.

Insecticides are also used in conventional **milling** processes but not organic ones. Pesticides are rarely used by organic farmers, because disease control is by fortification of the soil and plant defences. When pesticides are used, they must be natural and break down quickly in the soil, not leaving any residues. However, as described above, clearly not all organic farmers are obeying the rules.

As well as providing nutrients for grazing livestock, organic production systems provide food for wildlife. It is not clear whether

this is preferable to incorporating 'nature strips' into conventional farming systems. There are probable benefits of organic farming for biodiversity, but these are not well documented, because of the long-term nature of any trials.

Conclusions

Organic agriculture is a holistic production management system that promotes and enhances biodiversity, biological cycles and soil biological activity. It is based on minimal use of off-farm inputs and on management practices that restore, maintain and enhance ecological harmony. The result is that organic food has the appeal of having been produced 'more naturally' and not by so-called 'factory farms'. It is, however, more expensive to produce than conventional food, because it is more labour intensive, yields are generally lower and affected more by climate than conventional farms. Organic farming is conducted mainly on smaller farms that do not offer the economies of scale available on larger farms. Consequently, organic food is more costly to the consumer, but the products usually sell at a premium. The organic label is not a guarantee of food safety; the evidence from peer-reviewed publications indicates that some organic food has some advantages in terms of vitamins, minerals and antioxidants. There is evidence of increased pesticide residues in conventional products but residues are also found in organic produce, indicating that some organic farmers are not obeying the organic regulations. Meat, milk and eggs can be produced with an enhanced content of PUFAs by feeding the animals and birds organic **feed**, or feed containing fresh herbage. The risk of food-poisoning from organisms such as

E. coli in fresh organic vegetable produce can be higher because of the use of animal manure as fertilizer. A section of consumers – especially those who follow a healthy lifestyle – is attracted to organic foods because the way in which they have been produced is considered more environmentally friendly and the perception that the food is safer, more nutritious, healthier and tastier. The existence of a halo effect has been noted in the choice of organic foods by consumers. There are evident benefits to livestock welfare in organic systems, mainly because of the use of free-range practices, and also welfare of wildlife on and around organic farms. (RB; CJCP)

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Organic matter

Any material of which the carbon can be recovered as **carbon dioxide** as the result of an **oxidation** process. In regard to a diet, organic matter is equal to the weight lost from a dry sample due to combustion (**dry matter – ash**). In an animal, organic matter is the source of heat (**energy**) during the combustion process

whereby H_2O and CO_2 and other water-soluble end-products are produced. (NJB)

Ornithine

A **non-protein amino acid** ($C_5H_{12}N_2O_2$, molecular weight 132.2). It is a component of the **urea cycle** and is synthesized in the body primarily from **arginine**. Some ornithine synthesis occurs also from either glutamic acid or **proline**. (DHB)

Orotic acidUracil-6-carboxylic acid, $C_4N_2H_3(O_2)\cdot COOH$. The initial step in the production of orotic acid is the production of carbamoylphosphate ($NH_2\cdot CO\cdot OPO_3^{2-}$). Carbamoylphosphate can be produced by two **enzymes**: carbamoylphosphate synthase I (a **liver** mitochondrial enzyme related to **urea** synthesis) and carbamoylphosphate synthase II (a cytosolic enzyme related to **pyrimidine** synthesis). If the **urea cycle** is compromised, carbamoylphosphate produced from carbamoylphosphate synthase II combines with aspartate to produce carbamoylaspartate which, after two steps, gives rise to orotic acid, which can be excreted in **urine**. The amount of **nitrogen** excreted in the form of orotic acid is in the milligram range whereas that excreted as urea-N is in the gram range. The significance of elevated excretion of orotic acid is that it is an indication of a limitation of the urea cycle. (NJB)

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Osteoblast

Bone-forming cell. These plump-looking cells originate in the embryonic mesenchyme, differentiating from fibroblasts in the formation of bone tissue. They synthesize **collagen** and glycoproteins, forming the osteoid matrix before developing into osteocytes. Calcification occurs in areas furthest from the osteoblast location. (MMax)

Osteoclast
Bone-destroying cell, also known as osteophage. These large, multinucleated bone cells are involved in the breakdown and **resorption** of osseous tissue. Osteoclasts become activated in the presence of **parathyroid hormone** and are normally found lying in a cavity or groove of the underlying bone. (MMax)

Ostrich
The ostrich (*Struthio camelus*) is the world's largest living bird, standing around 2 m tall and weighing 100–150 kg. It is native to Africa and four subspecies, generally geographically separated, have been recognized largely on the basis of the colour of the skin and wing and tail feathers. Generally, males have black body feathers, unlike the brown-grey body feathers of the female; both genders have white (or brown) primary wing and tail feathers. In sexually active males the skin on the face, abdomen and legs flushes red. Young chicks are mottled brown, white and black, **moulting** out to brown-grey plumage in juveniles. The feathers are symmetrical and lack the interlocking barbules typical of other birds. Now considered to be a neotenous bird, the adult ostrich has retained **chick**-like characteristics (e.g. large eyes, soft downy

feathers) whilst becoming sexually mature.

The ostrich is **ratite**, exhibiting a flightless, cursorial lifestyle in open savannah, scrub and desert areas. Although capable of running at speeds of 40 km h^{-1}, this is usually only a response to a threat. Vegetation forms the main diet of the bird, which has a relatively broad palate. This is reflected in the alimentary tract, which is characterized by a large expandable **proventriculus**, a large muscular **gizzard** (which relies on swallowed stones to assist in grinding food) and a relatively **small intestine** compared with the very long **colon**. **Digestion** is assisted by microbial **fermentation** in the large paired caeca and proximal **colon** and the **short-chain fatty acid**s produced are absorbed in the distal colon. Micturition and **defecation** are separate events in the ostrich.

In wild situations, breeding is relatively opportunistic and generally reliant on environmental conditions (especially rainfall). Male ostriches establish and defend territories around which the females wander before choosing one male with which to establish a nest. Courtship involves an elaborate display by the male, including a booming call and showing the female potential nest sites. Mating can occur outside of established pairs and many females will lay some of their **eggs** in other nests. Egg laying takes place every 48 h and the clutch of about ten eggs can take 3 weeks to complete. The number of eggs in a nest can be much higher because of egg dumping by other females, but once **incubation** is established many of these eggs are pushed out (although it is unclear how the incubating female recognizes its own eggs). The egg is the largest

laid by any living bird (average of 1500 g, measuring 15 cm × 12 cm) and has a gross composition similar to that of the **domestic fowl** egg. Incubation takes 42 days and is carried out continuously, with the male sitting at night and the female sitting by day. Hatched chicks are about 30 cm tall and fully precocial, leaving the nest after 24–48 h to follow their parents to look for food and water. Typically, groups of chicks amalgamate to form crèches looked after by one pair of birds until they are well-grown juveniles. Adult height is reached by 12 months of age and sexual maturity is at 2–3 years.

For many centuries ostriches were persecuted for their feathers, which were used as human adornment. Aboriginal Africans also used empty **eggshells** as water carriers. During the 19th century it became apparent that slaughter of wild ostriches was not sustainable and in South Africa some birds were brought into captivity. Nevertheless, the ostrich remains threatened in much of its natural range. Captive breeding was fully established by development of an artificial incubator, though foster adult birds were used to rear most chicks. Farming was largely based around providing **grazing** on irrigated **lucerne** (alfalfa) supplemented by **maize**. Breeding stock were either kept in large 'free-range' groups or as pairs in small enclosures. Captive breeding programmes were also established to develop a bird more suited to a farming environment and for the regular plucking of feathers (once mature) from living birds. To a large extent this farming system still applies in South Africa.

The result was a rapid expansion of the worldwide market for

feathers and vast fortunes were made in the feather trade, particularly around Oudtshoorn, South Africa, which became (and remains) a major centre for ostrich farming. At this time ostriches were also exported to North America, Europe and Australia, where farming operations were established. World War I meant that the demand for ostrich feathers in fashion fell dramatically. By the 1930s only remnant farming operations remained in South Africa and had disappeared from other parts of the world.

After World War II, a marketing cooperative was established in South Africa that developed the market for leather tanned from the skin of ostrich slaughtered at around 12–14 months. Characterized by patches of raised quills, ostrich leather became a high-quality luxury product. Although dominated by the cooperative, the leather market led to a second expansion of ostrich farming in South Africa. In more recent times the leather market was also supplemented by sale of the high-quality leg **meat**.

International sanctions against South Africa during the 1980s produced a shortage of ostrich hides and ostrich farming became more attractive for other parts of the world. Aggressive marketing caused an extremely rapid spread of ostrich farming in the USA, which led to an increasing awareness around the world, with other African countries and Israel, Australia and Europe establishing ostrich farming operations.

Outside Africa, ostrich farming has been attempted in a wide range of climates and geographical conditions but the farms are usually small. Often breeding birds are kept in ‘trios’ (one male with two females) in small enclosures. Eggs are artificially

incubated and the chicks are intensively reared. Common problems have involved maintaining the health of birds, getting good **egg production**, **fertility**, hatchability, and poor survivability and **growth** rates of chicks. Commercial production and marketing of the products has also been a major restriction to development of an ostrich industry to match that of South Africa.

During the 1990s ostrich farming spread to almost all parts of the globe. Unfortunately, many factors, including **climate**, lack of experience, lack of capital investment and lack of marketing, have meant that many prospective ostrich farmers failed to secure a living. This was despite the increased interest in the low-fat red meat, which is produced entirely from the legs and hips (the breast **muscles** are very poor in this flightless bird). The market was further complicated by fraudulent marketing operations in several countries. Deregulation of the South African market in 1993 caused a rapid expansion in the availability of ostrich hides on the world market and the price plummeted. At the start of the 21st century the market recovered to a large extent and ostrich farming remains strong within South Africa. Elsewhere, though more widespread geographically, it is practised by relatively few people.

In its native habitat the ostrich is a **herbivore** feeding almost exclusively on vegetation. A wide variety of plants are consumed according to the prevailing flora in the local area. Green annual forbs and grasses are preferred but leaves, flowers and fruit from succulent plants will also be consumed. Selection of food items is by sight and the **beak** is used to strip the leaves. Plant species known to be toxic are avoided. Stones are a critical aspect of the

ostrich's diet because, employed in the muscular gizzard, they help to grind plant material before it passes into the intestines. Up to one-third of the bird's time is spent feeding, a behaviour that occurs in bouts, often whilst walking, interspersed with periods of vigilance. This pattern is maintained under captive conditions.

To digest plant fibre, ostriches rely on post-gastric microbial fermentation in the large caeca and very long colon. The passage rate for food is therefore slow (about 48 h in a juvenile bird), ensuring efficient fermentation of fibre to form **volatile fatty acid**s (VFAs). VFA levels of 171–195 mM have been recorded in the proximal colon and VFA production accounts for up to 76% of the daily **metabolizable energy** in a 50 kg ostrich.

The rise in interest in ostrich farming around the world during the 1990s stimulated interest in the nutrition of the ostrich in captivity. Traditionally in South Africa, the diet was based on lucerne (alfalfa), served freshly chopped, and maize. The young birds are typically allowed to graze on lucerne pasture but, as the birds grow, the ground is stripped bare and food has to be supplied on a daily basis. Feedstuffs for captive ostriches in other parts of the world are mainly pelleted formulated rations derived from a variety of vegetation and cereals. Pasture and **silage** prove effective as alternative husbandry techniques as long as the birds receive a concentrate **supplement**. In order to reduce feed costs, alternative sources of vegetation for rations, including *Phragmites* reeds, have recently been tested in South Africa with varying degrees of success.



An ostrich farm in South Africa. Photo courtesy of Kent Wang. Licensed under CC BY-SA 2.0.

There has been considerable research into the exact ingredients of ostrich rations, with the domestic chicken typically used as a comparison. Young ostrich chicks exhibit poor **digestibility** of both **fat** and **neutral-detergent fibre** (NDF) but these steadily improve as the birds grow to **maturity**. In some respects, ostriches resemble poultry (e.g. amino acid **metabolism**), but in others their **vegetarian** ancestry is clear. Post-gastric fermentation means that fibre utilization is very high. One study showed that, because NDF digestibility in an adult ostrich was over 60%, the apparent **metabolizable energy** of the test diet was 11.6 MJ kg^{-1}. This compares with a value of 8.3 MJ kg^{-1} for the same diet based on values derived from poultry.

One side effect of captivity is the habit of ostriches to consume items, including barbed wire and nails, that have no nutritional value. This behaviour is almost certainly a response to stress, induced by poor environmental conditions, and access to such material. Under good captive conditions ostriches will be too busy eating their normal rations to indulge in other less beneficial items. (DCD)

Outflow, rumen:
see Rumen

Ova:
see Ovum

Ovalbumin
Also known as egg **albumin** or the 'white of the egg'. It is one of a number of proteins present in the clear, viscous substance of the **egg**, having a slight yellowish tint and serving as a store of **amino acid**s for the developing embryo. This **protein** has been identified as one of the major allergens in eggs, resulting in some consumers having to avoid eggs.

A practical issue relating to ovalbumin is that during storage it is converted naturally to *S*-ovalbumin, a more heat-stable form. The white of a newly laid egg contains about 5% of the ovalbumin in the *S*-form, while more than 50% of the ovalbumin can be in the *S*-form by the time the egg is purchased by a consumer. Eggs with high *S*-ovalbumin content have runny whites, making the consistency of the egg-white a useful index of the age of the egg and how it has been stored. (RB; MMax)

Overfeeding
Overfeeding can be either spontaneous or imposed. Spontaneous overeating (**hyperphagia**) is when **voluntary food intake** is more than required to meet **nutrient requirement**s, resulting in excessive **fat** deposition. It is difficult to identify with certainty, because some apparent overeating may result from a mild

deficiency in one or more nutrients causing a compensatory increase in food intake to meet the requirement for the limiting nutrient. In meeting the need for the limiting nutrient, excess **energy** is consumed. Such apparent overfeeding may be evident in populations of animals in which individuals vary in their requirements for particular nutrients, because of intrinsic variation in **growth**, rate of lay, etc.

The term overfeeding is also applicable when animals are subjected to chronic food restriction, as, for example, with growing animals destined for breeding (e.g. growing gilts, **broiler breeder**s) when it is desirable to reduce growth rates to limit body weight at sexual maturity. Increasing daily rations much above recommended levels, or 'overfeeding', leads to heavier breeding animals which may have impaired health and reproductive performance.

Imposed overfeeding is the same as **force feeding**. (JSav)

Ovulation rate

In birds, the number of ova released from the single functional ovary during a given period. In laying birds, at peak production, this is one per day. However, ovulation rate does not always equate to rate of oviposition, as some ova miss the oviduct and are subsequently resorbed. Also, sometimes two ova develop within a single **eggshell**. In mammals, ovulation rate is the number of ova shed in one **oestrous cycle** from either one ovary in the case of single-ovulating species, or both ovaries in the case of multiple ovulators. (PDL; JJR)

Ovum

Unfertilized female gamete or **egg** cell (plural: ova). The ovum is a haploid cell containing the single set of chromosomes (forming a pronucleus), which the mother will contribute to the new individual at fertilization, when the haploid spermatozoon fuses with the ovum, creating a new diploid individual.

In mammals, the ovum consists of a pronucleus surrounded by cytoplasm and two small polar bodies, containing 'spare sets' of chromosomes resulting from the meiotic divisions that produced the pronucleus. The ovum is surrounded by a tough, clear, spherical shell – the zona pellucida. The ovum always contains an X chromosome, the sex of the new individual being determined when the ovum is fertilized by sperm containing either an X or a Y chromosome.

In birds, the ovum is much larger in relation to body size (up to about 20 g in the **domestic fowl**, for example). It is characterized by a large yolk, made up largely of **lipids**, which account for about one-third of the egg's weight and which will nourish the chick during **incubation**. A protective calcareous shell is formed around the egg after fertilization and before it is laid. Sex is determined by the ovum, which contains either a Z or a W chromosome. (PJHB)

Oxalates

Salts of oxalic acid (HOOC·COOH). One of the most prominent oxalate salts in urine is **calcium** oxalate. Oxalic acid is produced in the **catabolism** of **glycine** and **ascorbic acid**. It is found in asparagus, **spinach**, rhubarb and other vegetables and fruit. Dietary oxalates may cause primary oxaluria in which calcium

oxalate accumulates in the kidneys and other tissues (oxalosis). This may lead to kidney failure and uraemia. (NJB)

Oxaloacetate

A **dicarboxylic acid**, HOOC·CO·CH_2·COOH, derived either from the **transamination** of **aspartic acid** (HOOC·$CHNH_2$·CH_2·COOH) or from the **oxidation** of malic acid molecules (HOOC·CHOH·CH_2·COOH) in the **tricarboxylic acid (TCA) cycle**. It is essential for the oxidative **catabolism** of acetyl-CoA derived from **carbohydrates**, **fatty acid**s and **amino acid**s. It is a critical intermediate in the TCA cycle in regard to conversion of acetyl-CoA carbon to **carbon dioxide**, because it combines with acetyl-CoA to form citrate. It is also critical to **gluconeogenesis**, because it is the TCA cycle intermediate that provides carbon for **glucose** synthesis. (NJB)

Oxidation

The removal of electrons (in contrast to reduction, which is the addition of electrons). In aerobic **metabolism**, **substrates** are oxidized and the **energy** in the electrons removed from the substrates is carried by reduced co-factors (i.e. $NAD^+ \rightarrow NADH + H^+$; FAD → FADH) which interact with the mitochondrial electron transport chain to produce ATP from ADP. The final reaction in the electron transport chain is the reduction of **oxygen** to form water. In anaerobic metabolism, substrates are oxidized in the same way as in aerobic metabolism but a substance other than oxygen must be reduced (e.g. CO_2 reduced to **methane**). (NJB)

Oxidative decarboxylation

The removal of the carboxyl carbon from an α-**keto acid**. Oxidative decarboxylation involves an α-keto acid **substrate** such as **pyruvate** ($CH_3 \cdot CO \cdot COO^-$) or α-ketoglutarate ($^-OOC \cdot CH_2 \cdot CH_2 \cdot CO \cdot COO^-$). In the case of pyruvate, oxidized lipoic acid (RS·SR), **thiamine** diphosphate, **coenzyme** A and the appropriate **enzyme** all participate in the reaction. The oxidized form of lipoic acid (RS·SR) reacts with the two-carbon decarboxylation product of pyruvate (i.e. **acetate**) to form the reduced lipoate-SH/acetyl complex ($CH_3 \cdot CO \cdot SH \cdot$lipoamide·SH). The acetyl group of the acetyl·SH·lipoam ide·SH complex is transferred to reduced coenzyme A (CoASH) to form acetyl·S-CoA. The reduced lipoate (HS·lipoate·SH) is released and then oxidized by FAD to regenerate oxidized lipoic acid (RS·SR). A similar series of steps occur when α-ketoglutarate is the substrate. In this case succinyl·S-CoA is the product. (NJB)

Oxidized fats

Fats that have undergone oxidation by molecular **oxygen** resulting in the production of **peroxides** and **free radical**s. The oxidation is catalysed by heat, **light** and metals such as **copper** and **iron**. Oxidized fats become rancid and unpalatable, with an offensive **taste** and smell. If absorbed, the peroxides and free radicals in the fat can result in cellular damage and tissue death. Unsaturated vegetable fats are more susceptible to oxidative damage than saturated fats. Poor **growth** and lowered feed efficiency are expected. To prevent this detrimental effect, fats may have

antioxidants such as butylated hydroxytoluene (BHT), **ethoxyquin** and **tocopherol**s added to them. (NJB)

Oxygen

An element found in nature as a diatomic gas, O_2. It has an atomic number of 8 and an atomic weight of 15.9994. It makes up 20.946 ± 0.002% of the volume of dry air. The three isotopes of oxygen are ^{16}O, ^{17}O and ^{18}O. The heavy isotope ^{18}O is used as a tracer in chemical and metabolic studies. Oxygen is required for aerobic **metabolism**, because it is the terminal electron acceptor in the mitochondrial electron transport chain. The electrons (**hydrogen**) removed from **substrates** are used to reduce oxygen to water as part of the overall respiratory process. (NJB)

See also: Energy metabolism; Oxygen consumption

Oxygen consumption

Oxygen is consumed by animals at a rate of approximately 1–2 l g^{-1} of food metabolized. The amount of oxygen consumed is related more closely to the quantity of heat produced, being approximately 0.47–0.55 l kJ^{-1} of **energy** converted into heat.

The table gives the approximate oxygen consumption (litres per day) of growing farm animals at different body weights. For pregnant animals these estimates should be multiplied by approximately 1.5, for **laying hen**s by 1.75 and for lactating animals by 2, or even 3 for a champion cow. For **maintenance** conditions they should be reduced to about two-thirds. (JAMcL)

Oxygen consumption of growing farm animals

Body weight	Chickens	Sheep	Pigs	Cattle
50 g	2			
100 g	5			
200 g	10			
500 g	14			
1 kg	23			
2 kg	38	60		
5 kg		90	80	
10 kg		130	150	
20 kg		220	280	250
50 kg		360	500	500
100 kg			750	800
200 kg			1000	1200
500 kg				2000

See also: Haemoglobin

Oxytocin

A **peptide** hormone produced by the magnocellular neurosecretory nuclei of the posterior pituitary and by gonadal tissue. It is involved in the process of parturition and in the 'let down' of **milk** by the **mammary gland**. Oxytocin causes the contraction of **smooth muscle** in the uterus during parturition and its secretion is stimulated by the **suckling** stimulus in mammals, facilitating the ejection of milk from the mammary

gland. (JRS)

Oyster:
see Molluscs; Mollusc culture; Shellfish culture

Oyster shell
Oyster shells are almost pure **calcium** carbonate (95–99%) and are good sources of calcium for all classes of animals. Clam shells, conch shells, coral and coral sand can all be used for feeding. Shells that have been ground to coarse grit tend to be more palatable to **laying hen**s and help **grain** digestion in the **gizzard**, as well as producing strong **eggshells**. For laying hens the shells should be ground to 0.5–2.0 mm and mixed 2:1 with finely ground **limestone**. (JKM)

P

Pacific salmon
Pacific salmon comprise seven principally anadromous, semelparous species in the genus *Oncorhynchus*, namely the sockeye (*O. nerka*), pink (*O. gorbuscha*), chum (*O. keta*), chinook (*O. tshawytscha*), coho (*O. kisutch*), masu (*O. masou*) and amago

(*O. rhodurus*) salmon. The first five are naturally distributed around the Pacific Rim from the Bering Sea south to California and northern Japan. The last two are strictly Asian (Seas of Japan and Okhotsk). Coho and chinook salmon are commercially cultured.

Chinook salmon, a species of particularly high cultural, economic and ecological value, have exhibited declines in marine survival throughout their North American range (Welch *et al.*, 2021). Juvenile Chinook salmon may migrate to sea in the year that they emerge from the gravel (ocean-type) or spend one or more years rearing in **fresh water** (stream-type). They generally then spend 2–4 years in the ocean before returning to their river of origin to spawn (Quinn, 2018).



Chinook salmon in Idaho, USA. Photo courtesy of Bureau of Land Management. Licensed under CC BY 2.0.

Marine survival of Chinook salmon is calculated by marking smolts with coded wire tags and measuring the subsequent catch and return to the river of surviving adults; the smolt-to-adult survival. Within the Salish Sea, there is a perception of synchronous declines in smolt-to-adult survival of Chinook salmon (Riddell *et al.*, 2009) along with those of Coho salmon (*O. kisutch*)

(Beamish *et al*., 2010; Zimmerman *et al*., 2015). (RHP; QS)

See also: Salmon culture

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Pacific white shrimp (*Litopenaeus vannamei*)

Also known as the whiteleg shrimp. In the past two decades, there has been an increase in crustacean **aquaculture** production, reaching approximately 9.3 million tonnes in 2018, with *Litopenaeus vannamei* accounting for 52.9% of production output.

The white shrimp *L. vannamei* is a widely cultivated crustacean in the Pacific Rim countries, South America and China, because of its rapid growth, high disease resistance, and marketability.



Pacific white shrimp, also known as the whiteleg shrimp. Photo courtesy of Judgefloro. Licensed under CC0 1.0.

The rising demand for shrimp products and the associated increase in production has increased the demand for specially formulated feeds (i.e. for appropriate nutrient supply) that meet the needs of different breeding environments. The increase in crustacean production output is primarily due to aquaculture intensification, such as improved feed efficiency, feed formula and feeding management techniques and technological improvements, with considerable impact on **protein efficiency** and **nitrogen retention** (Wasielesky *et al*., 2006; FAO, 2020). Feed and protein efficiency are related to aquaculture fish growth and performance. Shrimp production performance has been reported to be primarily dependent on feed constituents in clear-water experimental systems and recirculating aquaculture systems (RAS) compared with semi-intensive or biofloc technology (BFT) aquaculture

systems, wherein shrimp are additionally dependent on natural food (Hargreaves, 2006). Highly intensive shrimp production in RAS and BFT systems are suitable alternatives for more sustainable production because of their high nitrogen residual management efficiency (Avnimelech, 1999; Crab *et al*., 2012) and ability to be combined with integrated multi-trophic aquaculture (Medina *et al*., 2016; Poli *et al*., 2019; Pinheiro *et al*., 2020; Schardong *et al*., 2020; Verdian *et al*., 2019). (QS)

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Pacu (*Piaractus mesopotamicus*)

A commercially important **freshwater fish** native to the rivers of Brazil. This large migratory fish reaches 60 cm in length and is a scavenger that eats vegetation, mostly fruit that falls into the water, as well as an occasional small fish or insect. Pacu is one of the first native fish species to be successfully cultured in Brazil. A market size of 1–2 kg can be attained in 18–20 months at **water temperatures** of 22–28°C. (SPL)

Palatability

The term palatable is defined as 'being pleasant to the **taste**' and hence the palatability of a food may be thought of as the degree to which an animal finds its taste pleasant. In ruminants, palatability usually designates those characteristics of a food that invoke a sensory response in the animal and is considered to be the corollary of the animal's **appetite** for the particular food (Baumont, 1996). Taste and smell are thought to be important determinants of palatability for mammals, while poultry are more affected by visual signals. Sheep, for example, have been shown to develop a liking for the taste of **monosodium glutamate** and to exhibit a preference for foods containing this additive. There is also evidence that ruminants prefer the smell of butyric acid to that of acetic acid. Young pigs find **sucrose** particularly attractive but are less influenced by other sweetening agents. Physical characteristics of foods are also thought to contribute to the sensory responses invoked and in this regard factors such as **particle size** and **dry matter** content can be regarded as factors affecting palatability. The palatability of a single food can be evaluated by the rate of eating at the beginning of the meal, while the palatability of different foods can be assessed by preference tests. Palatability is more likely to be achieved by providing fresh well-preserved foodstuffs of a type acceptable to an animal than by the use of attractive additives. (AJFR; RFEA)

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Palatability enhancers

Palatability can influence feed preference, tolerance and rejection, as well as intake if the access to feed is limited. **Fish product**s in feed for **aquatic organisms** enhance palatability, and their replacement by plant products reduces and retards intake. Palatability is determined principally by flavour, but texture and other feed attributes have the potential to influence palatability. The direct effect of flavour on **feed intake** is usually short term, but this can be important if access to feed is restricted, by time, space or **competition** with other animals. With repeated exposure, the palatability diminishes, a process known as self-**adaptation**. This involves animals savouring feed for longer to determine the taste induced by receptors. This is not the same as habituation, which functions at brain rather than receptor level. Flavours interact and the sensations they produce depend on nutrient status. Flavouring agents, such as sweeteners, added to animal feed can mask unpleasant flavours, such as bitter flavours from shea **nut** meal, cherko and **cocoa bean** meal, or salty flavours, such as in fish meal. Artificial sweeteners include talin, a product of the fruit of *Thaumatococcus danielli*, a West African plant, which has some liquorice aftertaste, and saccharin, which has a bitter aftertaste. Adding one flavour can mask another in a process known as cross-adaptation, for example between thaumatin, a sweetener, and the bitter **taste** produced by **tannins**. Sometimes mixtures of palatability enhancers suppress the taste of one or other, for example the suppression of the sweetness of thaumatin by **salt**, a phenomenon known as mixture suppression.

Sometimes palatability enhancers induce side tastes, with salt inducing a sweet taste, for example. Early experience of a flavour, even *in utero*, can enhance its palatability later in life.

Feeding stimulants are particularly important for **fish**, because uneaten food contributes to water pollution in aquatic systems. Palatability enhancers are most likely to be based on L-**amino acid**s, **betaine** or nucleosides and **nucleotides**, substances naturally found in the fishes' prey items. (CJCP; QS)

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Paleo diet

The Paleo or paleolithic diet, presumed to be consumed by cave dwellers, focuses on lean meat and includes fish, fruits, vegetables, nuts and seeds. Consumption of foods that became common when farming emerged about 10,000 years ago is restricted. This includes dairy, legumes and grains, all highly processed food and foods with high levels of salt and refined sugar. Claimed benefits include weight loss and improved regulation of blood sugar, triglycerides and appetite. (CJCP)

Palm kernel:

see Oil palm

Palmitic acid

Hexadecanoic acid, $CH_3{\cdot}(CH_2)_{14}{\cdot}COOH$, shorthand designation 16:0, a saturated 16-carbon **fatty acid** found in **animal fats** and

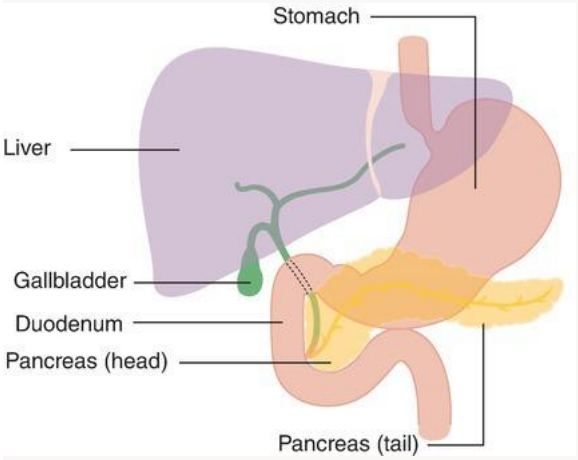
plant **oils**. (NJB)

Palmitoleic acid

cis-9-Hexadecenoic acid, $CH_3{\cdot}(CH_2)_7{\cdot}CH{=}CH{\cdot}(CH_2)_5{\cdot}COOH$, shorthand designation 16:1 n-9 (Δ^9), a 16-carbon **unsaturated fatty acid** found in nearly all **fats**. (NJB)

Pancreas

The pancreas, an accessory organ of **digestion**, plays an essential role in the digestive physiology of animals. It is located near the first part of the **duodenum** and appears as an elongated gland of loosely connected aggregated nodules.



The position of the pancreas in the human gastrointestinal tract. Licensed under CC BY-SA 4.0.

These are composed of pancreatic acini, with exocrine functions, and the islets of Langerhans, which have endocrine functions. The exocrine function is to produce and secrete fluids necessary for digestion in the **small intestine**. The endocrine function is to produce and secrete the important metabolic hormones: **insulin** and **glucagon**.

The exocrine products are secreted into the duodenum via the pancreatic duct. Secretion is controlled in part by autonomic nerves and in part by the **gastrointestinal hormone**s: **gastrin**, **secretin** and **cholecystokinin** (CCK). The secretory rate per unit of body weight (ml kg^{-1} h^{-1}) is higher in chicken (about 0.7) than in mammals (e.g. about 0.1 in sheep).

The exocrine secretions of **enzymes** and proenzymes are increased by parasympathetic stimulation when the **stomach** contents enter the intestine. In omnivores and non-ruminant **herbivore**s (e.g. pig and horse), parasympathetic stimulation also increases the secretion of water and **electrolytes**, which are needed for **fermentation** in the **large intestine**. Gastrin potentiates the parasympathetic effect on the pancreas. Secretin release is stimulated by acid perfusion of the duodenum and causes the pancreas to secrete **bicarbonate**. CCK is secreted in the response to the presence of **protein** and **lipid** in the duodenum and causes the pancreas to secrete enzymes and proenzymes.

In the horse, the rate of enzyme secretion is low in comparison with that of other species, because most ingested food requires microbial fermentation. The composition of **pancreatic juice** changes during development and alterations in composition can also be induced by changes of diet.

Pancreatic fluid contains bicarbonate, which neutralizes the acid **digesta** from the stomach, and an array of enzymes and precursors necessary for the digestion of proteins (**trypsin**, **chymotrypsin**, **elastase**, **carboxypeptidase**s), lipids (**lipase**, **phospholipase**s), **starch** (**amylase**) and **nucleic acid**s

(nuclease and **ribonuclease**). All proteases and **phospholipase** A_2 are secreted as inactive proforms in order to prevent damage to the pancreatic tissue. Active trypsin plays a central role in the activation of all enzyme precursors in the duodenum and a potent **trypsin inhibitor** in pancreatic tissue prevents premature activation of trypsin. (SB)
See also: Pancreatic hormones; individual pancreatic enzymes

Pancreatic diseases
Pancreatic conditions include inflammation, atrophy and neoplasia. Pancreatitis is potentially very painful. Pancreatic diseases may affect either the exocrine function (the production of **enzymes** – proteases, **amylase**, **lipases** and nucleases – for **digestion**) or the endocrine function (the production of **glucagon** and **insulin** from cells in the islets of Langerhans).

Loss of exocrine function is often reflected in fatty faeces, loss of weight and increased appetite. Release of these digestive enzymes within the gland causes acute pancreatitis, severe pain and **hyperlipidaemia**.

Insulin is the major anabolic **hormone** in animals and stimulates **protein synthesis**, **polysaccharide** production from **monosaccharide**s and **lipid** synthesis from **fatty acid**s. In **diabetes** mellitus (sugar diabetes) there is a permanent high blood **glucose** level, even during fasting. The kidneys will eliminate excess glucose but require water to do this, leading to excess urination and drinking (a temporary glucosuria may be due to other factors). Diabetes mellitus is usually due to a failure of the β cells in the pancreas to produce insulin but may be due to an excess

of insulin **antagonist**s. It is often seen in dogs and cats but is uncommon in large domestic animals. (EM)

Pancreatic hormones
Hormones released from **pancreatic islet**s, primarily involved in the regulation of **metabolism**. They include: **insulin** and **glucagon**, which regulate blood **glucose** levels; somatostatin, a potent inhibitor of **growth hormone** secretion; and pancreatic polypeptide, which is believed to act by partially inhibiting exocrine pancreatic function. (GG)

Pancreatic islets
The islets of the pancreas, also known as the islets of Langerhans; the functional units of the endocrine portion of the pancreas. Islet cells make up less than 2% of the total pancreatic mass but secrete **hormone**s that are absolutely essential to **metabolism**, including **insulin** from β-cells, **glucagon** from α-cells, somatostatin from δ-cells and pancreatic polypeptide. (GG)

Pancreatic juice
The secretion of the pancreas, an alkaline juice containing a very high content of **bicarbonate** and numerous digestive **enzymes**. The high content of bicarbonate serves primarily to neutralize the highly acid **chyme** produced in the **stomach** that passes into the **duodenum**. The digestive enzymes include the inactive precursors of proteases (**trypsinogen**, **chymotrypsinogen**, proelastase, procarboxypeptidase A and B), **amylase**, **lipases** (including the inactive precursor of **phospholipase** A_2) and

nucleases. After activation in the duodenum, initiated by activation of **trypsin** by **enterokinase** and the activation of lipase from **bile** acids, the enzymes have a potent capacity to degrade proteins, **starch**, **lipids** and **nucleic acid**s, respectively. (SB)

Pancreatin
Freeze-dried pancreatic tissue (usually from pigs) containing the various pancreatic enzymes, including proteases (**trypsin**, **chymotrypsin**, **elastase** and **carboxypeptidase**s), **amylase**, **lipase** and **ribonuclease**. (SB)

Pancreatitis:
see Pancreatic diseases

Pancreozymin:
see Zymogens

Pangas (catfish) 'nei'
Pangasius spp., a carnivorous species and also a voracious feeder; termed 'nei' by FAO ('not elsewhere included', not possible to identify to the species and more than one species is included in the same group). It feeds on decaying animals and vegetative matter (Talwar and Jhingran, 1991).



Juvenile giant pangasius fish (*Pangasius sanitwongsei*). Photo courtesy of Hectonichus. Licensed under CC BY-SA 3.0.

In rivers, it preys on snails and other **mollusc**s (IUCN Bangladesh, 2000). The pangas catfish, *Pangasius pangasius*, attains sexual maturity at the fourth year of its life (Rahman, 1992), breeds between June and August (David, 1963), or July and October in Bangladesh (Rahman, 1992). Both male and female broods of *P. pangasius* can mature in captivity (Khan and Mollah, 1998). Initially pangasius monoculture came from Thailand, and farming of this species is still a common practice in South-east Asian countries, especially the Philippines, Thailand and Vietnam (Dey *et al*., 2005; Ahmed, 2007; Belton *et al*., 2011; Alam, 2011). Pangasius has been cultured in Vietnam, Thailand, Bangladesh, Myanmar and other regional tropical Asian countries because of rapid **growth** following the implementation of artificial **reproduction**, responses to external feeding, high survival rates, and ability of this species to grow at high stocking densities. Currently, Vietnam is the largest pangasius producer, in total 1.2 million tonnes in 2017, constituting a major proportion of the world pangasius production and export market (VASEP, 2017).

(QS)

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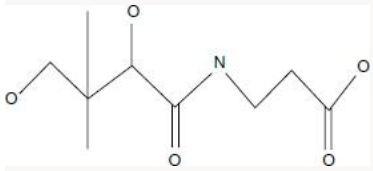
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Pantothenic acid

A water-soluble B **vitamin**, $HOCH_2 \cdot C(CH_3)_2 \cdot CHOH \cdot CO \cdot NH \cdot (CH_2)_2 \cdot COOH$, a combination of pantoic acid and β-**alanine**. Only D-pantothenate is biologically active. It is a component of the enzyme co-factor **coenzyme**-A and part of the acyl carrier **protein** involved in **fatty acid synthesis**. Coenzyme-A is found in the cytoplasm and in the mitochondrial matrix in free form as CoASH or in bound form, for example as acetyl-CoA. In the cytoplasm it is also found as 4′-phosphopantetheine as part of the acyl carrier protein that is involved in fatty acid chain elongation. About 80% of the pantothenic acid in tissues is found as CoA, which is widely distributed in nature because it is a participant in enzyme reactions involved in the **catabolism** and synthesis of **carbohydrates** and fatty acids (individual steps and the **citric acid** cycle), the catabolism of some **amino acid**s and synthesis of **cholesterol** and porphyrins. CoA in food is hydrolysed by a phosphatase in the digestive tract to pantetheine (pantothenyl cysteamine) and absorbed, along with pantothenate, by a **sodium**-dependent transporter. In experimental animals fed **pantothenic acid**-deficient diets, no single set of symptoms has been observed.

A unique goose-stepping has been reported in deficient pigs. A spontaneous deficiency of pantothenic acid is not expected, presumably due to its wide distribution in nature. (NJB)



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Parakeratosis

A condition in which the stratum corneum of the skin is thickened, scaly and cracked: it differs from **hyperkeratosis** in that the keratinocytes remain nucleated. It is seen in growing pigs suffering from **zinc** deficiency (caused either by a diet containing less than 100 ppm of zinc or secondary to high concentrations of **calcium**, or of **phytates**). It does not cause itching (as distinct from mange mites) and does not normally occur in young pigs (as distinct from greasy pig disease). In calves, the condition is inherited (Adema disease) and may respond to treatment with zinc in the feed. Parakeratosis of the **rumen** has been described in cattle fed heat-treated **lucerne** but appears not to cause clinical illness. (WRW)

See also: Skin diseases

Parasitization, effects on feeding

Gastrointestinal parasites present a serious risk to the health of **grazing** livestock, with affected individuals experiencing low **growth** rates, sickness and death. Some **plant secondary compounds** have antiparasitic function, as they can poison parasites in just the same way that greater concentrations can poison the host. **Tannins** are particularly effective in reducing faecal egg counts. Livestock even increase their selection of these feeds when they are carrying a higher pathogen load. (CJCP)

Parathyroid

An **endocrine gland** responsible for regulating blood **calcium** concentration. Some animals (e.g. pig, rat) have one pair of parathyroid glands; others (e.g. ruminants, humans) have two pairs. The glands are located within the neck region, often with one pair residing within the thyroid gland and one pair just cranial or caudal to the thyroid gland, depending on the species. **Blood** is supplied to the parathyroid glands by branches of the carotid arteries. Cells of the parathyroid are capable of sensing the calcium concentration in the blood: when it falls below normal (2.25–2.5 mM in most species), the gland secretes parathyroid hormone; as the blood calcium concentration returns to normal, the secretion is reduced.

It is vital to life that calcium concentration be maintained within a fairly narrow range. When it is too low the animal will not be able to form new bone, control nervous or muscular function properly (which may result in **tetany** or **muscle** weakness; *see* Milk fever), form blood clots, or maintain normal intracellular calcium

concentrations. If blood calcium concentration exceeds normal limits, calcium precipitates within the soft tissues of the body, disrupting their function.

Parathyroid hormone is a **peptide** of 84 **amino acid**s and it has three distinct actions. Initially it increases renal tubular reabsorption of calcium from the glomerular filtrate, decreasing urinary calcium loss. This is sufficient to restore blood calcium concentration to normal levels if the perturbation in blood calcium is small. With larger decreases in blood calcium concentration, continued secretion of parathyroid hormone increases **resorption** of calcium from bone. Specialized bone cells known as **osteoblast**s have receptors for parathyroid hormone on their surface. These cells recognize the parathyroid hormone signal and initiate bone resorption activity by stimulating a second bone cell, known as an **osteoclast**, to begin to degrade the organic matrix of the bone to free bone minerals (primarily calcium and **phosphorus**) for transport to the blood to increase blood calcium concentration.

In addition, parathyroid hormone can stimulate the production of a second hormone, 1,25-dihydroxycholecalciferol, by the kidneys. The precursor for this hormone is **vitamin D**, which is supplied in the diet or produced in the skin. The 1,25-dihydroxycholecalciferol produced in response to parathyroid hormone stimulation of the kidney acts on the intestine to stimulate the active transport of calcium across the epithelium. Without this hormone, dietary calcium is only poorly absorbed.

A secondary effect of parathyroid hormone is on phosphorus **metabolism**. Parathyroid hormone increases resorption of

phosphorus from bone at the same time as it increases resorption of bone calcium. To prevent a build-up of phosphorus in the blood as a result of bone phosphorus resorption, parathyroid hormone also increases phosphorus excretion by the kidneys and, in the case of ruminants, the salivary glands. (JPG)

Parathyroid diseases

Diseases involving the parathyroid gland fall into two categories: those associated with excessive parathyroid **hormone** activity (**hyperparathyroidism**) and those associated with abnormally low parathyroid hormone activity. Excessive parathyroid hormone activity results in depletion of bone **calcium**, leading to osteoporosis and predisposing the animal to bone fracture. Excessive parathyroid hormone secretion is commonly associated with diets low in calcium. In some cases diets that are excessively high in **phosphorus** can interfere with calcium **absorption**, resulting in excessive parathyroid hormone secretion. In companion animals and humans, tumours of the parathyroid gland commonly result in uncontrolled secretion of parathyroid hormone, leading to **hypercalcaemia**. Low parathyroid hormone activity may also be caused by parathyroid gland tumours. Of greater significance, especially in ruminants, is the failure of the target tissues of parathyroid hormone, bone and kidney, to respond to parathyroid hormone stimulation. Dietary **cation**–anion balance affects **blood** pH, which alters tissue responsiveness to parathyroid hormone. **Milk fever** in dairy cows is often the result of metabolic **alkalosis** induced by diets high in **potassium**. Low blood **magnesium** concentration can also impair the action of

parathyroid hormone on its receptors in bone and kidney, resulting in **hypocalcaemia**. (JPG)

Parietal cells
Cells in the parietal glands, which are located in the parietal area in the **stomach**. Their function is to secrete HCl, which is produced by an enzymatic process using CO_2, H_2O and NaCl. The other product, $NaHCO_3$, is transferred to the **blood**. (SB)

Parity
The number of pregnancy and **lactation** cycles completed by an animal. Thus, a primiparous animal (heifer, gilt, ewe lamb) is in its first pregnancy or lactation – its first parity; a multiparous animal (cow, sow, ewe) is in its second or subsequent parity.

Most farm animals enter their first parity before reaching their mature body weight. Therefore, in addition to the **nutrient requirement**s for pregnancy and lactation, they also have nutrient requirements for continued **growth**. Production level (**milk** yield or number of offspring) also generally increases with parity. This is particularly noticeable when comparing animals in their first and second parities.

In dairy cattle, **liveweight** increases until the third or fourth parity and milk yield may not reach a plateau until the fifth parity. The lactation curve of a heifer (first parity) is noticeably flatter than that of a cow in its second or subsequent parity. This is because the secretory tissue of the **mammary gland** develops during the first lactation.

In pigs, liveweight increases until the sixth parity and **litter**

size may increase until the third parity. Gilts are first mated at a relatively young age and light weight, compared with cattle, and so growth during the first three parities requires a higher proportion (up to 20%) of total nutrients. (PCG)

Parotid glands
A pair of salivary glands located near the ears. The parotid glands are one of the three known pairs of salivary glands (parotid, submandibular, sublingual). They secrete water and the enzyme ptyalin, which is involved in **starch hydrolysis**. The parotid glands contribute about 20% of the 1.5 l of **saliva** secreted per day in humans. (NJB)

Particle size
The size of food particles in gut contents depends both on the nature of the food eaten and the extent to which it is comminuted by **chewing**. In **ruminant animal**s, ingested food is chewed and ensalivated until it is in a suitable state for swallowing. During periods of **rumination**, reticulorumen contents are regurgitated into the mouth, where the more solid fraction is thoroughly re-chewed and swallowed. Long food particles in the reticulorumen tend to form a bubbly floating mat while being rapidly fermented, and avoid onward passage. Small, dense, well-fermented particles sink to lower levels and tend to be selected for onward passage through the reticulo-omasal orifice. Particle size is important in determining which undigested feed particles leave the **rumen**. Particles less than about 1.2 mm have an almost 100% probability of leaving the rumen, with the probability rapidly declining as

particle size increases. Feed particle size, or the size of partly digested particles in the rumen, influence **feed intake** and the extent of feed **digestion**. The time for which particles are retained in the reticulorumen determines the extent of digestion of potentially degradable fibre. Grinding and **pelleting roughage** diets will reduce particle size and so reduce **retention time** and the extent of fibre digestion in the reticulorumen. Voluntary intake is greater when feed particles are small, because they pass rapidly into the lower digestive tract and this allows the rumen to be refilled.

A spectrum of particle size can be described by sieving rumen content (or other material), either dry or in fluid suspension, through a series of sieves of differing mesh size under standard conditions (Kennedy, 1984). (RNBK; GMcLD)

See also: Dilution rate

Reference and further reading

Kennedy, P.M. (ed.) (1984) *Techniques in Particle Size Analysis of Feed and Digesta in Ruminants*. Occasional Publication No. 1, Canadian Society of Animal Science, Edmonton.

Kaske, M. and Engelhardt, W. van (1990) The effect of size and density on mean retention time of particles in the digestive tract of sheep. *British Journal of Nutrition* 63, 457–465.

Parturient paresis

This hypocalcaemic disorder affects dairy cows at the onset of **lactation**, when the **mammary gland** suddenly imposes a large demand for **calcium**. The disease occurs because the calcium homeostatic mechanisms of the body fail as a result of diet and

advancing age of the cow. (JPG)
See also: Milk fever

Passage rate:
see Transit time

Passive immunity:
see Immunity

Pawing behaviour
Animals, such as sheep and horses, that are routinely kept in snowbound territory effectively use pawing to scrape away the snow from the ground to reveal pasture. The behaviour may also be used to stimulate activity in newly born offspring and as an intention-to-escape behaviour in captive animals. It may damage the floor of the animals' enclosure and in horses may redirect to kicking the walls of the enclosure. The ability of horses to paw the ground is used in dressage. In bulls the behaviour may indicate an intention to charge. (CJCP)

Pea (*Pisum* spp.)
High levels of **sugar**, **starch** and undegradable **protein** make peas a valuable raw material in high-nutrient-density beef and dairy feeds. They are typically steamed, flaked or micronized to increase their **digestibility**. Some varieties may contain **trypsin inhibitor**s and **lectins**, which limit their inclusion in pig and poultry diets. Heating (e.g. by **extrusion**) can destroy most of these. Other varieties, low in trypsin inhibitors, can be used without extrusion in diets for growing and finishing pigs. Peas can be

included in diets for dairy and beef cattle, ewes, growing and finishing pigs, sows, calves and lambs, and breeder and layer chickens. Peas are usually ground and pelleted before inclusion in poultry diets. They are not typically included in diets for young pigs or chickens. (JKM)

The nutrient composition of peas.

	Nutrient composition (g kg^{-1} DM)							**Energy** (MJ kg^{-1})
	Dry matter (g kg^{-1})	**Crude protein**	**Crude fibre**	**Ether extract**	**Ash**	**NDF**	**MER**	**MEP**
Dried peas	860	260	70	16	35	190	13.6	13.0
Field peas	130	210	60	15	25	110	11.7	–

DM, dry matter; MEP, metabolizable energy for poultry; MER, metabolizable energy for ruminants; NDF, neutral-detergent fibre.

Peak meat

The concept of 'peak meat' describes a point in human consumption of **meat**-based products, including **beef**, **chicken**, **pork** and mutton, beyond which per capita intake no longer increases over time. Historically, improvements in income have been associated with increasing levels of meat consumption. However, awareness about negative environmental and health-related consequences from excessive meat consumption is contributing towards consumers making conscientious decisions in some countries to reduce their intake. Beef production in particular has a very significant environmental impact associated with high greenhouse gas emissions, pollution and land use, contributing to **climate** change and biodiversity loss. The health benefits of beef have also been put under scrutiny, with the World Health Organization (WHO) classifying fresh red meat as probably carcinogenic and processed red meat as carcinogenic.

Globally, per capita meat consumption continues to be on the rise and only three countries are believed to have achieved peak meat. They are: New Zealand, where per capita **meat production** dropped by 11.5 kg per person per year between 2000 and 2019 (from 86.7 kg to 75.2 kg); Canada, by 6.3 kg (from 76.5 kg to 70.2 kg); and Switzerland, by 3.1 kg (from 54.7 to kg 51.6 kg). Furthermore, there is also evidence that beyond a per capita income of US$40,000 per year, the direct correlation between rising meat consumption and increased wealth no longer holds.

Meat production and consumption can be severely impacted by climate change, associated extreme weather events and other natural calamities as well as geopolitical tensions. Despite the

vulnerability of the livestock sector to such factors, they are not seen to be at the core of the concept of peak meat. (DM)

Further reading

Whitton, C., Bogueva, D., Marinova, D. and Phillips, C.J.C. (2021) Are we approaching peak meat consumption? Analysis of meat consumption from 2000–2019 in 35 countries and its relationship to Gross Domestic Product. *Animals* 11, 3466. doi: 10.3390/ani11123466

Peanut:

see Groundnut

Pecking

The act of birds, such as chickens, turkeys and pheasants, directing the **beak** at an object with the aim of ingesting feed, litter, grit etc., imbibing fluids, or attacking or courting another individual. Pecking another bird typically involves an attack on the vent or feathers of the other bird. This helps to establish a 'pecking order' or hierarchy for priority of access to resources. **Feather pecking** is not necessarily aggressive and may take the role of a redirected **foraging behaviour**. Vent pecking is directed at another animal's **cloaca** and may draw the attention of other birds if **blood** appears. **Cannibalism** may ensue. This is more common in well-lit environments and in large groups of birds. (CJCP)



Pecking may be used for ingestion of food, and it is used extensively by chickens when they are kept under natural conditions. Photo courtesy of Alex Ford. Licensed under CC BY 2.0.

Pectic substancesPolysaccharides in plant tissue, **gums** and mucilages. Their primary structural component is a chain of (1→6)-linked residues of α-D-**galacturonic acid**. This main chain may be modified extensively, for example by methyl **esterification** of carboxyl groups, acetylation of hydroxyl groups, inclusion of **rhamnose** residues or addition of neutral **sugar** side-chains. Pectic substances are common in certain fruits, seeds, leaves, bark and roots. The main commercial sources are citrus peel and apple pomace. (JAM)
See also: Carbohydrates; Dietary fibre; Galactouronans; Rhamnogalactouronans; Storage polysaccharides; Structural polysaccharides; Uronans; Uronic acids

Pectins:
see Pectic substances

Pellagra
A condition caused by deficiency of **niacin** (nicotinic acid) or its

precursor **tryptophan**. It is occasionally seen in pigs fed a diet high in unsupplemented **maize**. Signs include **diarrhoea**, dermatitis and loss of **hair**. (WRW)

See also: History of nutritional sciences; Skin diseases; Vitamin deficiencies

Pellet binders in fish feed

Pellet binders are incorporated into fish feeds to improve stability in water, increase pellet firmness, and reduce the amount of fines produced during processing and handling. Among the most widely used binders are **sodium** and **calcium** bentonites, lignosulphonates, **hemicellulose**, carboxymethylcellulose, alginate, **guar gum** and some inert polymeric binders. **Cereal grain**s provide **starch** that, when gelatinized, gives a durable, water-stable pellet. Certain feed ingredients such as **whey**, **wheat** gluten, **soybean** protein concentrate, pregelatinized starches and **molasses** produce good-quality pellets. Most binders are considered to be inert and have limited or no nutritional value. However, incorporation of alginate and guar gum in diets for **rainbow trout** and some **marine fish** reduced **feed intake**, increased moisture content of faeces and lowered the **digestibility** of **protein** and **lipids** (Storebakken, 1985). Wood *et al*. (1954) showed that carboxymethylcellulose at 2% in the diet of **trout** caused no growth depression. (QS)

References

Storebakken, T. (1985) Binders in fish feeds. 1. Effect of alginate and guar gum on growth, digestibility, feed intake and passage through the gastrointestinal tract of rainbow trout. *Aquaculture* 47, 11–26.

Wood, E.M., Griffin, P.J. and Snieszko, S.F. (1954) Acute sulfamethazine toxicity in young salmon. *The Progressive Fish Culturist* 19, 64–67.

Pelleted feed

A blend of raw materials that has been ground, conditioned and pressed into uniform pellets. The pellets may have a diameter of 1.5–19 mm and an average length of approximately 2.5 times their diameter, depending on their intended use. Smaller pellets are used for young animals and smaller species, larger ones for animals fed directly on the ground.

Pelleting increases the **bulk density** of feed, making it cheaper to store and transport. Pellets also flow more easily and quantities are measured more accurately through on-farm automated feeding systems. The raw materials will not separate once pelleted, thus ensuring that the animals receive exactly what is intended. This is particularly important when the feed contains micro-ingredients such as vitamins and medicines. Less feed is spilled and wasted by animals given pellets than by those given meal. In addition, the **conditioning** process required in order to pellet feed improves its **digestibility** and therefore its value to the animal.

Pelleted feed can be a complete balanced feed or part of a complete diet; for example, protein **concentrate**s are specially designed to be mixed with cereals. To supply a balanced diet for the particular species, the concentrate would contain materials rich in protein supplemented with minerals and vitamins. (MG)

See also: Coating; Compound feed; Feed mixing; Quality control in feed mills

Pelleting

The process of forming feed into pellets. Mixing and pressing ground raw materials has a number of advantages. It increases **bulk density**, which facilitates bulk storage, transport and the metering of automated feeding systems. It reduces the risk of the constituent ingredients separating over time, which is particularly important if the feed is medicated. It allows for a degree of formulation change to accommodate fluctuations in the supply of raw materials without any noticeable difference to **feed intake**. Finally, it decreases waste on the farm.



Pelleted corn stover. Photo courtesy of Idaho National Laboratory. Licensed under CC BY 2.0.

Pellets must be uniform, dust-free and hard enough to withstand handling and storage between manufacture and feeding. To achieve these aims the meal must be suitably prepared by grinding and **conditioning**. Materials need to be ground to a grist with a good particle distribution and then conditioned. Conditioning is usually carried out by passing the meal along a horizontal barrel with steam and **molasses** (if used) injected along its length. Revolving paddles along a central spindle blend the

steam and molasses with the meal, making it more pliable and compressible. The steam injection raises the temperature of the meal, which aids the absorption of the liquids. Ruminant feeds may also be held for 20–30 min, immediately after conditioning, in a vessel called a ripener, where stirring arms aid conditioning.

Once the meal has been conditioned it is forced through a die under pressure to form the pellet. Most pelleting machines use a ring die, developed in about 1910. Meal drops into the centre of a rotating die, which is a metallic ring of variable diameter and thickness, depending on the equipment being used and the final product required. The die normally rotates around two or three fixed rollers that compress the conditioned meal through holes, forming the pellets. The friction further heats the pellet, aiding the ensuing chemical reactions between the **starch**, **protein** and **sugars** present in the raw materials and any artificial binder added. Finally, to avoid condensation and the risk of moulding, the pellets must be cooled to within a few degrees of ambient temperature before the product is stored. (MG)

PentosansPolysaccharides comprising a large number of **pentose** residues joined by *O*-glycosidic linkages. Pentosans are widely distributed in plants; they are found in woody tissue, leaves, fruit and seeds. (JAM)
See also: Arabinoxylans; Carbohydrates; Dietary fibre; Hemicelluloses; Xylan

Pentose
A **monosaccharide** containing five carbons. Major naturally

occurring pentoses include the aldoses L-**arabinose** and D-**xylose**, both of which are widely distributed in plants as constituents of **polysaccharide**s, and D-ribose, the only sugar in **ribonucleic acid** (RNA) which is found in all plant and animal cells. The pentose derivative 2-deoxyribose is the only sugar in **deoxyribonucleic acid** (DNA). The ketopentose L-xylulose is an abnormal constituent of **urine** in idiopathic pentosuria. (JAM)

Pentose phosphate pathway

A metabolic pathway in the cytoplasm of cells by which **glucose** is converted via glucose-6-phosphate to one of two pentose (5-carbon) sugars: ribose 5-phosphate or xylulose 5-phosphate. This pathway produces nicotinamide adenine dinucleotide phosphate (NADPH), which provides reducing equivalents for **fatty acid** biosynthesis.

Ribose is the pentose sugar found in nucleosides (adenosine, guanosine, cytidine, uridine and thymidine) and in enzyme co-substrates such as NAD, NADP, FAD, CoA and vitamin B_{12}. (NJB)

Pepsin

A proteolytic enzyme (EC 3.4.23.1) in the **stomach**, secreted as the inactive precursor pepsinogen. The activation of pepsinogen is an autocatalytic process involving the removal of a **peptide** from the NH_2-terminal of pepsinogen by active pepsin in the presence of hydrogen chloride (HCl). Pepsin has optimal activity at pH 1.8–3.5 and initiates the **hydrolysis** of dietary proteins in the stomach by cleaving peptide linkages that involve aromatic and acidic **amino acid**s. (SB)

See also: Digestion

Pepsinogen:
see Pepsin

Peptidase
A hydrolytic enzyme secreted by the **pancreas** or the **brush border** of the small **intestinal mucosa**. The pancreatic enzymes include the **endopeptidase**s **trypsin**, **chymotrypsin** and **elastase**, as well as **carboxypeptidase** A and B, which are **exopeptidase**s. The pancreatic peptidases are secreted as inactive **zymogen**s that must be activated to become functional. Those in the brush border are active without activation. They include enteropeptidase, **aminopeptidase**, carboxypeptidase and endopeptidases. Dipeptidases are brush border peptidases that cleave a **dipeptide** to yield the two free **amino acid**s. (NJB)

Peptide
A molecule formed of two or more **amino acid**s linked by peptide bonds R·CHNH·CO·R. A **dipeptide** has one peptide bond, a tripeptide has two, and so on. The term peptide is not well defined: a peptide may contain two to ten amino acids whereas a polypeptide may contain 10–100 amino acids. Some dipeptides of note are **carnosine** (β-alanylhistidine), anserine (β-alanyl-1-**methylhistidine**) and **balenine** (β-alanyl-3-methylhistidine). **Glutathione** (γ-glutamylcysteinylglycine) is a tripeptide that is involved in protection against oxidative damage and in **oxidation**–reduction reactions in the cell. Polypeptide **hormone**s

of note in animal **metabolism** are shown in the table. (NJB)

Polypeptide hormones active in animal metabolism.

Source	Polypeptide hormone
Endocrine pancreas	Insulin, glucagon, somatostatin
Gastrointestinal tract	Gastrin, cholecystokinin, secretin, gastrin inhibitory peptide
Posterior pituitary	Antidiuretic hormone (arginine vasopressin), oxytocin
Hypothalamus	Thyrotropin-releasing hormone (TRH), gonadotropin-releasing hormone (GnRH), corticotropin-releasing hormone (CRH), growth hormone-releasing hormone (GHRH), somatostatin
Anterior pituitary	Adrenocorticotropic hormone (ACTH), thyroid-stimulating hormone (TSH, also called thyrotropic hormone), luteinizing hormone (LH), follicle-stimulating hormone (FSH), growth hormone (GH), prolactin

Source	Polypeptide hormone
Other	Insulin-like growth factors I (IGF-I) and II (IGF-II), epidermal growth factor (EGF), fibroblast growth factor (FGF), transforming growth factors (TGF-α and TGF-β), nerve growth factor (NGF), hepatocyte growth factor (HGF), interleukins (IL-1, IL-2, IL-6, etc.), colony-stimulating factor, erythropoietin, atrial natriuretic peptide (ANP), angiotensin II, endothelin

PeptidoglycansPolysaccharide–peptide molecules in which parallel polysaccharide chains are covalently cross-linked through peptide bridges consisting of four, or occasionally five, **amino acid**s, many of which are in their uncommon D-forms. Peptidoglycans are cell wall components of **algae** and major supporting structures of bacterial cell walls. In bacteria, the peptide portion of the molecule varies with the bacterial strain, but the **disaccharide** repeating unit in the polysaccharide chain always appears to consist of *N*-acetylglucosamine and an acidic sugar, *N*-acetylmuramic acid. In Gram-negative bacteria, the cross-linking usually involves the formation of **amide** linkages between the carboxyl groups of D-**alanine** residues in one chain and the ω-

amino groups of the diamino acids in another chain. Cross-linking is more extensive in Gram-positive bacteria. (JAM)
See also: Carbohydrates

Pericarp
The part of a fruit that develops from the ovary wall of a flower and which may be dry and hard or soft and fleshy, depending on the type of fruit. The pericarp can be made up of three layers: the outer skin (epicarp or exocarp), the middle layer (mesocarp) and the inner layer (endocarp). (ED)

Periodontal disease
Disease primarily affecting the **teeth**, gums or jaws. The teeth of older sheep fed on roots (turnips, fodder beet) over several winters may become loose and eventually lost, making it difficult for the animal to eat sufficient roots to survive. (JMF)

Peristalsis
Propulsive movements of the gut by which the food is propelled. Peristalsis consists of a moving ring of constriction in the wall of a tubular organ. The rings reduce the lumen diameter, pushing the bolus of food ahead of them along the gut. Peristalsis is a universal type of propulsive **motility**, occurring in all parts of the **gastrointestinal tract**, beginning in the oesophagus. (SB)

Perosis
A condition seen in young birds in which the hock joint is greatly swollen, the birds are severely lame and may show 'spraddle legs'. The term now preferred to describe the condition is

chondrodystrophy, defined as a generalized disorder of the growth plates of long bones such that growth is impaired, while mineralization and appositional growth remain normal, resulting in shortened long bones, enlargement of hock joints and often secondary valgus or varus deformations (Waldenstedt, 2006). In severe cases, the gastrocnemius tendon may also become displaced from the medial condyle.

This condition is seen in chickens, ducks and turkeys. It is caused by a deficiency of **manganese**, **choline** and **zinc**, either singly or in combination, although deficiencies of **pyridoxine**, **biotin**, folic acid and **niacin** may also be involved. For prevention, diets for growing chickens, ducks and turkeys should be formulated to ensure that the nutrients in question (especially manganese) are in optimal balance and of high bioavailability. Excess levels of dietary **calcium** and **phosphorus** need to be avoided. In turkeys, chondrodystrophy may be due to an inherited deficiency of **galactosamine**. (RB)

Reference

Waldenstedt, L. (2006) Nutritional factors of importance for optimal leg health in broilers: a review. *Animal Feed Science and Technology* 126, 291–307.

Peroxide

Any compound with a bivalent O·O group. Because one of the oxygen atoms is not tightly bound, oxygen can be released which results in peroxides being strong oxidizing agents. In **metabolism** of aerobic organisms, **superoxide** anions (O_2^-) are produced and can be involved in the production of hydrogen peroxide (HO·OH).

Under conditions where free ferrous **iron** is available, it can be oxidized to ferric iron with the production of a hydroxyl radical (OH·) which may also lead to the production of lipoperoxides, RO·OH. (NJB)

Pescatarian

A person who follows a mainly lacto-ovo **vegetarian** diet and does not eat any **meat**, except **fish** and seafood. This may be because they wish to gain the health benefits claimed for both vegetarian food and fish and avoid the health problems suggested to be associated with meat from terrestrial animals. It can also be a transition diet to a completely vegetarian diet. The term was invented in the 1990s in the USA. Historically, several religious groups followed a pescatarian diet in the belief that is more pious. (CJCP)

Pesticides

Natural or synthetic chemicals or biological agents used to control a variety of pests (weeds, insects, pathogens, molluscs and vertebrate pests) that injure or compete with crops, animals or humans. They include herbicides and insecticides. Most pesticides are very specific to the target organism but some may accumulate to levels that may be harmful to crops, animals or humans. Strict regulatory requirements are placed on the use of pesticides in most countries, and tolerance limits are set and monitored to avoid harmful residues.

Herbicides are generally applied early in the season to control undesirable plants in crops and thus are generally dissipated by the

time an animal consumes the crop. When applied properly, currently licensed herbicides seldom develop residues that are toxic to animals. Dinitro compounds (dinoseb) are the only highly toxic class of herbicides. Moderately toxic herbicides include bipryidyl (paraquat), carbamate (EPTC) and triazine (artizine) compounds. Low- to non-toxic herbicides include chlorobenzoic acid (dicambba), chlorophenoxy acids (2,4-D), glyphosate, substituted **urea** (diuron) and sulphonylureas (metsulphuron).

Insecticides are generally applied to crops later in the season, or applied directly to grains to prevent insect damage. Many insecticides are applied directly to livestock to reduce pest problems. Thus, their concentrations may be higher, and they are generally more toxic than herbicides. Classes of common insecticides include chlorinated hydrocarbons (DDT), organophosphorus compounds (parathion), carbamates (carbaryl) and pyrethrins. (MHR)

Peyer's patches

Aggregated lymphatic nodules in the **mucosa** of the **small intestine**, especially in the **ileum**. Together with the tonsils and the lymphoid structures of the appendix, they are the initial site of many of the interactions between food **antigen**s and the animal's immune system. (SB)

pH

The negative $\log_{10}$ of the concentration of H^+. Thus, pH 7 corresponds to a concentration of 10^{-7} M H^+, which is neutral. Values below pH 7 correspond to acidic conditions and those above

pH 7 correspond to alkaline conditions, respectively. In the **stomach**, pH values can be as low as 1.5 (in rabbits) and 2–3 in pigs. In the **duodenum**, the pH value is generally about 7 in most farm animals but changes slightly along the tract according to the microbial production of **short-chain fatty acid**s and the secretion of **bicarbonate**. In the faeces of cattle and horses, the pH value is generally below 7, but in those of pigs, sheep and hens it is normally above 7. (SB)

Pharmafood

A food or nutrient for which claims of medical or health benefits are made. (MFF)

See also: Functional food; Nutraceutical

Phenolic compounds

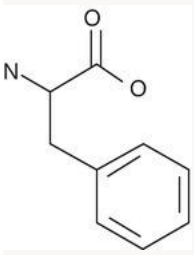
Compounds that have one or more hydroxyl groups (·OH) attached directly to a benzene ring (C_6H_6) replacing one of the hydrogens. Phenol ($HO{\cdot}H_5C_6$) is the simplest. Other variations are cresols (methyl phenol, $HO{\cdot}H_4C_6{\cdot}CH_3$), xylenols (dimethylphenol, $(CH_3)_2H_3C_6{\cdot}OH$), resorcinols (*meta*dihydroxybenzene, $(HO)_2{\cdot}H_4C_6$) and naphthols ($C_{10}H_7{\cdot}OH$). The amino acid **tyrosine** is a phenol. The **catecholamines** and related compounds, dopa, **dopamine**, **epinephrine** and **norepinephrine** are all phenolic compounds. (NJB)

Phenylalanine

An essential aromatic amino acid ($C_6H_5{\cdot}CH_2{\cdot}CH{\cdot}NH_2{\cdot}COOH$, molecular weight 165.2) found in protein. Phenylalanine can be

irreversibly hydroxylated to **tyrosine** and can therefore satisfy the physiological requirement for both of these amino acids, with about half the requirement being satisfied by phenylalanine and the other half by tyrosine. Phenylalanine + tyrosine are seldom, if ever, deficient in practical diets for animals, because most feed ingredients are rich in these amino acids.

After being metabolized to tyrosine, the main degradative pathway consists of **oxidation** of tyrosine to homogentisic acid and then to fumarate and acetoacetate, and ultimately to CO_2. Some of the phenylalanine or tyrosine not used for **protein synthesis** and not catabolized to CO_2 is used for synthesis of several important body compounds. Some of the tyrosine is iodinated to the hormone thyroxine, some is metabolized through **dopamine** to **norepinephrine** and **epinephrine** (both vasoactive **amine**s), and some is metabolized via the **copper**-containing enzyme tyrosinase to the pigments melanin (black) and dopachrome (red). The latter two compounds are synthesized primarily in dermal pigment cells known as melanocytes. Ultraviolet **light**, melanocyte stimulating hormone (MSH) in the pituitary gland and **melatonin** in the pineal gland function to regulate the synthesis of these pigments. (DHB)



See also: Essential amino acids; Thyroid

Phosphatidylcholine
Derivative of phosphatidic acid in which the phosphate group of diacylglycerol-3-phosphate is esterified with **choline**. Also known as **lecithin**, phosphatidylcholine is the most abundant **phospholipid** of the cell membrane and is one of the major structural phospholipids in the brain, comprising approximately 15% of the total **lipid**. Some lecithins are very effective **emulsifier**s and surface-active agents that prevent adhesion. They are synthesized from fatty acyl-CoAs and **glycerol** by several enzymatic steps that are shared with **triacylglycerol** synthesis. The **fatty acid** in the *sn*-1 position is usually saturated; that in the *sn*-2 position is usually unsaturated. (JAM)

Phosphatidylethanolamine
A derivative of phosphatidic acid in which the phosphate group of diacylglycerol-3-phosphate is esterified with ethanolamine. Phosphatidylethanolamines, also called cephalins, are the major structural **phospholipid** in the brain, comprising approximately 20–25% of the total **lipid**, and are also the precursor of **phosphatidylserine**. Phosphatidylethanolamine is synthesized from fatty acyl-CoAs and **glycerol** in several enzymatic steps that are shared with **triacylglycerol** synthesis. The **fatty acid** in the *sn*-1 position is usually saturated; that in the *sn*-2 position is usually unsaturated. (JAM)

Phosphatidylglycerol
A **phospholipid** consisting of **glycerol** esterified in the *sn*-1 and *sn*-2 positions with **fatty acid**s, and in the *sn*-3 position with

glycerol-3-phosphate. Synthesized in eukaryotes and bacteria from **triacylglycerol**s and glycerol-3-phosphate. Constituent of most phospholipids. The fatty acid in the *sn*-1 position is usually saturated; that in the *sn*-2 position is usually unsaturated. (JAM)

Phosphatidylinositol
A derivative of phosphatidic acid in which the phosphate group of diacylglycerol-3-phosphate is esterified with **inositol**. In eukaryotes it is the major **phospholipid** in plasma membranes, where it plays a central role in signal transduction. The **fatty acid** in the *sn*-1 position is usually saturated; that in the *sn*-2 position is usually unsaturated. (JAM)

Phosphatidylserine
A derivative of phosphatidic acid in which the phosphate group of diacylglycerol-3-phosphate is esterified with **serine**. A slowly metabolized structural **phospholipid** found in most tissues, and major structural phospholipid in the brain. Derived from phosphaditylethanolamine in mammals (phosphaditylethanolamine + L-serine α-phosphatidylserine + ethanolamine) and synthesized from cytidine diphosphate-diacylglycerol in bacteria. The **fatty acid** in the *sn*-1 position is usually saturated; that in the *sn*-2 position is usually unsaturated. (JAM)

Phospholipase
One of a group of lipolytic enzymes, e.g. phospholipase A_2 (lecithinase A; **phosphatidylcholine** 2-acylhydrolase; EC 3.1.1.4),

which is secreted as an inactive precursor from the **pancreas** into the **duodenum**, where it is activated by **trypsin**. The active enzyme hydrolyses **phospholipid**s into **fatty acid**s and lysophospholipids. (SB)

Phospholipids
Derivatives of phosphatidic acid (diacylglycerol-3-phosphate) in which the phosphate is esterified with the hydroxyl of a suitable alcohol. Phospholipids include phosphatidic acid and **phosphatidylglycerol**, **phosphatidylcholine**, **phosphatidylethanolamine**, **phosphatidylinositol**, **phosphatidylserine**, lysophospholipids, plasmalogens and sphingomyelins. All of these are phosphoacylglycerols except for the sphingomyelins, which do not contain **glycerol**. Phospholipids are main **lipid** constituents of cell membranes and contain hydrophobic (**fatty acid**) and hydrophilic (frequently an **amino acid**) polar ends. (JAM)
See also: individual phospholipids

Phosphorus (P)
A non-metallic element with an atomic mass of 30.97. Phosphorus exists in biological systems combined primarily with four **oxygen** atoms to form the phosphate radical. About 70% of the phosphate in the body is in organic forms while 30% is inorganic. The large majority of the latter is in the **sodium** and **potassium salts** of $H_2PO_4^-$ and HPO_4^{2-}, and a small amount of PO_4^{3-}. Phosphorus is an essential **nutrient**, with a large amount in the bony structures of the body, where it combines with **calcium** in hydroxyapatite

crystals in a 2:1 ratio of Ca:P. Phosphorus as the phosphate radical plays many roles in the metabolic machinery of the body. One of the most important is in the molecular structure of **nucleic acid**s to form the genetic code. Phosphates as **phospholipid**s also are important in the **maintenance** of cell membrane integrity. Another very important role is in the transfer of metabolic **energy** in the form of high-energy phosphate bonds such as phosphoenolpyruvate, 1,3-diphosphoglycerate and phosphocreatine, and **nucleotides** such as ATP, ADP, GTP and others.

Because phosphate is ubiquitous, its concentration in plant material can be fairly high, ranging from 0.1% to 0.3% in hays and **grasses** and 0.4% to 0.8% in **grain**s and seeds, and over 1% in **oilseed** meals and **cereal** grain **by-product**s. Much of the phosphorus in grains and seeds is in the form of phytic acid and is not as available for **absorption**, as are the inorganic forms. This is especially true for non-ruminant animals, which do not have active **phytases** in the intestine that hydrolyse the phytic acid to release P. Microbial phytases are commonly added to the diets of pigs and poultry to aid in phosphorus utilization. In the presence of calcium, phytic acid can bind certain **trace element**s, such as **zinc** and **iron**, and reduce their absorption. If the animal is consuming low to marginal amounts of the trace elements, the reduced absorption rate can lead to signs of deficiency.

Animals grazing over-ripe **dry season** grasses, especially if they have grown on phosphorus-deficient soils, will show signs of phosphorus deficiency. These include inappetence (**rumen**

microorganisms require phosphorus and a deficiency reduces the rate of fibre **digestion**), bone disorders and **lameness**, and low **fertility**.

Inorganic P is readily absorbed from the **small intestine**, an active process that is stimulated by 1,25-dihydroxy vitamin D_3, the hormone metabolite of **vitamin D**. The normal concentration of free phosphorus in plasma is about 30 mg l^{-1}. The phosphorus status of an animal is most often determined by measuring this parameter. Because phosphate is involved in metabolic **energy** transfer, deficiency signs can be manifested in many ways, including **anorexia**, lethargy, joint stiffness and nervous-system disorders.

Because of its importance in metabolic regulation, the dietary requirement for P is high relative to other minerals. According to the US National Research Council, the P requirement for beef and dairy cattle is 3 g kg^{-1} diet for growing and lactating animals; for sheep it ranges from 1.6 to 3.8 g kg^{-1}; for poultry and horses it is 3–4 g kg^{-1}; and for pigs it ranges from 4 to 7 g P kg^{-1} diet, depending on age, with younger animals requiring more than older ones. The severity of high P intake is tied to the amount of calcium consumed. A low Ca:P molar ratio in the diet can lead to soft-tissue calcification, with the kidney being more affected than other organs. A dietary Ca:P molar ratio of less than 1 is not advised. (PGR; GMcLD)

See also: Availability; Phytate

Further reading

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Phosphorus utilization efficiency

The sources of dietary phosphorus depend on animal species. For example, strict **carnivore**s obtain phosphorus only from animal-sourced foods, whereas omnivores acquire phosphorus from both animal- and plant-sourced foods. Inorganic phosphorus in some compounds can be effectively used by all species of animals. In all animals, **digestion** (such as the **hydrolysis** of **nucleic acid** and **phytate** into phosphate (PO_4^{3-})) is the first and crucial step for the utilization of animal- and plant-sourced phosphorus in diets, whereas phosphorus-containing inorganic compounds must be readily dissolved and dissociated in the lumen of the **gastrointestinal tract**.

Although hydroxyapatite present in animal-sourced foods such as **meat** and **bone meal** is barely soluble in water at neutral pH, this mineral is readily dissolved and dissociated in the gastric fluid (e.g. pH 2–3 in pigs) of the **stomach** to yield phosphate. In plant-sourced foods, *phytate* constitutes 60–80% of total *phosphorus* in **cereal**s, **legumes**, **nuts** and **oilseed**s. Phytate must be hydrolysed by **phytase** present in foods and derived from gastrointestinal microbes to phosphate for the utilization of dietary phosphorus. Phosphate in the intestinal lumen is absorbed by the

small intestine via three Na^+-dependent phosphate transporters against an electrochemical gradient: **sodium**–phosphate co-transporter, phosphate transporter-1 and phosphate transporter-2. **Vitamin D** stimulates the expression of these transporters in the small intestine. Phosphate enters the portal vein as a free anion and is taken up by extra-intestinal cells through Na^+-dependent phosphate transporters. The digestibilities of phosphorus in animal-sourced foods are generally greater than those in plant-sourced foods (Li *et al*., 2016; She *et al*., 2017). Ruminants are assisted by ruminal microbial phytase and, therefore, have a greater ability to utilize dietary phosphorus than non-ruminants. For example, the digestibility of dietary phosphorus in ruminants is generally about 64% for forages and 70% for concentrates (Humer and Zebeli, 2015).

The rate of the retention of dietary phosphorus in the body of 3-week-old broilers ranges from 16% to 72%, depending on the plant-sourced feedstuff (see table). About 24% and 59% of dietary phosphorus are retained in the body of growing pigs fed diets containing low- and high-level phytate, respectively (Lee *et al*., 2021). The rate of the retention of dietary phosphorus in the body of growing calves fed low, medium and high levels of phosphorus is 1.6%, 40% and 38%, respectively (Challa and Braithwaite, 1988). Dietary **supplementation** with phytase can enhance the digestibility and the utilization efficiency of phosphorus in both poultry and pigs fed plant-based feedstuffs, as well as forage-fed high-producing ruminants (Humer and Zebeli, 2015). Juvenile largemouth bass fed a conventional fish meal and soy protein-

based diet retain 35–40% of dietary phosphorus in the body (Li *et al.*, 2020). The utilization of dietary phosphorus is affected by: its intake and the intestinal health of animals; the dietary content of protein, minerals (particularly **calcium** and **fluoride**), **energy** and vitamin D; animal species, disease, **environmental temperatures** and air pollution; and the quality of drinking water. (GW)

Retention of plant-, animal-, and inorganic-sourced dietary phosphorus in the body of 3-week-old broilers

Foodstuff	Total phosphorus ($g\ kg^{-1}$), as-fed basis	Retention in broilers (% of total phosphorus)
Plant-sourced		
Beans	4.9	52
Lupin	3.0	72
Maize	3.0	29
Peas	4.1	41
Rapeseed	10.9	33
Rice bran	17.2	16
Soybean (heat-treated)	5.5	54
Soybean meal	7.1	61
Sunflower meal	11.9	38
Wheat	3.4	48

Foodstuff	Total phosphorus ($g\ kg^{-1}$), as-fed basis	Retention in broilers (% of total phosphorus)
Wheat middlings	10.8	36
Animal-sourced		
Bone meal	76	59
Fish meal	22	74
Meat meal	29	65
Meat and bone meal	60	66
Inorganic phosphorus		
Calcium sodium phosphate ($CaNaO_4P$)	180	59
Dicalcium phosphate ($CaHPO_4$)	183	83
Dicalcium phosphate (dihydrous) ($Ca(H_2PO_4)_2 \cdot H_2O$)	181	77

Foodstuff	Total phosphorus ($g\ kg^{-1}$), as-fed basis	Retention in broilers (% of total phosphorus)
Monocalcium phosphate [$Ca(H_2PO_4)_2$]	226	84
Monodicalcium phosphate (hydrous)[a]	213	79
Monodicalcium phosphate[b]	200	80
Monosodium phosphate (NaH_2PO_4)	224	92
Defluorinated phosphate [$Ca_4Na(PO_4)_3$]	182	86

Adapted from Li *et al.* (2016).

[a] $Ca(H_2PO_4)_2 \cdot H_2O + CaHPO_4 \cdot 2H_2O$

[b] $Ca(H_2PO_4)_2 + CaHPO_4$

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Phosphorylation

A process whereby an **enzyme** (a protein kinase) utilizes ATP to add a **phosphorus** atom to another molecule, most often a specific **serine**, threonine or **tyrosine** residue in a **protein**. Other **amino acid**s (**histidine**, **lysine**, **arginine** and aspartate) can also be phosphorylated. This modification of the protein may activate (turn on) or inactivate (turn off) some function, usually enzymic, of the protein. The process is reversed by

dephosphorylation, which is catalysed by enzymes called protein phosphatases. (NJB)

Photoperiod

The period of **light** within a light/dark cycle that is interpreted as day; it is synonymous with day length. It is the most potent part of a lighting regime and it regulates the endocrine system through the pineal gland and its product, melatonin, which is secreted during the hours of darkness. Photoperiod can thereby influence virtually every aspect of production. Photoperiod influences the physiology of many mammalian species, resulting in seasonal cycles of reproductive activity, growth, food intake and pelage growth.

Wild animals show well-defined breeding seasons, but the nature and extent of these are more variable in domestic animals. Domesticated sheep, deer, goats and horses exhibit seasonality of breeding whereas cattle and pigs do not. In sheep, deer and goats (short-day breeders), onset of sexual activity is triggered by the decreasing photoperiods of autumn. There are important breed differences in the duration of the breeding season; for example, the season is shorter for feral sheep breeds and for breeds of temperate latitudes (e.g. Scottish Blackface) than for tropical breeds or breeds of Mediterranean origin. Use of **melatonin** treatments to mimic short days is effective in advancing the breeding season in these species. Conversely, in mares (long-day breeders), reproductive activity is triggered by the increasing photoperiods of spring and the breeding season may be advanced by artificial light treatments. In cattle and pigs, oestrus occurs regularly throughout the year but both species show a period of reduced **fertility** in the summer

period.

Photoperiod also has a profound effect on **growth** and **appetite** in seasonally breeding animals. Sheep and deer exhibit lower rates of growth and **voluntary food intake** in winter than in summer, triggered by the decreasing and increasing photoperiods of autumn and spring, respectively. Thus low intake and **energy** demand in short days coincide with the winter period of food shortage, providing an adaptive survival strategy. The amplitude of the appetite cycle is greater in males than in castrates or females, and differences between breeds reflect the differences in photoperiod sensitivity of their breeding activity. In production systems with winter housing, growth rates of lambs and deer can be enhanced in artificial lighting regimes by long (> 12 h) photoperiod. It follows that photoperiod and nutrition interact to affect age at **puberty** in these seasonal species. If spring-born offspring are not sufficiently well nourished and well grown by the autumn, their first breeding season is delayed until the following autumn. In cattle and pigs, growth and appetite are not significantly affected by photoperiod, although long day lengths tend to increase **milk** yield in dairy cows.

Photoperiod also influences pelage growth and **moulting** in deer, sheep and goats, the timing of the winter and summer pelage being appropriate for optimum survival. Thus, fleece and fibre growth are highest in autumn and winter, with clear impact for **wool**, cashmere and mohair production.

For avian species, photoperiods can be arbitrarily categorized as sexually stimulatory (> 10 h) or sexually non-stimulatory (< 10 h).

Birds are generally reared on a non-stimulatory photoperiod prior to transfer to a stimulatory one when rapid gonadal development is required. Sexually sensitive birds reared on increasing photoperiods (spring hatched) mature earlier than birds held on constant photoperiods, which mature earlier than birds given decreasing photoperiods (autumn hatched). The degree of advance or delay in sexual maturity depends on the age at which the photoperiod is changed, the size of the change and the initial and final photoperiod. The earliest **maturity** for pullets reared on constant photoperiods occurs with a 10 h photoperiod, and the maximum advance in maturity is achieved by transferring pullets from 8 h to 14 h at 9–10 weeks of age. Once in lay, birds on longer photoperiods tend to lay more **eggs** and produce larger eggs, but have higher **feed intake**s, thinner shells and higher mortality rates. **Egg production** increases with photoperiod by about 2% h^{-1} to reach a plateau at between 10 and 14 h, depending on **genotype**. Feed intake increases by about 1.3 g h^{-1} and egg weight by 0.1 g h^{-1} with increasing photoperiod. However, shell quality and mortality are both adversely affected by longer photoperiods. Photoperiods of > 12 h do not significantly affect body weight gain in broilers and sexually immature turkeys, though ultra-long photoperiods reduce feed conversion efficiency in broilers but improve it in older turkeys (as they become sexually mature). Mortality rate and the incidence of leg problems are positively linked to photoperiod in broilers and turkeys. In growing pullets, broiler chickens and male turkeys, body weight gain is positively correlated with photoperiod, principally because of the increased

feeding opportunity on longer photoperiods, but severe feed restriction can prevent birds responding to a stimulatory lighting regime. When exposed to photoperiods that are interpreted as sexually stimulatory, male turkeys that have reached the age threshold for sexual development also have faster growth rates because of elevated plasma testosterone concentration. The effect of photoperiod on growth in female turkeys is equivocal. (PDL; CLA)

Phylloquinone
2-Me-3-phytyl-1,4-**naphthoquinone**, the form of **vitamin K** produced by plants. (JS)

Physical activity:
see Activity, physical

Phytase
An **enzyme** produced by microbes (e.g. *Aspergillus niger*) that is capable of releasing the bound **phosphorus** from **phytate**, which is the major form of phosphorus in plant tissue. Phytases are produced commercially and can be added directly to diets to release phosphate from phytate while in the intestinal tract. The greatest activity of added phytase is found in the contents of the **stomach** and upper **small intestine** in pigs and in the crop and **proventriculus** in chickens. The addition of 500–1500 units of phytase kg^{-1} diet results in nearly complete release of phytate phosphorus. This not only increases the utilization of plant phosphorus but also reduces the need for supplemental

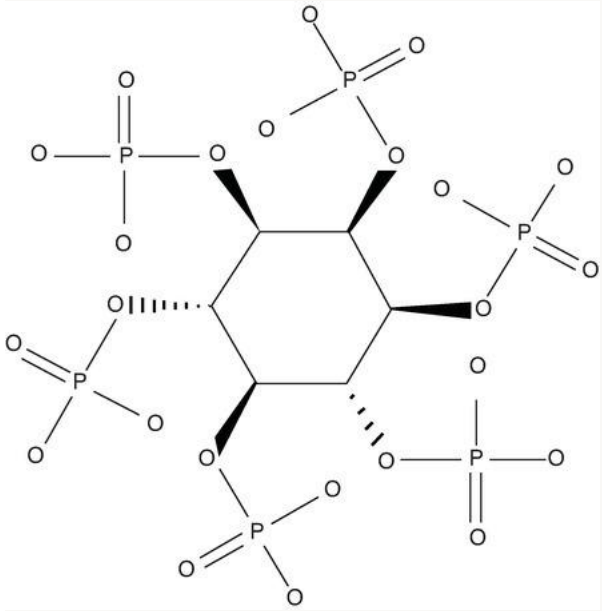
phosphorus, resulting in lower phosphorus losses in manure. Because **rumen** bacteria produce phytase, it is not necessary to add it to the diets of **ruminant animal**s. (NJB)

Key reference

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Phytate

Phytic acid is inositolhexaphosphoric acid, $C_6H_6(OPO(OH)_2)_6$. Phytates behave as chelating agents: metals known to be **chelate**d by phytate are **calcium**, **cobalt**, **copper**, **iron**, **magnesium**, **manganese**, **nickel**, **selenium** and **zinc**. Phytates are the major form in which **phosphorus** is found in plants and the phosphorus in **cereal**-based diets consequently has a low bioavailability. In **maize**, phytate is found mainly in the germ in a water-soluble form. In **legumes**, phytate is associated with protein. (NJB)



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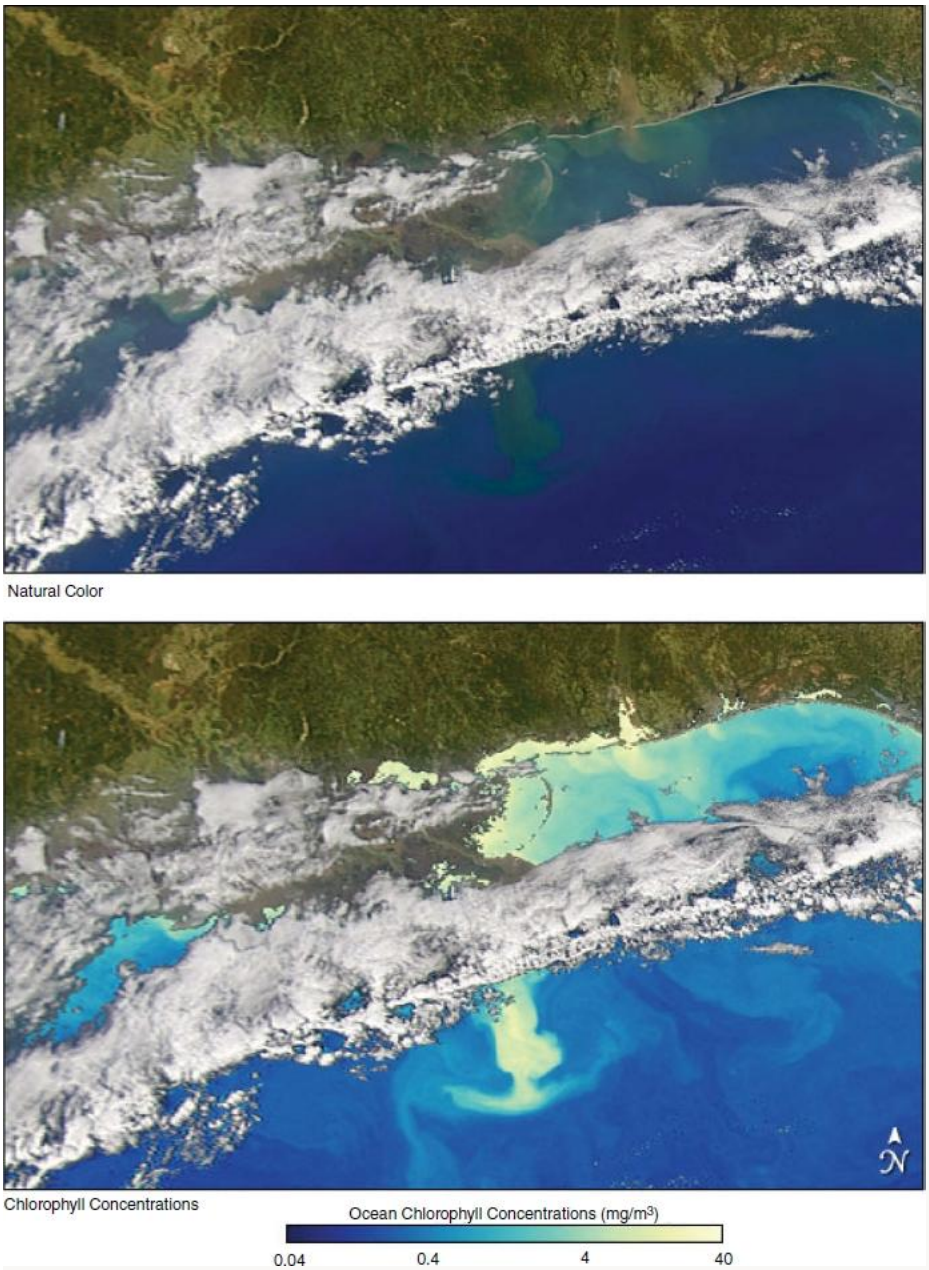
Phytohaemagglutinins

Proteins of plant origin that possess multiple **carbohydrate** binding sites. They cause the clumping or agglutination of **blood** cells. (SEL)

See also: Lectins

Phytoplankton

Phytoplankton, or microalgae, are primary producers in the aquatic food web. They use **chlorophyll** to convert solar **energy**, inorganic elements, **nitrogen** and **carbon dioxide** into **carbohydrate**, **protein**, **lipid** and **carotenoid**s.



Phytoplankton bloom in the Gulf of Mexico, as shown by chlorophyll concentrations. Photo courtesy of NASA Goddard Photo and Videl. Licensed under CC BY 2.0.

Algae

in **marine fish** culture have been used to increase the nutritional value of **rotifers**, as a direct source of nutrition for **fish larva**e, to provide background feeding for surviving prey in the rearing tanks and to maintain **light** and **water quality**. Most of the algal species used for rotifer feeding in commercial marine fish culture belong to Chlorophyceae, Prasinophyceae,

Eustigmatophyceae, Prymnesiophyceae, Cryptophyceae or Bacillophyceae. There are two predominant species: *Nannochloropsis* (Eustigmatophyceae, greenish yellow algae) and *Isochrysis* (Prymnesiophyceae, golden brown flagellate). Starter master cultures are commercially available, as are systems for containment, lighting and liquid nutrient media.

Selection of a suitable microalgal species is based on the nutritional requirements of the target fish species, the **enrichment** and growth of the intermediate rotifer prey, algal size and **fatty acid** content and, more pragmatically, the ease with which the algae can be maintained in mass culture. Algal growth is further dependent on intense illumination between 400 and 700 nm, **temperature** control within the species-specific optimum range, water filtration and sterilization, salinity and pH control, nutrients, aeration for suspension of cells and as a source of inorganic carbon, as well as maintaining ubiquitous stringent hygiene. Algae are generally harvested in the exponential growth phase when cells begin to divide at a constant rate. Generally, small culture volumes achieve higher cell densities, due to the availability of light, but densities of < 150 million cells ml^{-1} have been reported with high-density *Nannochloropsis* systems. More common cell densities range between 2 million and 40 million cells ml^{-1}. (KP)

See also: Aquatic organisms; Live fish food

Phytotoxins

Also termed toxalbumins, phytotoxins are **protein** compounds produced by certain plants that provoke antibody responses. Major

phytotoxins are **ricin**, found in castor **bean** (*Ricinus communis*), and robin, in black locust (*Robinia pseudo-acacia*). These highly toxic compounds produce depression, poor appetite, paralysis, abdominal pain, bloody **diarrhoea**, cardiac irregularities and sometimes death. (JAP)
See also: Lectins

Pig
Pigs are characterized by being hoofed (two major and two minor digits on each foot), polytocous, simple-stomached and omnivorous, having a robust but sensitive nasal disc (snout) and a sparse bristly coat. Typically the domestic pig has 38 chromosomes (2*n*) but the number can vary and 36 (2*n*) is common in wild pigs (Bosma, 1976).

Pigs are members of the mammalian Order Artiodactyla (the even-toed ungulates) and belong to the Suborder Suina (Suiformes). At this level there are three families. Pigs are a branch of the Family Suidae and are distantly related to the peccaries (the Family Tayassuidae) and the hippopotamuses (the Family Hippopotamidae). Within the Suidae there are several genera, but wild pigs of the genus *Sus* are exclusively native to Eurasia. There are some ten species or sub-species occurring in this area, of which many are very local and considered to be endangered. The domesticated pig is primarily descended from the wild boar (*Sus scrofa scrofa* L.) and some breeds may have genes from the Indian crested pig, *Sus crystatus* or *S. vittatus*.



Pigs rooting at pasture on a farm in the USA. Photo courtesy of USDA. No copyright.

Pigs have a poor ability to use fibrous leafy or woody materials. They compensate by being formidable excavators of roots using their specialized snout and their well-developed neck and shoulder muscles (m. brachio cephalicus). Roots are a rich source of **sugars**, **starch** and **hemicelluloses**, which they digest easily. Pigs have virtually no ability to **sweat**, and cope with heat by lying in water or wallowing in mud. In hot environments, provision should be made for mist spraying or for them to wallow. Although they have only a sparse coat, adults can survive winter cold because of the thick layer of subcutaneous **fat** which, when vaso-constricted, provides good insulation. They are also adept at finding and using shelter if given the opportunity. In adults, there is considerable sexual dimorphism, males being larger than females, with well-developed tusks and a 'shield' of **collagen**-reinforced

subcutaneous fat over the shoulders.

Pigs have been domesticated and eaten for several thousand years, particularly in the Far East. Several religions regard the animal as 'unclean' and this has a historic basis. Traditionally, pigs have been kept in poor conditions and in close association with human habitation. They are opportunist omnivores and will readily consume small animals, carrion and other animal's excrement. Unfortunately, these traits can give rise to important zoonoses. If pigs pick up the eggs of the tapeworm *Taenia soleum* from human faeces, these develop and form cysts in the muscles and internal organs. Inadequately cooked **pork** from such pigs can then infect humans with tapeworm and may also cause a dangerous brain damage in a condition known as neurocystercercosis. Pigs can also become infected with the roundworm *Trichinella*, which can give rise to the painful condition in humans known as trichinosis. However, in developed countries, strict hygiene regulations and **meat** inspection ensure that human and animal health are paramount and that the meat is perfectly safe.

The many different breeds of pig found across the world reflect past and present local needs. In earlier times, pigs were bred to produce fat meat, prized both for food energy in winter and when rendered to **lard** as a cooking fat. Pigs were also bred for hardiness (Duroc breed), the ability to **forage** (e.g. Iberian pigs and acorns), an ability to utilize poor-quality and waste food products (pot-bellied pigs) and the ability to withstand extremes of heat and radiation from the sun (dark-skinned and black-haired breeds, e.g. the Iberian Entrepelado). The high-water mark of such diversity

was probably the late 19th century. In developed countries, modern marketing methods have resulted in a dramatic loss of diversity in breed types. Selection objectives have focused on large size, feed utilization, leanness and, in terms of colour, white skin and white bristles. Many high-quality markets regard dark bristles deeply embedded in the skin and fat as distasteful. Now, modern hybrids (the product of several breeds) contain a high proportion of genes from the Yorkshire (Large White) and Landrace breeds. Adult boars can weigh as much as 500 kg and adult females 400 kg. At the other end of the scale there are many breeds of miniature pig which are finding an increasing role as pets and as **laboratory animal**s with a physiology similar to humans. An extreme type is the Mexican Cuino, in which the adults do not usually exceed 15 kg.

In modern hybrids, **puberty** for males and females is reached between 150 and 200 days of age depending on breed, nutrition and social environment. Unbred young females are called maiden gilts, and females embarking on gestation for a second litter are usually considered as **sows**. Uncastrated males are referred to as boar**s** or entires, and castrated males as hogs or barrows. The average length of the oestrous cycle is about 21 days. Gestation length is on average about 115 days (3 months, 3 weeks and 3 days) but this can range from 112 to 118 days. The number born in a single **litter** is between 8 and 14 with an average **birth weight** of about 1.3 kg. **Piglet**s that are small at birth (< 1 kg) are very vulnerable and neonatal mortality often runs at 15% or more. Prolific Chinese breeds such as the Meishan can average 14 or more and may produce as many as 24 piglets in a single litter.

In nature, piglets become nutritionally independent of the dam after about 12 weeks, but most farmers practise a degree of **early weaning** at 3–5 weeks of age. Segregated early weaning (at about 14 days) is a component of a specific health strategy in which piglets, still primed with passive immunoglobulins from the colostrum, are moved to a clean rearing environment, so preventing the transfer of important diseases from dam to offspring. Special diets are required for early-weaned pigs, incorporating easily digested proteins and preferably some **dried milk** products. From about 10 weeks of age (30 kg) pigs are normally fed diets based on **cereal** (mainly for **energy**) and **oil**-extracted **soybean** (high in **protein**) or their equivalent. **Nutrient requirement**s and diets are given by NRC (2012) and English *et al*. (1996). Under commercial conditions, pigs growing from 30 kg to 100 kg have growth rates of around 600–800 g per day with a ratio of feed to live gain of about 3.3:1. However, in specialized healthy environments with low stocking densities (e.g. boar-performance testing stations), growth rates can exceed 1500 g per day with feed/gain ratios as low as 1.9:1.

Slaughter weights vary according to local market preferences. Pigs slaughtered for light pork are usually marketed at 65–70 kg live weight, for the quality bacon market at 90–100 kg and for manufacturing and detailed butchering at about 120–140 kg. Entire males have a superior feed conversion, growth rate and leanness compared with females and castrates. In many countries, however, male pigs not destined for breeding are castrated because of concerns about '**boar taint**' in the meat. The odour is associated

with the presence of **skatole** and a steroid androstenone (5α-androst-16-en-3-one), which is closely related to the male sex pheromone (Lundström *et al*., 1994). A number of studies have shown that at weights of less than 100 kg this is not a major consideration with consumers and **castration** is not practised in countries such as the UK, Denmark or Australia (Willeke *et al*., 1993). **Pig meat** is one of the most versatile of all meats and is 'manufactured' into a wide range of products, including ham, bacon and sausages. High-value products include Parma and Iberian hams and fermented sausages such as salami and chorizo.

In the year 2000, on a world basis, 91 million tonnes of pig meat were produced. This exceeded the combined total for beef, sheep and goats by 33% and the combined total for chicken and turkey by 50% (FAO, 2002), making pig meat the most popular of all meat types. (VRF)

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Pig, essential nutrients

Life **maintenance** and **growth** of pigs are supported by nutrients from diets. Naturally, pigs will eat seeds, roots and insects to obtain nutrients, whereas in pig production, pigs receive processed feeds as a source of nutrients. A **diet** is composed of several to many feedstuffs with distinctly different nutrient composition and is formulated to provide nutrients meeting the requirements based on the growth stage and physiological status. Feedstuffs can be grouped by the major nutrients they are providing, including **energy** feeds, **protein supplements**, **mineral** supplements, **vitamin** supplements and non-nutritive **feed additives**. Certain nutrients must be provided to pigs from feeds because they are not synthesized, or not sufficiently synthesized, in the body. Therefore, feeds should contain essential nutrients meeting the requirement of pigs. Nutrients are categorized into water, carbohydrates, protein and amino acids, fats and fatty acids, minerals and vitamins.

1. ***Water:*** Water is an essential nutrient for pigs. Water can be obtained from drinking and from feeds, as feedstuffs contain water. Another source of water for pigs is nutrient **oxidation**.

Water has critical functions in pigs including thermal regulation, nutrient dilution, **metabolism** and lubrication.

2. ***Carbohydrates:*** **Monosaccharide**
is the basic unit of carbohydrates, including **glucose**, **fructose**, **galactose**, ribose, **xylose**, **mannose**, etc. Once absorbed into the body, glucose will be oxidized to generate **energy**. Other monosaccharides will be converted to glucose or intermediates of glucose metabolism before the oxidation. Two monosaccharides can link together to form disaccharides, which include **maltose**, **isomaltose**, **sucrose**, **lactose**, cellubiose, etc. **Milk** co-products contain high levels of **lactose** whereas other disaccharides are not mainly found in typical feedstuffs. **Oligosaccharide**s are composed of several monosaccharides, which include **raffinose**, **stachyose**, **verbascose**, fructo-oligosaccharides, manno-oligosaccharides, xylo-oligosaccharides, etc. **Polysaccharide**s are composed of many monosaccharides, which include **starch**, **cellulose**, fructan, **mannan**, **xylan**, glucan, **arabinoxylans**, **galactomannan**, glucomannan, etc. The largest portion of carbohydrates found in typical feedstuffs is polysaccharides. Polysaccharides can be divided into starch vs. **non-starch polysaccharide**s (NSPs) based on **nutrient availability** to pigs. Starch is highly digestible in the **gastrointestinal tract** of pigs whereas NSPs are not. Some NSPs are relatively soluble, absorbing water, whereas others are relatively insoluble. Soluble NSPs can cause **viscosity** of **digesta** in the upper gut and also are fermentable by gut microbiota. Insoluble NSPs can cause increased passage

rate of digesta in the gut and are less likely to be fermented by gut microbiota compared with soluble NSPs.

3. ***Proteins and amino acids:*** Body **protein** is synthesized from **amino acid**s. Among the 20 proteinogenic amino acids, nine of them cannot be synthesized *de novo* in the body and are nutritionally essential: **lysine**, threonine, **methionine**, **tryptophan**, **valine**, **leucine**, **isoleucine**, **phenylalanine** and **histidine**. **Cysteine** and **tyrosine** are formed from methionine and phenylalanine, respectively. Five amino acids (**arginine**, **glutamate**, **glutamine**, **glycine** and **proline**) are synthesized *de novo* but become nutritionally essential for pigs upon specific conditions and thus are called conditionally essential amino acids. For example, arginine is essential for newborn and pregnant pigs and glutamine for all ages of pigs during immunological challenge. The remaining four amino acids are synthesized *de novo* in the body and their dietary provision may be crucial for animal growth: **alanine**, **asparagine**, aspartate and **serine**. Typical pig feeds based on cereal **grain** and **legume** seed meals often do not include sufficient amount of lysine, threonine, methionine and tryptophan, requiring their **supplementation**; they are called limiting amino acids. **Availability** of supplemental amino acids allows nutritionists to reduce **crude protein** in pig feeds. Currently, ten amino acids are commercially available as supplements, including lysine, threonine, methionine, tryptophan, valine, isoleucine, histidine, arginine, glutamate and glutamine.

4. ***Lipids:*** **Lipids** include **fats** and **fatty acid**s. Triacylglycerides are composed of **glycerol** and three fatty acids. Thus fatty acids determine the property of lipids. Fatty acids can be synthesized in the liver and **adipose tissue**s in pigs, except for two **unsaturated fatty acid**s: **linoleic acid** (C18:2, omega-6 series fatty acid) and **linolenic acid** (C18:3, omega-3 series fatty acid), which are called **essential fatty acid**s. This is because animal cells lack an **enzyme** called Δ^9-desaturase. These can be further elongated and desaturated to be **arachidonic acid** (C20:4, omega-6 series), **eicosapentaenoic acid** (EPA, C20:5, omega-3 series) and DHA (**docosahexaenoic acid** (DHA, C22:6, omega-3 series), which are typical examples of **polyunsaturated fatty acid**s (PUFAs). Lipids from plant-based feedstuffs (plant **oil**) often contain high levels of unsaturated fatty acids whereas lipids from animal-based feedstuffs (**animal fat**) often contain high levels of **saturated fatty acid**s. In pig feeds, various lipid sources can be used, including **corn oil**, **soybean** oil, **lard**, tallow, poultry fat and **by-product**s (A-V blend oil and restaurant grease). Linoleic acid, **oleic acid** (C18:1) and **palmitic acid** (C16:0) are the most abundant fatty acids in pig feeds.
5. ***Minerals:*** There are at least 20 minerals essential to pigs. Minerals represent < 5% of the animal body. Depending on the amount found in the body, they are grouped as macrominerals (**calcium**, **phosphorus**, **magnesium**, **sulphur**, **sodium**, chlorine and **potassium**) or microminerals (e.g. **iron**, **copper**,

manganese, **zinc**, **cobalt**, **iodine**, **selenium** and **boron**). These minerals are essential and should be provided from diets.

5. ***Vitamins:*** There are at least 13 vitamins that have been identified. Vitamins are required in small amounts for their functions in the body. Depending on their **solubility**, vitamins are grouped into **fat-soluble vitamins** and **water-soluble vitamins**. Fat-soluble vitamins include **retinoid** (**vitamin A**), **cholecalciferol** (**vitamin D_3**), **tocopherol**s (**vitamin E**) and **menadione** (**vitamin K**). Water-soluble vitamins include **thiamine** (vitamin B_1), **riboflavin** (vitamin B_2), **niacin** (vitamin B_3), **pyridoxine** (vitamin B_6), **cobalamin** (vitamin B_{12}), **pantothenic acid**, folic acid, **biotin** and **ascorbic acid** (**vitamin C**). Pigs cannot synthesize most of vitamins except for cholecalciferol, niacin and ascorbic acid. However, their biosynthesis is often not sufficient in pigs, requiring dietary supplementation. (SWK)

Pig feeding

The feeding of pigs is typically divided into stages based on the production cycle and housing changes. **Suckling piglet**s derive most of their nutrients from the sow's **milk**, but it is common practice to offer some solid feed (**creep feed**) or supplementary milk if **weaning** age is greater than 3 weeks.



Piglets suckling a contented sow on pastureland. Photo courtesy of Woodlywonderworks. Licensed under CC BY 2.0.

After weaning, and depending on weaning age, pigs will be fed a series of two to four different diets until reaching a weight of 20–30 kg. These diets are initially of high **digestibility** and nutrient density, but decrease in quality and cost as the pigs mature and achieve higher voluntary intake. Pigs are normally fed frequently to **appetite** or *ad libitum* at this time, although slight feed restriction in the first few days may reduce the risk of health problems. The number of different diets fed in the growing and finishing phase will depend on the size of the farm and the housing arrangements. Since the **nutrient requirement**s of the pig change continuously as it grows, with appetite increasing and the required **protein:energy ratio** in the diet decreasing, greatest efficiency is achieved by making frequent changes to the diet specification. This is possible on large units with all-in all-out buildings, where all pigs in the feeding system are of similar age and weight, but it is

impractical on smaller units where buildings contain a mixed-age population. In this situation the best compromise diet to meet the needs of all the different pigs must be selected, but this will inevitably either restrict the performance of the younger pigs or oversupply the older animals. Whilst this problem could be overcome by blending two different diets, this is not common practice. On most farms, therefore, two or three different diets are fed during the period from 25 kg to slaughter, depending on the logistics of housing and food supply. It is increasingly common with modern selected genotypes to feed these diets *ad libitum* throughout the life of the pigs. However, in situations where castrated males, unimproved genotypes, heavy slaughter weights or very strict **carcass** fat limitations are present, it is normal practice to restrict the amount of food given after 60–70 kg **liveweight**. This reduces **fat** deposition and improves carcass quality and feed utilization efficiency, but also reduces growth rate.

Within the breeding herd, the requirements of the gestating and lactating **sows** are very different and it is common to have two separate diets for these stages. On smaller units, a single diet can be used for all **sows** if some inefficiency is accepted. Gestating **sows** are normally fed a restricted amount of feed in one or two daily meals to meet their limited requirements for **maintenance**, **growth** and pregnancy but prevent **obesity**. In a group-feeding system, this can give rise to **competition** between animals for food, penalizing young and low-ranking animals. To avoid this, sows may be individually housed and fed in stalls or separately tethered (now being phased out by law in the European

Community), temporarily confined in individual stalls during feeding or fed individually in turn by computer-controlled feeding stations. In **lactation**, sows are normally housed individually in farrowing crates and must achieve a high **feed intake** to meet the demands for milk production. They are normally fed an increasing amount of feed from the time of farrowing until fed to appetite by 7–10 days of lactation. High feed intake is encouraged by providing fresh feed two or three times daily, or by feeding *ad libitum* with plentiful water available. A diet with high nutrient density helps to minimize **body condition** loss in young animals, which have limited appetites. This is especially important in countries with high **environmental temperatures** that reduce voluntary feed intake.

The diets fed to pigs are generally based on **cereal**s and vegetable proteins, which provide the most cost-effective ingredients in the majority of situations. However, since the pig is an omnivore, it can efficiently utilize a very wide range of raw materials and was historically used to convert unwanted **by-product** materials into valuable **meat**. Commercial compound diets are usually formulated from the available raw materials by computer, using a least-cost formulation process, such that all essential nutrients are supplied in the correct balance at the lowest unit cost. Nutritional knowledge is used to set the appropriate nutrient targets for each production stage, and to impose constraints on the permitted inclusion levels of individual raw materials where this is necessitated by the presence of antinutritive factors, or by detrimental influences on **palatability**, **meat**

quality or diet manufacturing processes.

Pigs do not produce the necessary **enzymes** for fibre **digestion** and, unlike ruminants, do not have a highly efficient gut **fermentation** system which enables them to perform well on high-**forage** diets. Adult animals can utilize fibre through microbial fermentation in the **large intestine** but the energy yield and efficiency of this process are low in younger animals, where gut capacity is more limited and rate of passage more rapid. Although it is possible to feed pigs on bulky vegetable material, such as root crops and fresh or ensiled herbage or cereals, this presents logistical difficulties in large intensive production units and it is normal to offer only a single compound diet. This diet can be presented in meal or pellet form, or as a liquid feed. Raw materials such as **cereal**s are generally ground to reduce **particle size** and thus improve **digestibility** by facilitating **enzyme activity**. Since excessive fineness of grind can result in **gastric ulcer**ation, a 4–5 mm screen is recommended. Digestibility can be further enhanced by the **pelleting** process, in which heat and pressure are applied. The main benefits of pelleting lie in the enhancement of feed intake and reduction in feed wastage which occur under practical feeding conditions. Dry **compound feed**s can be handled in bulk from manufacture to trough using pneumatic and mechanical auger systems. Alternatively, automation can be achieved in wet feeding systems, which also permit liquid by-products to be incorporated on-farm. Ingredients are mixed in the correct proportions, often under computer control, and the final feed, with a water:meal ratio of 3:1 or 4:1, is then pumped to the destination building via a

pipeline system. Timed valves regulate the amount of feed dispensed to each pen. In addition to reducing feed costs by allowing the use of by-products, liquid feed can enhance intake and growth rate. (SAE)

Pig meat

The body tissue of the pig that enters the human **food chain** and is the main end-product of the feeding of commercial growing pigs. Typical lean **muscle** tissue of **pork** contains approximately 70% water, 20% **protein**, 9% **lipid** and 1% **ash**. The **amino acid** composition of the muscle protein is relatively invariant (see table). The ratio of lean to fat will depend on the joint selected, the **genotype** and nutrition of the pig and the extent of post-slaughter fat trimming. A typical loin or shoulder joint will have a fat content of approximately 40%, whilst a leg joint will typically contain only 20%. At the extreme, trimmed lean **pork** may have a fat level as low as 3.5%. Some breeds, such as the Duroc and Hampshire, produce meat with a higher level of intramuscular or 'marbling' fat and this may improve eating quality. The **fatty acid** composition of pig meat (see table) typically shows a saturated:unsaturated ratio of 0.6–0.7. This ratio can be modified by the level and composition of the feed given to the pig. Pigs that are very lean at the time of slaughter tend to have less saturated fat, whilst those with higher **body fat** content, derived from diets based on **cereal**s, produce more saturated fat. If the diet included ingredients high in **oil**, the fatty acid composition of that **oil** is rapidly reflected in body fat composition, with changes being apparent in 1–2 weeks. (SAE)

Amino acid and fatty acid composition of pig meat.

Amino acid composition [a]	**(% of cooked pork meat)**	**Fatty acid composition** [b]	**(% of total fatty acids)**
Arginine	1.8	14:0	1.5
Cystine	0.37	14:1	0.5
Histidine	1.2	15:0	0
Isoleucine	1.4	16:0	24.0
Leucine	2.3	16:1	3.5
Lysine	2.6	17:0	0.5
Methionine	0.78	18:0	14.0
Phenylalanine	1.2	18:1	43.0
Threonine	1.3	18:2	9.5
Tryptophan	0.37	18:3	1.0
Tyrosine	1.0	20:0	0.5
Valine	1.6	20:1	1.0
Others			1.5

Reference: [a]USDA Nutrient Database for Standard Reference (2001). [b]Wood, J.D. (2017) Meat composition and nutritional value, In: Toldra, F. (ed.) *Lawrie´s Meat Science*, 8th edn. Woodhead Publishing, Sawston, Cambridge, UK, pp. 635–659.

Pig meat quality

Within the pig industry, **pork** quality is associated with a multitude of factors that each set their own level of importance from the

producer to the consumer. Quality attributes that are the most influential are **muscle** pH, lean colour, intramuscular **fat** percentage, sensory characteristics and fat quality. Muscle pH is a key driver in the formation of lean colour post-mortem, with lean defects occurring at low and high measures of pH that differ from the normal pH (5.6) of **meat**. Intramuscular fat is deposited at a rate and amount related to the genetics of the animal, days on feed, and nutritional value of the product being fed. Muscle pH, lean colour and intramuscular fat percentage play a key role in the consumer's overall sensory experience. Current export/import markets serve as a segregation method for pork **carcass**es with varying degrees of quality. Each country sets relevant pork quality standards based on their consumers' needs: pork with different quality factors can be separated and sold to the market with the most potential for consumer acceptance.



Pig meat quality is influenced by slaughter method, nutrition and many other factors. Photo courtesy of Joaquin Uy. Licensed under CC BY 2.0.

Fat quality and texture are essentially a separate evaluation of

pork quality, and in recent times this has become an industry standard in the evaluation of overall quality. In general, pork fat quality can be explained with three factors: firmness; oiliness/wetness; and amount of floppiness present. All three of these factors can be attributed to the level of **unsaturated fatty acid**s in comparison with **saturated fatty acid**s within the carcass. The demand for leaner pork and the economics of achieving low-cost formulation within feedstuffs has increased the level of 'soft fat' carcasses and carcass parts observed within the industry. Bacon, the most recognizable pork product, is severely affected by poor fat quality. This is why USDA currently assigns the grade of 'U.S. Utility, carcasses with unacceptable quality' to any carcass that contains soft or oily fat. Current measures of pork quality are defined by many external factors, including **nutrition**.

The quality of fat in pig carcasses is a major consideration when diets are formulated. Techniques such as **iodine** value and 'belly flop angle' tests in conjunction with overall appearance are used to determine quality levels of the fat present. The most identifiable method of controlling fat quality in pork is maintaining an adequate ratio of saturated to unsaturated fatty acids present in the diet. When pigs are fed a **corn**- and **soybean** meal-based diet with no added **supplementation** of fats/oils, fat is typically deposited as saturated/monounsaturated fatty acids. For a **polyunsaturated fatty acid** to be deposited into the fat, a direct source would have to be fed in the diet. Feed sources such as dried distillers' **grain**s are a great source of energy in the diet, but at levels exceeding 10%, fat becomes increasingly soft and oily (a

decrease in fat quality) in nature due to its high polyunsaturated fatty acid content. Feedstuffs containing high levels of polyunsaturated fatty acids are not 'bad' products, but their level of inclusion must be at a rate that produces adequate iodine values (70 or higher) or pass the 'belly flop angle test'. Pork containing higher levels of polyunsaturated fatty acids is more susceptible to **lipid** oxidation and subsequent oxidative **rancidity**. Products containing higher levels of unsaturated fatty acids tend to have a reduced shelf-life, and the olfactory experience drastically decreases once the fat within the product begins to oxidize heavily. Maintenance of quality in relation to polyunsaturated fatty acids is critical to the shelf-life and overall sensory experience in pork products.

The optimal pork colour can be found at a pH around 5.6. Values that are too low result in pale discoloured lean meat associated with a pork quality defect known as pale, soft and exudative (PSE). Values that are too high are associated with the pork quality defect known as dark, firm and dry (DFD). Control of pH and subsequent colour in the lean can be modified by a variety of methods. One method that is commonly used is withdrawal from feed for a period before slaughter, typically 12–24 h. The idea behind feed withdrawal is that by reducing **feed intake** before slaughter, total **glycogen** present in the **muscle** can also be reduced. With reduced glycogen content, pH will drop at a lesser rate, resulting in a higher ultimate pH and a darker lean colour. However, this method is not fool-proof, due to outlying variation that can be triggered by genetics and animal handling before

slaughter. In addition, extended feed withdrawal periods could result in long-term stress and extensive glycogen depletion, which can result in DFD pork.

Supplementation of **feed additives** in a pig diet, such as **magnesium**, can also play a role in managing pH and colour in post-mortem muscle. Feeding magnesium for a few days before harvest aids in more acceptable colour development and control of pH-related factors such as drip loss. The use of **vitamin E** as a diet supplement can ultimately increase the colour stability and shelf-life of pork products, in addition to producing pork that is more desirable in colour. The success of these supplements is highly dependent on their inclusion rate and time during the finishing stage of pig feeding.

Intramuscular fat is deposited within the muscle and is typically one of the last sites of fat deposition during the growth of the animal. Intramuscular fat is best accumulated when diets are relatively high in energy content and low in total protein. This type of formulation allows for greater deposition of fat throughout the entire carcass. Drawbacks to this type of diet are that **backfat** tends to be deposited at a much higher rate, resulting in lower overall carcass cutability. Furthermore, deprivation of protein content within the diet causes decreased growth characteristics, making it highly unreasonable for producers to use. Although pork marbling can be increased via diet, increased intramuscular fat percentage is more often controlled through genotypic selection. (TES; JWS)

Pig meat quality and carcass composition, effects of

nutrition

The decades between 1990 and 2009 saw global aggregate **meat** consumption per capita increase by 24%. Although the largest gains in meat consumption have been in **poultry meat**, during this time per capita **pork** consumption rose by 20% and it remains the most eaten meat worldwide in both absolute and per capita amounts. Changing demographics will see an increasing focus on product quality in many markets and therefore factors that contribute to **meat quality** will be of increasing importance for future pork production. In this context the nutrition of pigs prior to slaughter is an important consideration.

Carcass features

Intramuscular **fat** is one of the leading contributors to flavour and juiciness of meat and therefore consumer acceptability. Genetic selection for reduced subcutaneous fat has resulted in reductions in intramuscular fat (IMF), with corresponding reductions in sensory attributes such as juiciness and flavour. In some countries there are financial penalties when **carcass** fatness passes beyond prescribed limits, and therefore maximizing eating quality through adequate intramuscular fat deposition, without attracting financial penalties, represents a challenge for pork production.

Nutritional strategies to improve IMF in finisher pigs include low-protein finisher diets and use of conjugated **linoleic acid** supplements. Reducing **protein** concentrations to a range of approximately 12–18% increases IMF and marbling, while the effects on subcutaneous fat are minimal. This effect has been observed in multiple breeds and crossbred pigs, which are

particularly prone to reduced IMF, due to their increased rates of **muscle** growth. Furthermore, reductions in the amino acid, **lysine**, are particularly important when increasing IMF and marbling, as it is a limiting amino acid for muscle growth.

Conjugated linoleic acid is a collective term describing positional and geometric **isomer**s of linoleic acid. Conjugated linoleic acids are a product of biohydrogenation of PUFAs by the **rumen** microbiome and have health benefits, such as anticarcinogenic activity. When supplemented to pigs, conjugated linoleic acid influences fat accretion and nutrient partitioning. In particular, conjugated linoleic acid has been observed to reduce overall fatness in pigs, representing reductions in subcutaneous fat deposits.

Overview of the effects of nutrition

The primary focus of the formulation of pig diets is to provide adequate energy and nutrients for growth. Nutrition influences meat quality on multiple levels, be they sensory, which relates to the appearance and hence consumer purchasing intent, or physicochemical, relating to the structure and consumer experience, including factors such as fat composition, colour, post-mortem biochemistry and **collagen** content.

Fats and oils

Fats and **oils** are included in pork diets to increase the caloric density of the feed, improving feed efficiency and reducing voluntary **feed intake**. The type and quality of the fat used can have markedly different effects on meat quality.

Polyunsaturated fatty acids (PUFAs) are **fatty acid**s that

contain more than one double bond and they are found in **soybean** oil, **sunflower**, **corn**, palm, canola, rapeseed and **linseed** oils. In contrast, **saturated fatty acid**s contain no double bonds and are typically the result of *de novo* synthesis or from animal sources such as tallow. The degree of unsaturation of fats and oils is measured by the **iodine** value (IV), which is measured in grams of iodine per 100 g of fat and increases with PUFA **supplementation**.

There are health benefits associated with supplementing with PUFAs, but this must be offset by the effects on meat quality. Supplementation with PUFAs such as soybean oil increases the concentrations within fat depots, such as the back and belly fat in the pig, and can result in processing difficulties. Higher fat unsaturation reduces the melting point, which results in reduced fat rigidity and 'soft bacon', which has a reduced yield as it is more difficult to bone out and slice. There have been mixed results in replacing PUFAs with tallow during the finishing period to offset the fat softness, and this may in part be due to the long residence time of some PUFAs in **adipose tissue**, the inclusion timeframe and the inclusion concentration. Further effects of PUFAs on meat quality are in the shelf-life and meat quality. Reductions in shelf life arise as the unsaturated bonds in PUFAs are prone to **oxidation**, resulting in **rancidity** during storage and a reduced shelf life. Oxidation of PUFAs in meat includes oxidation by reactive oxygen species (ROS), or **lipid** hydroperoxides, but photooxidation can also occur during the display of fresh meat. Oxidative stability can be improved via the addition of fat-soluble

antioxidants such as **vitamin E**. Alternatively some PUFAs have strong antioxidant properties and supplementation of rapeseed or linseed oils to pigs has been observed to reduce **lipid peroxidation** in stored chops. Furthermore, rapeseed and linseed oils improve the colour of stored meat. This has been observed by increasing a* (redness) values, indicating an increase in oxymyoglobin, which is associated with improved consumer acceptability.

Large-scale **ethanol** production and brewing have resulted in large supplies of dried distillers' **grain**s (DDGs), which can be included in pig diets with minimal effects on growth performance when fed at 20–30%. DDGs have a **digestible energy** (DE) and **metabolizable energy** (ME) similar to corn, but they contain approximately 8–12% oil in the form of PUFAs. Although DDGS improve growth rates, the PUFA content results in increases in the iodine value (IV) of the pork, which can reduce in fat firmness and other meat quality problems associated with PUFAs. Therefore, it is recommended that DDGs be limited in the final 3–4 weeks pre-slaughter.

Antioxidants

Vitamin E

Unsaturated fatty acids contain reactive methylene bridges, which are particularly prone to oxidation reactions, forming lipid peroxides. In turn, lipid peroxides continue to react with adjacent lipids in a chain reaction known as lipid peroxidation. Fat-soluble vitamins such as **vitamin E** contain an unpaired electron and react with lipid peroxides. The lipid hydroperoxides have half-lives of

milliseconds to seconds, and the new tocopheryl radical has a half-life of approximately 48 h. Therefore, the scavenging of lipid hydroperoxides by vitamin E effectively terminates the propagation of further lipid peroxides and it is due to this property that it is often referred to as a 'chain-breaking' antioxidant. Vitamin E naturally occurs in feed bases, but as it is susceptible to oxidation, supplementation with vitamin E **acetate** is commonplace. Vitamin E acetate is an **ester** with acetic acid that has prolonged shelf-life and is converted to vitamin E once absorbed. When fed to grower finisher pigs, vitamin E is incorporated into muscle tissue where it reduces lipid peroxide formation, which is associated with **rancidity**, increases in drip loss and paler meat colour. Therefore, the addition of vitamin E is a useful countermeasure to improve shelf-life and reduce the incidence of off flavours associated with rancidity, including in pigs supplemented with unsaturated fats. Further benefits of vitamin E are the reduced oxidation of myoglobin, contributing to lighter-coloured pork and reduced drip loss.

Selenium

Selenium is an essential nutrient and **trace element**, with beneficial roles for health, growth and carcass traits. The effects of selenium are mediated through selenoproteins, of which there are approximately 45 different vertebrate types with a wide distribution in the body. Most selenoproteins are oxidoreductases, performing roles in selenium transport, **immunity**, thyroid **hormone**s and **metabolism** of reactive oxygen species (ROS). Feeding selenium above typical inclusion rates of 0.2–0.3 mg kg^{-1}

has additional health benefits, with five selenoproteins responsive to increased selenium supplementation, although expression with other nutrient combinations can activate expression of other selenoproteins. The best-characterized of the selenoproteins in terms of pork quality is **glutathione peroxidase** (GP_x). Removal of reactive ROS occurs by exogenous vitamin-based removal and by bulk enzymatic degradation. Glutathione peroxidase forms part of the enzymatic removal pathway, which along with **superoxide** dismutase and catalase forms the bulk of ROS removal.

Selenium is supplemented in either inorganic forms, such as **sodium** selenite, or organic forms, such as selenomethionine. While both forms are beneficial to pork production, the **organic compound**s are the natural forms existing in the feed base. Furthermore, the organic forms of selenium have increased oral absorption and incorporation into muscle and other tissues and therefore usually offer benefits over the inorganic forms. For example, both forms reduce drip loss and improve parameters of colour such as a*, but in direct comparisons between inorganic and organic selenium supplementation the organic forms have had greater improvements.

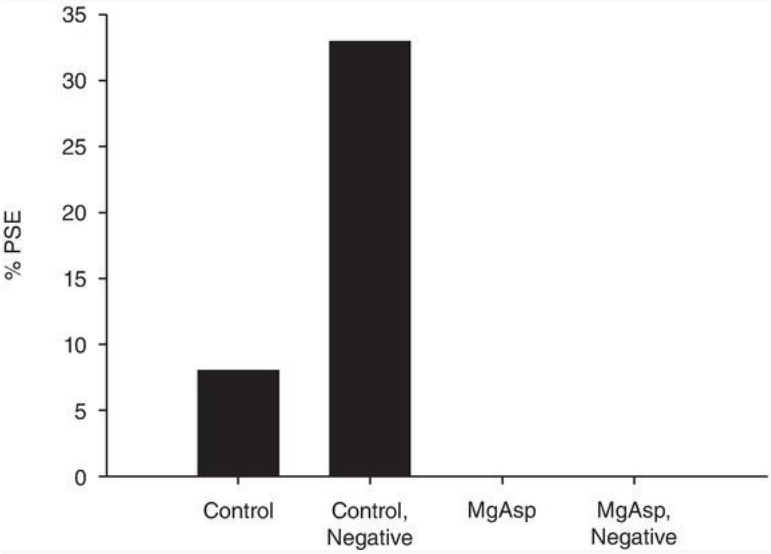
Glycogen and post-mortem pH

The concentrations of **glycogen** in the muscle determine the potential for pH reduction post-mortem and ultimate pH of meat (pH_u). Pork with low glycogen concentrations results in higher pH_u, which can lead to dark firm dry (DFD) meat, which is associated with reduced consumer acceptability. Alternatively, pork with pH_u below 5.5 can appear as ‘pale, soft, and exudative’ (PSE).

The development of PSE is caused by not just the lower pH_u, but also accelerated rates of pH fall. Glycogen depletion pre-slaughter can increase the incidence of DFD meat. This is more a result of pigs spending too long in lairage off feed, fighting or in cold temperatures, but supplementation with **sucrose** or other digestible **carbohydrate** sources pre-slaughter is effective in increasing muscle glycogen concentrations and preventing high pH_u pork. There are concerns that this may increase the incidence of PSE, which is far more prevalent than DFD, and therefore diets that lower glycogen pre-slaughter are of more relevance. This can be achieved by formulating diets with low digestible carbohydrate and compensating the caloric intake by increased **protein** and **fat** concentrations. There are discrepancies between experiments, in part due to differences in gender and muscle, but this approach has been demonstrated to slow the rate of pH decline and improve parameters of **meat quality** such as water-holding capacity.

Other approaches for reducing post-mortem glycogen metabolism and rapid rates of pH fall include additives that reduce stress. One example is **magnesium**, which when supplemented as magnesium aspartate, **chloride** or sulphate reduces the rate of post-mortem pH decline, reduces the lightness of meat and improves drip loss. In industry-based experiments magnesium aspartate has been demonstrated to reduce the incidence of PSE pork, even in the presence of negative handling with electrical prodders (see figure). Magnesium exerts some of its effects on the central nervous system, where it is antagonistic to **calcium** entry to voltage gated ion channels. The displacement of calcium

attenuates excitatory responses, leading to the reduction in stress **hormone**s, such as adrenaline and cortisol. The interaction with glycogen arises through an attenuated stress response and reduced rates of **glycolysis** to **lactate**. Interestingly, **alkaloid**s derived from *Macleaya cordata* extracts reduce the incidence of PSE in broilers and stress responses in pigs. However, results on the incidence of PSE in pigs and wider effects on pork quality are currently lacking.



Addition of 40 g magnesium aspartate (MgAsp) per day for 5 days before transport to abattoir completely removed incidences of PSE pork, even when negatively handled with electric goads. (Adapted from D'Souza *et al.*, 1998.)

Collagen

Collagen is deposited alongside the **skeletal muscle** fibres as the muscle grows in a process known as fibrinogenesis. Additionally, as the animal becomes older the collagen forms crosslinks, which increase the robustness of the collagen sheets and reduce the collagen **solubility**. **Turnover** of collagen in skeletal muscle is

mediated by matrix metalloproteinases (MMPs) and, in contrast to the skeletal muscle fibres, collagen does not undergo substantial proteolysis during the ageing process post-mortem. Therefore, the contribution of collagen to intrinsic pork quality is a product of fibrogenesis and crosslinking while in the grower-finisher stage. Nutrition has indirect effects on collagen content by modulating **growth** rates, as the age of an animal when it reaches slaughter will influence the degree of crosslinking. However, direct effects of nutrition have been observed with the inclusion of **lecithin** during the grower-finisher phase. Lecithin is a generic term for amphiphilic lipids such as glycerophospholipids, and **phosphatidylcholine**. Due to its amphiphilic properties, lecithin is sometimes used as an **emulsifier** in pig diets. Lecithin also contains anti-fibrogenic properties, preventing collagen accumulation during hepatic fibrosis. When fed to finisher gilts for 6 weeks, lecithin reduced the expression of types I and III procollagen via COL1A1 and COL3A1. When fed for 14 weeks to growing pigs, lecithin reduced overall collagen content and instrumental measurement of chewiness. Further improvements in **dressing percentage** were observed, along with reductions in L* and a* which are associated with improved consumer acceptability (Akit *et al*., 2016).

Betaine

Betaine is a methylated tripeptide synthesized in plants. When consumed by animals, betaine serves two primary functions. As an osmolyte, betaine can be accumulated in tissues undergoing osmotic stress and reduce the activity of cellular ion pumps. This

has the effect of reducing **maintenance** energy, with multiple experiments showing that betaine has improved growth rates. Alternatively, betaine can be metabolized, providing methyl groups to reactions such as DNA **methylation** and the **methionine** cycle. The effects of betaine on the sensory attributes of pork are poorly investigated but merit attention, due to documented effects on instrumental meat tenderness, colour and intramuscular fat (Dunshea *et al*., 2005). (JC; FD)

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distillers dried grains with solubles in swine diets. *Journal of Animal Science* 87, 1292–1303. doi: 10.2527/jas.2008-1290

Pigeon pea (*Cajanus cajan*)

An important **grain legume** in the tropics. It is grown mainly for its seed, which has an apparent **metabolizable energy** of 1–14 MJ kg^{-1} for sheep and poultry. The **forage** material can be fed to ruminants. (TA)

Piglets

The nutritional management of young piglets is critical for both growth and health. In the first weeks of life, piglets can exist solely on their mother's **milk**. Immediately after birth, the colostrum (first milk) provides not only a source of nutrients but also immunoglobulins, which can be absorbed intact from the gut to provide systemic immune protection. This absorptive ability is lost within the first day after birth and, whilst immunoglobulins in milk still provide local protection within the gut, the nutritional role of the milk assumes primary importance. Daily milk intake increases from about 500 g per pig in the days after farrowing to a maximum of 800–1000 g when milk yield peaks at about 3 weeks. The intake that is achieved by each individual piglet depends on the teat that it is **sucking**. Within the first day of life, a 'teat order' is established and each piglet always returns to the same teat. Stronger piglets tend to appropriate and defend the higher-yielding **mammary glands**, whilst weaker piglets are relegated to poorer glands, often in the posterior region of the udder. By about 2 weeks of age, the **appetite** of the piglets exceeds the available milk and piglets start

to look for other food. This is usually provided in the form of **creep feed** when **weaning** occurs at more than 3 weeks of age. Piglets then progressively increase their solid food intake as their own **nutrient requirement**s continue to increase while the milk yield of the sow declines.

Commercial production impairs the natural evolution of **feeding behaviour** by imposing abrupt **early weaning**. This imposes a major nutritional challenge, since the composition of the sow's milk to which the pigs are accustomed (see table) is very different to that which can be supplied by a compound diet.

Composition of sow's milk.

	% **Fresh milk**	% **Milk energy**
Crude protein	6	21
Fat	10	65
Lactose	5	14
Water	79	

Sow's milk provides a diet with concentrated **energy** in the form of highly digestible, emulsified **fat**. It also provides **sugar** (**lactose**) and easily digestible **protein** (**casein**). Thus the digestive **enzymes** of the **suckling** piglet are adapted to dealing with these **substrates**, whilst the ability to digest more complex **carbohydrates**, proteins and fats is very limited. As the piglet starts to consume solid food, the activity of the enzymes such as **amylase**, **maltase** and **sucrase**, necessary to digest more complex diets, is induced. However, when weaning occurs abruptly

at 3 weeks of age or less, the piglet will have little experience of solid food and an immature enzyme system. It also has poorly developed acid secretion and difficulty in providing the optimal pH for gastric digestion and neutralization of ingested pathogens. This, together with the removal of protective milk immunoglobulins, makes the piglet very vulnerable to pathogenic bacteria in the environment.

During the suckling phase, the surface of the **small intestine** is covered by finger-like **villi** which project into the lumen of the gut and maximize the surface area for **absorption**. Immediately following weaning, these villi can often become stunted, resulting in poor absorptive capacity. This is a consequence of inadequate **feed intake** during the weaning transition. To minimize the problems experienced at weaning, the nutritional strategy must be to maximize consumption and digestion of solid feed. **Palatability** of the diet is therefore of great importance. Both palatability and **digestibility** can be enhanced by inclusion of milk powder or related products such as casein and **whey** powder. Flavourings and sweeteners are also often included in diets for newly weaned piglets, although scientific evidence for their efficacy is limited.

Because voluntary feed intake is initially low, a high-nutrient-density diet is desirable to minimize body tissue **catabolism** after weaning. Diets typically contain a high level of **oil** (up to 10% in specialist diets for piglets weaned very early) but it is important that this is of good quality, with adequate **antioxidant** and **vitamin E** also present in the diet. Since amylase activity is initially poorly developed, precooking the **cereal** component of the

diet to rupture the **starch grain**s is also beneficial. **Flaking**, micronizing or extruding are common commercial methods. A high level of fibre in the diet is undesirable, since the greater dietary bulk and dilution of energy are deleterious when appetite is limiting, and the small gut capacity of the young piglet leaves little scope for **fermentation**. However, some readily fermentable fibre such as that derived from **oats** or **sugarbeet** can be beneficial in promoting a favourable gut microflora and reducing colonization by pathogenic bacteria.

The nature of the protein component of the diet is just as important as the **energy source**, since poorly digested protein can cause **diarrhoea**. The most digestible proteins are those in milk products. Other **animal protein**s such as fish meal and meat meal (provided that they are dried at low temperature) are the best substitute, though the use of meat meals is now prohibited in some countries, due to concern about possible transmission of disease agents. Vegetable proteins are less digestible and are often associated with **antinutritional factors** with which the young piglet is poorly equipped to cope. For this reason, the inclusion rate of ingredients such as **soybean** meal, which may contain **protease inhibitor**s and **lectins**, should be limited whilst products such as rapeseed meal, with unpalatable **glucosinolate**s, should be completely omitted. However, vegetable **protein isolate**s, from which antinutritional and antigenic factors have been removed by previous thermal, chemical and enzymatic treatment, can provide an acceptable alternative to animal proteins. In order to optimize **amino acid** balance and reduce the

total amount of **crude protein** that must be digested, the use of synthetic amino acids can be very beneficial.

Although not directly nutritional, other aspects of raw material selection for piglet diets must also be considered. Because of the difficulty that the piglet initially experiences in secreting adequate **hydrochloric acid**, a lower buffering capacity of the diet assists in achieving an optimal gastric pH for **enzyme activity**. Selection of ingredients with a low acid-binding capacity and minimizing inclusion of powerful buffers such as **limestone** (calcium carbonate) will facilitate digestion and minimize risk of diarrhoea.

It is usual to feed newly weaned piglets *ad libitum* to maximize feed intake. Since feed freshness is an important factor in palatability, the frequent feeding of small meals to appetite may be practised as an alternative in the first week after weaning. However, with poorer quality diets it may be necessary to restrict feed intake in the first week to prevent overtaxing of the immature **digestive system** and resultant diarrhoea. This approach requires that adequate trough space be provided to enable all piglets to eat simultaneously. The appetite of the young piglet increases rapidly in the post-weaning period. As intake and digestive **maturity** improve, the cost of the diet can be reduced by lowering nutrient density and increasing inclusion of less sophisticated raw materials. It is therefore common to feed two, or even three, different diets in the period between weaning and 20 kg **liveweight**. (SAE)
See also: Runt

Pigments:
see Carotenoids; Yolk pigment

Pine needle poisoning

Typically associated with late-term **abortion** in cattle induced by the labdane resin acid, isocupressic acid, found in ponderosa and other pines and some juniper species. Occasional toxicoses occur, resulting in nephrosis and neurological dysfunction. The associated toxins are the abietane-type resin acids (abietic and dehydroabietic acid), present in high concentrations in the new growth tips of pine branches. (KEP)

Pineapple (*Ananas comosus* (L.) Merr.)

A perennial stemless plant with narrow fibrous leaves. Chopped leaves can be fed fresh, dried or ensiled to ruminants. Up to 20 kg fresh leaves per day can be fed to cattle without harmful effects. Leaves are not used for non-ruminants. The main product is the fruit, from which the outer peel and central core are discarded as waste. Waste, also called pineapple **bran**, accounts for half of the total fruit weight, equivalent to about 10 t ha^{-1}. Waste can be fed fresh or dried. It is also sometimes fed with **molasses** but is palatable in its own right. The fermented pulp is more acceptable to cattle than the fresh material. Waste, mixed with grass, is a good **roughage** feed for ruminants, and can be fed to both dairy and beef cattle and sheep. It has moderate ruminant **metabolizable energy** (10.8 MJ kg^{-1} DM) and fibre (418 g kg^{-1} DM) contents, but it is low in **protein** (45 g kg^{-1} DM) and **phosphorus** (13 g kg^{-1} DM). Pineapple waste can be used in feed for older pigs but adversely affects growth and feed conversion efficiency in chicks, even at low levels of inclusion. (LR; GMcLD)

Nutrient composition of pineapple (% dry matter).

	DM (%)	**CP**	**CF**	**Ash**	**EE**	**NFE**	**Ca**	**P**
Fresh leaves	20.6	9.1	23.6	4.9	1.6	60.8		
Dried waste (bran)	87.6	3.5	16.2	5.2	0.5	74.6	0.29	0.11

CF, crude fibre; CP, crude protein; DM, dry matter; EE, ether extract; NFE, nitrogen-free extract.

Typical ME content and digestibility (%) of major constituents (abbreviated as above) in pineapple leaves and bran for ruminants

	CP	**CF**	**EE**	**NFE**	**ME** (MJ kg^{-1})
Ruminants					
Leaves	77.1	81.8	60.2	76.0	11.52
Waste (bran)	0	76.7	0	79.2	10.85

ME, metabolizable energy.

Further reading

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Pining

Term used (also pine) to describe the symptoms of a deficiency of **cobalt** in sheep and cattle. In ruminants, cobalt is used by **rumen** bacteria to synthesize **vitamin** B_{12} and other cobalt-containing analogues, whereas in non-ruminants a source of vitamin B_{12} is required in the diet rather than cobalt. The disease causes loss of appetite, stunted growth, matting of the coat (which is usually in poor condition), sunken eyes, **anaemia** and eventually death. It can be most effectively remedied by an intra-ruminal cobalt bullet. (CJCP)

Pinocytosis

A method of **absorption** in which cells of the **small intestine** engulf large molecules or ions in a manner similar to that in which an amoeba engulfs its food. Pinocytosis occurs in newborn mammals and allows the large immunoglobulins from colostrum to be absorbed intact. (SB)

Placentophagia

In eutherian placental mammals the placenta is usually eaten shortly after birth. This has the advantage of recycling the nutrients

contained within and reducing the possibility of predators finding weak neonates. (CJCP)

Plaice
A common name applied primarily to two species of right-eyed North Atlantic **flatfish** (Pleuronectidae). The American plaice (*Hippoglossoides platessoides*, called the long rough dab in England), a **cold-water species** of commercial importance in Canada, is distributed on both sides of the North Atlantic. The European plaice (*Pleuronectes platessa*), an important commercial flatfish in Europe, ranges from the Mediterranean Sea to the White Sea. (RHP)

Plane of nutrition
A description of the nutritional regimen relative to some reference value such as the **maintenance** requirement or the intake when food is offered *ad libitum* (e.g. 1.50 × maintenance; 0.90 of *ad libitum*). It is not a precise term and is variously used to refer to food intake by weight, **energy intake** or the intake of particular nutrients. (MMacL)
See also: Energy requirements

Plankton:
see Phytoplankton

Plant oestrogens
Many plants contain substances which, when consumed by animals, act like the female hormone, **oestrogen**. These substances, termed phyto-oestrogens, are found in **lucerne** (alfalfa), clovers, peas,

beans and other feeds. In some cases the chemical structure of the phyto-oestrogens is similar to that of mammalian oestrogens. Phyto-oestrogens bind oestrogen receptors in the brain and reproductive tract, which can cause premature growth of the uterus in young animals. Because phyto-oestrogens may have a negative feedback effect on the **hypothalamus**, they can also decrease the amount of natural oestrogen produced by the animal's ovaries. Without the natural ovarian oestrogens, the subsequent **fertility** of the animal consuming these plants may be affected. Oestrogenic compounds can also be found in plant material as a result of fungal **contamination**. Zearalenone is a **mycotoxin** found in mouldy **maize**, **wheat**, **barley** and other grains. It can cause severe reproductive problems in animals, especially pigs. In controlled amounts, zearalenone has been incorporated into implants and used as a **growth promoter** in beef animals. (JPG)

Plant oils:
see Cottonseed; Groundnut; Linseed; Oilseed; Rape; Soybean

Plant secondary compounds
This is an umbrella term for compounds in plants that inhibit food **digestion**, increasing metabolic costs, and may have toxic effects on **herbivore**s. As such they represent a defence against consumption. They include flavonoids, **tannins**, **saponin**s, **alkaloid**s, **amino acid**s, **cyanogenic glycosides**, **glucosinolate**s and **terpenes**. At low concentrations or intake, they may inhibit diseases through their toxic effects within the **gastrointestinal tract**. (CJCP)

Plantain (*Musa sapientum*)

A large, herbaceous, shrub-like plant 1–2 m tall, with very broad leaves and large flowers. It grows mainly in tropical and subtropical regions.



Banana plantain in Costa Rica. Photo courtesy of KraYa. Licensed under CC BY-SA 4.0.

Both unripe and ripe plantains may be useful in animal nutrition. They have been reported to contain (%) the following: moisture, 70 and 67; **starch**, 12 and 0; fermentable **sugar**, 0.08 and 20.47; **sucrose**, 1.34 and 4.56; fatty substances, 0.21 and 0.58; **nitrogen** substances, 3.04 and 4.72; **crude fibre**, 0.36 and 0.17; **tannin**, 6.53 and 0.34; and **ash**, 1.04 and 0.95, respectively (Zargari, 1997). Plantain fruit is very useful for children and the elderly, due to its good nutritional value and the ease of its digestion, being rich in carbohydrates (22%) and containing 370 kJ **energy** per 100 g. Plantain fruit is a good source of **potassium** (358 mg 100 g^{-1}), rendering it beneficial in food programmes

(Ranjha *et al*., 2022). The peel is usually wasted but is also rich in nutrients (Thomas and Krishnakumar, 2017; Nuriyasa *et al*., 2022). (AS; BH-G; CJCP)

See also: Banana

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Plasma:

see Blood plasma

Plastic ingestion

This is a problem in the oceans, on the land and in waste piles in places with no proper waste collection. The impact is primarily causing impaction in the gut, but also can spread pollutants such as PCBs and plasticizers to the ingesting animal's body. Plastic is synthetic polymers made of diverse materials and cannot replace fibre in the diet of ruminants or other animals, because it is inert. Filter-feeding marine invertebrates can also ingest microplastics.

The indigestion can be direct or via contaminated food, the latter similarly posing threats to humans.

Microplastics comprise both breakdown products of large plastic pollutants, such as plastic bags and straws, and directly applied plastic products, such as particles used to clean the undersides of boats. Plastic fishing nets are commonly ingested and have caused the death of whales from gastric impaction. Similar to this, large quantities of plastic bags have been found in the rumen of emaciated cattle in India, these animals having to roam the streets in search of feed. The absence of rubbish collection encourages widespread pollution with plastic bags and containers, to which cattle, birds and other livestock or wild animals are attracted looking for food. Scavenging farm animals in particular may consume plastic in their search for nutrients in the contents of plastic bags and bottles in the vicinity of human settlements.



Squirrel eating plastic bag containing a discarded sandwich. Wildlife are particularly prone to plastic consumption problems. Photo courtesy of Bluesbby. Licensed under CC BY- 2.0.

As a material, the plastic is inert from a digestive perspective, and it takes many centuries to degrade naturally. When consumed

in large quantities, the plastic can accumulate in the gastrointestinal tract and block apertures. Emergency rumenotomies are often required to prevent such animals dying of obstructive blockages. For example, nearly all street cattle in India have health problems caused by plastic ingestion. Large areas of the world's oceans are also contaminated with plastics, some of which cause obstructive blockages in marine life.

If left in the natural environment, some plastics break down under the elements to microplastics, which are similarly inert but easier to digest, while others remain intact for a long period of time. It is estimated that a single plastic bottle takes 450 million years to decompose. Many countries are now attempting to control the use of plastic through recycling, bans or replacing it with other materials. (CJCP; DM)

Poisoning

Animals are susceptible to a wide range of poisons or toxins derived from plants (see table), **microorganism**s or chemicals. Many feeds for farmed animals contain naturally occurring toxic substances such as **gossypol** in **cottonseed** and **haemagglutinin**s in **legume** seeds; grazing animals may be accidentally exposed to the poisons of bracken and ragwort. Feeds may be contaminated with fungal toxins such as **ergot** and **aflatoxin**. A number of infectious microorganisms produce toxins that lead to gastrointestinal disorders. Animals may also be exposed to herbicide and **pesticide** residues. (MFF; MHR)

Poisonous plants.

Scientific name	Toxin	Disease
North America		
Hymenoxys odorata	Hymenoxin	Gastroenteritis
Zigadenus spp.	Steroidal alkaloids	Convulsions
Conium maculatum	Piperidine alkaloids	Birth defects, respiratory arrest
Delphinium spp.	Norditerpene alkaloids	Paralysis, bloat, respiratory failure
Astragalus, *Oxytropis* spp.	Swainsonine	Wasting disease, neurological dysfunction
Astragalus spp.	Nitropropanol	Emphysema, locomotor dysfunction
Lupinus spp.	Quinolizidine alkaloids	Respiratory paralysis
	Piperidine alkaloids	Crooked calf disease
Senecio spp.	Pyrrolizidine alkaloids	Liver disease
Cassia spp.	Unknown	Myopathy
Eupatorium rugosum	Tremetol	Trembles
Pinus ponderosa	Isocupressic acid	Abortions in cattle

Scientific name	Toxin	Disease
South America		
Palicourea marcgravii	Monofluoracetic acid	Heart failure
Arrabidaea spp.	Unknown	Sudden death
Mascagnia spp.	Unknown	Sudden death
Ateleia glazioviana	Unknown	Heart fibrosis, abortion
Baccharis coridifolia	Trichothecenes	Gastroenteritis
Cestrum spp.	Parquin	Liver necrosis
Senecio spp.	Pyrrolizidine alkaloids	Liver disease
Pteridium aquilinum	Ptaquiloside	Enzootic haematuria, anaemia, neurological disease
Solanum malacoxylon	Vitamin D_3-like glycoside	Metastatic calcification
Nierembergia veitchi	Vitamin D_3-like glycoside	Metastatic calcification
Australia and New Zealand		
Coriaria spp.	Tutin	CNS lesions
Acacia georginae	Fluoroacetate	Heart failure

Scientific name	Toxin	Disease
Gastrolobium, *Oxylobium*	Fluoroacetate	Heart failure
Erythrophloeun chlorostachys	Cassaine	Cardiotoxin
Crotalaria spp.	Pyrrolizidine alkaloids	Liver, lung and kidney lesions
Cycas, *Macrozamia* spp.	Methyo-azoxymethanol	Liver necrosis, gastroenteritis
Indigofera spp.	Indospicine, nitrotoxin	Birdsville disease
Homeria spp.	Bufadienolides	Gastroenteritis
Lantana camara	Lantanin	Liver damage
Pimelea spp.	Unknown	Gastroenteritis
Pteridium esculentum	Ptaquiloside	Enzootic haematuria, anaemia, neurological disease
Swainsona spp.	Swainsonine	Wasting disease
Neobassia proceriflora	Oxalates	Kidney damage
Tribulus terrestris	Unknown	Liver disease, secondary photosensitivity

Scientific name	Toxin	Disease
Heliotropium spp.	Pyrrolizidine alkaloids	Liver disease
Echium plantaginium	Pyrrolizidine alkaloids	Liver disease
South Africa		
Dichapetalum cymosum	Monofluoroacetate	Heart damage
Pachystigma spp.	Unknown	Heart failure
Tribulus terrestris	Unknown	Secondary photosensitivity
Lantana cannara	Lantanin	Liver damage
Lasiospermum bipinnatum	Furanosesquiterpene	Liver damage, secondary photosensitivity
Asaemia axillaris	Furanosesquiterpene	Liver damage, secondary photosensitivity
Senecio spp.	Pyrrolizidine alkaloids	Liver disease
Geigera spp.	Sesquiterpene lactones	Gastroenteritis
Pennisetum clandestinum	Oxalates, nitrates	Respiratory failure
Ornithogalum spp.	Unknown	Diarrhoea

Scientific name	Toxin	Disease
Gnidia spp.	Daphentoxin	Diarrhoea
Salsola tuberculatiformis	Unknown	Distocia
Crotalaria spp.	Pyrrolizidine alkaloids	Lung lesion
Europe		
Colchicum autumnale	Colchicin	Gastroenteritis
Solanum dulcamara	Solasodin	Birth defects
Ranunculus acer	Protoanemonin	Gastroenteritis
Brassica spp.	Isothiocyanates	Gastroenteritis
Taxus baccata	Taxines	Cardiac arrest
Quercus spp.	Tannins	Gastroenteritis
Senecio jacobeae	Pyrrolizidine alkaloids	Liver disease

See also: Aflatoxins; Algal toxins; Alkaloids; Aspergillosis; Botulism; Bracken fern; Carcinogens; Castor bean; Cyanide; Cyclopropenoic fatty acids; Deoxynivalenol; Dioxin; Endotoxins; Ergot; Fumonisins; Gizzerosine; Glucosinolates; Gossypol; Heavy metals; Herbicide residues; Insecticide residues; Kale; Lathyrism; Lead; Lectins; Leucaena; Lupinosis; Marine toxins; Mercury; Mimosine; Mustard; Mycotoxins; *N*-nitroso compounds; Nitrosamines; Ochratoxins; Pesticides; Phytotoxins; Pine needle

poisoning; Poisonous plants; Polychlorinated biphenyls; Polycyclic aromatic hydrocarbons; Ragwort poisoning; Ricin; Saponins; Solanin; Thiocyanates; Trichothecenes; Vicine; Vomitoxin.

Further reading

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Pollards:

see Milling by-products

Polyamines

The polyamines spermidine ($NH_2{\cdot}(CH_2)_4{\cdot}NH{\cdot}(CH_2)_3{\cdot}NH_2$) and spermine ($H_2N{\cdot}(CH_2)_3{\cdot}NH{\cdot}(CH_2)_4{\cdot}NH{\cdot}(CH_2)_3{\cdot}NH_2$) are derived from the amino acid, **ornithine**, which is decarboxylated to provide the four-carbon diamino compound, **putrescine** ($NH_2{\cdot}(CH_2)_4{\cdot}NH_2$), and **methionine**, which provides its amino-N and 2, 3 and 4 carbons via ***S*-adenosylmethionine**. Spermidine is converted to spermine by a second addition of the methionine amino-N and 2, 3 and 4 carbons obtained from *S*-adenosylmethionine. In sheep fetuses, **arginine** is decarboxylated

to form agmatine, which is hydrolysed to putrescine and **urea**. By contrast, pig conceptuses lack the enzymes for converting arginine to agmatine. Polyamines are required for cell proliferation and growth. Since they have multiple positive charges, they are found associated with the polyanions DNA and RNA. (NJB; GW)

Polychlorinated biphenyls (PCBs)

Biphenyls consisting of two chlorinated benzene rings joined together. PCBs are structurally similar to the insecticide DDT. PCBs were used as non-flammable **oils** in transformers, condensers and paints, as well as other industrial applications. Because they are persistent environmental contaminants, their industrial use has been greatly restricted. They are toxic to wildlife, especially birds, and cause impaired egg hatchability, tissue damage and mortality. 'Aroclor' is a common PCB. (PC)

Polychlorinated biphenyls as pollutants

PCBs were once commonly used in the electroplating industry as plasticizers in paints and other products, as well as in a large number of other industrial uses, causing them to enter the air, water and soil. As a result of their long half-life and resistance to degradation, PCBs accumulate in the **food chain**. They have no **taste** or smell in contaminated food. An estimated 2–3 million tonnes were produced worldwide between the 1920s and 1980s. Since the recognition of their potential carcinogenicity and adverse effects on **reproduction**, immune and nervous systems of animals in the 1970s, levels of use have gradually declined.

For humans, food is the major source of exposure, particularly

fish and shellfish, dairy and **animal fat**, as PCBs bind tightly to soil and, in the ocean, accumulate on the surface of the seabed. There have been some major **poisoning** incidents in Asia when **rice** contaminated with PCBs and their breakdown products was consumed. Because of harm to human and environmental health, the importation of these chemicals was banned in Australia in 1975; their use was prohibited in the USA from 1979 and in the UK from 1981 and an international ban was introduced soon after. (CJCP; DM)

Polycyclic aromatic hydrocarbons (PAHs)
Compounds composed of carbon and **hydrogen** that contain two or more fused aromatic rings. There are approximately 163 PAHs, many of which are known for their carcinogenic and mutagenic properties. PAHs containing four or more rings that are not co-linear are carcinogenic, e.g. 1,2-benzathracene. PAHs are formed both naturally, from biosynthesis, natural combustion and long-term degradation followed by synthesis from biological material, and from anthropogenic sources through incomplete combustion of organic material. Their occurrence in complex environmental mixtures makes their detection, identification and quantification challenging. (JEM)

Polydipsia
Drinking to excess, usually in association with stress. (CJCP)

Polyenoic fatty acids:
see Polyunsaturated fatty acids

PolyglutamatesTetrahydrofolate

substrates ($PteGlu_n$) found in foods and cell extracts. The form absorbed from food in the intestine is tetrahydrofolate monoglutamate ($PteGlu_1$). In cells, polyglutamates ($PteGlu_{1–7}$) are formed by successive additions of γ-**glutamate**, the most abundant form being the pentaglutamate. Addition of γ-glutamates lowers the K_m for these **substrates**. (NJB)

Polyphenols

Compounds that contain more than one hydroxylated phenyl group. Although the term polyphenol is more correctly limited to **lignan**s, **lignin** and **tannins**, which are polymers, it is also used to refer to other **phenolic compound**s such as hydroxy **cinnamic acid**s, monolignols and flavonoids. Plant polyphenols have several nutritional effects. Tannins inhibit the digestion and absorption of protein. Lignin prevents the **fermentation** of cell wall **polysaccharide**s by anaerobic gut microorganisms. Many flavonoids have **antioxidant** properties that are similar to **vitamin E**. (NJB)

Polysaccharides

Carbohydrate polymers that contain periodically repeating structures in which the dominant, but not necessarily exclusive, interunit linkages are of the *O*-glycosidic type. This classification includes polymers consisting entirely of **monosaccharide** monomers as well as proteoglycans, **peptidoglycan**s, **lipopolysaccharide**s and teichoic acids. Homopolysaccharides are polymers of a single monosaccharide (e.g. **glucose** in **starch**

and **cellulose**). Heteropolysaccharides have more than one monosaccharide in the polymeric structure (e.g. **arabinose** and **xylose** in **arabinoxylans**). (JAM; JDR)
See also: Carbohydrates; Dietary fibre; Hemicelluloses; Pectic substances

Polyunsaturated fatty acids (PUFAs)Long-chain fatty acids (C-18 to C-22) that contain more than one unsaturated (·HC═CH·) carbon–carbon linkage. They are classified into two groups: n-3 and n-6. In the n-3 group the first double bond is between carbons 3 and 4, counting from the terminal methyl (CH_3·) carbon, and in the n-6 group the first double bond is between carbons 6 and 7 from the methyl end. For example, **linolenic acid** (all-*cis*-9,12,15-octadecatrienoic acid) is designated 18:3 n-3 and **arachidonic acid** (all-*cis*-5,8,11,14-eicosatetraenoic acid) is designated 20:4 n-6. PUFAs for aquatic animals are mainly linolenic acid, arachidonic acid, ARA, EPA, DHA, all major **essential fatty acid**s. (NJB; QS)

Pond:
see Fish pond

Pork
The unprocessed meat of pigs. **Pig meat** is also cured, and may additionally be smoked, to produce ham and bacon. (MFF)

Postabsorptive state
The state of an animal after it has digested and absorbed the nutrients consumed in a meal. (JMW)

Potassium (K)

An alkali metal with an atomic mass of 39.098. Potassium is absolutely essential in the diet of animals. In mammalian systems, it is usually associated with the intracellular fluid. The **intestinal absorption** of K is not regulated per se, but is facilitated by a number of pumps, co-transporters and conductance channels. These include (located in cell membranes and involving K exchange) the Na,K-ATPase pump, the H,K-ATPase pump and the Na-Cl-K co-transporter. The body maintains a fairly constant amount of K. The kidneys eliminate about 95% of K absorbed beyond the body's needs and the other 5% is excreted through the **gastrointestinal tract**.

One of the key roles of K, along with **sodium**, is in the maintenance of an electrical potential across the membranes of all cells. This is accomplished to a great degree by the Na^+/K^+ pump in the membrane that exchanges three Na ions inside the cell for two K ions outside the cell. The Na/K pump is an ATPase and is especially important in the propagation of impulses in **muscle** and nerve cells.

The US National Research Council recommends from 6 g K kg^{-1} diet for growth to 7 g kg^{-1} for early **lactation** in beef cattle, and 10–10.7 g kg^{-1} diet for lactating dairy cows, depending on the milk yield, but only 6 g K kg^{-1} diet for growing heifers, bulls and gestating beef cows. The K requirement for growing pigs ranges from 1.7 to 3 g kg^{-1} diet, depending on the age of the animal: young growing pigs require more than adults. The K requirements for

growing turkeys and laying turkey hens are 4–7 and 6 g kg^{-1} diet, respectively; the K requirement for growing **broiler chicken**s is 3 g kg^{-1} diet across all age groups of the birds; the K requirements for Leghorn-type **laying hen**s are 1.3–1.9 g kg^{-1} diet, depending on the amount of daily **feed intake** (80–120 g per hen). For growth and maintenance of horses the requirement is 3 g kg^{-1} of diet, but it increases to 3.5 to 4.2 g kg^{-1} diet for lactating mares and working horses. The requirement for sheep ranges from 5 to 8 g kg^{-1} diet. Almost all farm animal feedstuffs are reasonably high in K concentration, but **grain**s have less than forages. Thus, under normal feeding practices, animal diets may require **supplement**s of K salts.

Potassium deficiency can depress plasma K concentrations, which can result in muscle paralysis and cardiac dysfunction in animals. Ingestion of high amounts of K can reduce **magnesium** absorption and enhance the onset of **tetany**, especially in ruminant animals. (PGR)

See also: Chloride

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Potato (*Solanum tuberosum*)

Potatoes may be fed to ruminants either raw or cooked. They can be fed whole to adult cattle but, to avoid the risk of them becoming stuck in the gullet, they can be fed from low troughs or they can be mashed or chopped. Dairy cattle can be given potatoes at 15 kg per day and beef cattle at 20 kg per day or < 12% of the diet, and ewes at 3% of diet. However, as potatoes have a laxative effect they should be introduced gradually. Due to the structure of the **starch** granules, non-ruminants digest raw potato starch poorly: most is digested by hindgut **fermentation**. Raw potatoes also contain a **protease inhibitor**. Cooking renders the starch highly digestible and also inactivates the protease inhibitor. For these reasons, potatoes should be cooked before being fed to young pigs and poultry. Sows can adapt to eating raw potatoes at < 6 kg per day or 15% of the diet, while weaners can be fed at 10%. Heavily soiled, rotten, green and sprouted potatoes should not be fed to livestock, or the sprouts should be removed before they are fed to pigs or poultry as they contain toxic **alkaloid**s. Ensiled potato haulm can be fed to cattle at < 20 kg per day but may have a high **ash** content, due to soil inclusion. Potato processing wastes include sludge, peelings and potato chip scraps. (JKM)

Nutrient composition of potato.

		Nutrient composition (g kg^{-1} DM)				
	Dry matter (g kg^{-1})	**Crude protein**	**Crude fibre**	**Ash**	**Ether extract**	**NFE**
Haulm	230	109	270	135	43	443
Haulm silage	250	128	176	224	108	364
Fresh tubers	200–241	103–121	20–40	50–55	2–5	781–818
Fresh peelings	212	99	33	61	5	802

Poult
A young **turkey**. (CN)

Poultry
A general term applied to domesticated avian species but frequently used in the narrower context of **domestic fowl**. (KJMcC)
See also: Chicken; Ducks; Game birds; Goose; Guineafowl; Ratites; Turkey

Poultry by-products:
see Feather meal; Hatchery waste; Poultry offal meal

Poultry droppings

Unlike mammals, poultry do not possess separate openings for the excretion of urine and faeces. As a result the excreta in birds is a combination of urine and faeces, expelled via the **cloaca**. This process in birds explains the absence of a bladder and involves the excretion of nitrogenous breakdown products in the form of uric acid, which appears as a white paste or a dry, white powder in the droppings. Very little water is required for this process in birds, compared with the excretion of urine in cattle or pigs, and is related to their ancestry from reptiles and the need for a light body weight to enable the bird to fly. Caecal waste is also deposited on the excreta, appearing as a light-brown froth, which should not be confused with **diarrhoea**.

Chickens may produce > 250 g of droppings per day, but this can vary markedly with amount of feed eaten and total urine output. Depending on dietary composition, poultry droppings may have a high **nutritive value** and can be used as a fertilizer. (RB)

Poultry feeding

This general term applies to the feeding of any domestic avian species at any stage of production. (KJMcC)

See also: Chicken; Ducks; Game birds; Goose; Guineafowl; Ratites; Turkey

Poultry litter:

see Litter

Poultry manure

This can be almost pure **poultry droppings** (excreta), if collected under cages, or a mixture of excreta and bedding (**litter**) if obtained from a broiler house or a deep-litter system for **laying hens**. Therefore the moisture and nutrient contents can vary widely. Poultry manure is usually spread on land, where it provides useful amounts of **nitrogen** and **phosphorus**, thus reducing the need for artificial fertilizer. (KJMcC)

Poultry meat

The four main species of domesticated poultry used for **meat production** are **domestic fowl**, **turkey**, **goose** and **duck**. The **carcass** yields of poultry (as a percentage of the **liveweight**) are around 71–74%. The edible **meat yield** (also as a percentage of liveweight) ranges from around 29% in ducks to 34% in geese, 44% in meat-line strains of domestic fowl and 51% in turkeys. Both the carcass yield and the edible meat yield depend on the slaughter weight and the figures quoted should only be used as guidelines. In general, breast meat of poultry has a greater economic value than leg meat. Of the edible meat approximately 35% is breast meat, 38% leg and thigh meat and 27% wing and other meat. Although the breast meat in turkey (38%) is a greater proportion of the edible meat than in domestic fowl (34%), there is a greater proportion of wing and leg meat in turkeys (39%) than in domestic fowl (29%). These figures represent average ranges and will depend on the genetic strain of the poultry.



Chicken meat from free-range chickens in Indonesia. Photo courtesy of Sakurai Midori. Licensed under CC BY 3.0.

One of the main differences between breast and leg meat is the appearance, breast meat being generally lighter in colour due to having less myoglobin than the leg **muscles**. There are biochemical differences between the breast and leg muscles that reflect their original use for flight. The breast muscles predominantly contain 'fast glycolytic' (type IIB) muscle fibres, i.e. those that can contract fast and have an enzyme profile for a glycolytic-type **metabolism**. For example, the pectoralis major, the main muscle in breast meat, has 100% fast glycolytic-type fibres. The leg muscles, on the other hand, have a predominantly oxidative metabolism. For example, the illiotibialis, one of the leg muscles in domestic fowl, has 40% oxidative fibres at 20 weeks of age. The proportion of oxidative fibres increases with age in this muscle.

Although the water contents of the breast and leg muscles are similar, the dark leg meat has a higher **fat** content (5.5%) and less **protein** (19%) than breast meat (3.2% and 22%, respectively). The

collagen content is higher in the thigh muscle (17 mg g^{-1} dry matter (DM)) than in the breast muscle (8 mg g^{-1} DM). In the thigh muscle the amount of collagen increases with age and its **solubility** decreases with age.

The **fatty acid** profile of the meat reflects the fatty acid profile of the diet. For example, increasing the proportion of fish meal in the diet results in increased concentrations of 22:6 n-3 fatty acids in both the white and dark meat of broilers. Increasing the proportion of n-3 **polyunsaturated fatty acid** (PUFA) content can lead to reduced oxidative stability and increased **rancidity** during refrigerated storage. Feeding **vitamin E** (α-**tocopherol**) results in increased incorporation of this into the muscle and this can act as an **antioxidant**. (BMM)

See also: Meat composition; Meat quality

Poultry metabolic disorders related to nutrition

A malfunction of the body, tissues, or organs due to disturbances in metabolic or physiological processes such as **growth** or increased workload (e.g. cardiac output) in modern commercial poultry. These growth and production-related disorders results in failure of the body's cardiovascular haemodynamics and **antioxidant** defence systems. Poultry metabolic disorders occur primarily in two body systems: (i) cardiovascular and (ii) musculoskeletal (those impacting **muscle** and skeletal development). These disorders are commonly associated with fast growth in meat-type **broiler chicken**s and turkeys. The most common cardiovascular disorders include pulmonary arterial **hypertension** syndrome

(**ascites** syndrome), sudden death syndrome in broilers and turkeys, spontaneous turkey cardiomyopathy, round heart disease in broilers, ruptured aorta in turkeys, **atherosclerosis** in turkeys and broilers and epicardial fibrosis in broilers. Broilers are susceptible to ascites syndrome when their pulmonary vascular capacity is inadequate to accommodate the requisite cardiac output. In severe cases, metabolic disorders affecting cardiovascular system are accompanied by ascitic-like conditions and sudden death. Those affecting the skeletal system are accompanied by **leg weakness** and leg or joint abnormalities (e.g. angular bone deformities), leading to reduction in growth and **lameness**, affecting animal **welfare** as well as economic aspects. Recently certain muscle (*pectoralis major*) quality attributes such as **myopathy**, wooden breast (myodegeneration and necrosis) and white striping (white striations of intramuscular **fat** and **connective tissue** parallel to muscle fibres) has been associated with fast growth, affecting visual quality, **carcass** downgrades and consumer acceptance of broiler chicken meat. Other categories of metabolic disorders affecting egg-laying hens include hepatic- and kidney-related disorders, leading to fatty liver haemorrhagic disease and peroxidative dysfunction in young chicks, called nutritional encephalomalacia, affecting the brain. Dietary imbalances (excess or deficiency) of nutrients include: **arginine** (the **substrate** for **nitric oxide** production); n-6 to n-3 **fatty acid** ratio, affecting the **arachidonic acid** cascade and pro-inflammatory vasoactive **eicosanoid**s (e.g. **prostaglandin**s, thromboxanes, **leukotriene**s) synthesis; **antioxidant**s (e.g.

tocopherols, **selenium**), affecting **lipid peroxidation** and oxidative stress; and other nutrients such as **vitamin A**, **vitamin D**, **biotin** and ascorbate. These are all associated with the aetiology of metabolic disorders of nutritional origin in poultry. (GC)

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Poultry offal meal

The viscera, feathers, etc., obtained during slaughter and processing account for up to 30% of **poultry meat** production. Spent hen meal, arising from complete **rendering** of **laying hen**s at the end of the productive cycle, is a recent variant. These **by-product**s are potentially good sources of nutrients (particularly **protein** and **amino acid**s) if properly processed. Typically, poultry offal meal contains around 600 g protein kg^{-1} and is a good source of amino acids. The protein contents of spent hen meal and

feather meal are around 670 and 820 g kg^{-1}, respectively. However, the amino acid content and availability of the latter are relatively poor. (KJMcC)

See also: Blood meal; Fish products; Meat products

Prawn

A freshwater crustacean, the Malaysian giant prawn, farmed primarily in Asia but experimentally cultured in other areas of the world. 'Prawn' is sometimes used to distinguish larger shrimp. (DEC)

See also: Crustacean feeding; Shrimp

Key reference

New, M.B. and Valenti, W.C. (2000) *Freshwater Prawn Culture: the Farming of* Macrobrachium rosenbergii. Blackwell Science, Oxford, UK, 443 pp.

Prawn nutrition

Prawns belong to the Dendrobranchiata suborder of the order Decapoda under Class Crustacea (Dzidzornu 2018). The commonly cultured prawn species in the world include giant freshwater prawn (*Macrobrachium rosenbergii*), painted river prawn (*Macrobrachium carcinus*), oriental river prawn (*M. nipponense*), monsoon river prawn (*M. malcolmsonii*), Amazon river prawn (*M. amazonicum*) and Cauque river prawn *(M. americanum*). Different species of prawns have different dietary requirements for nutrients. Globally, prawns have been farmed for several decades, primarily in Asia and the Americas. Most prawn species are omnivores and their natural diets consist of a variety of plant and

animal materials (D'Abramo and New, 2010). Here, dietary **nutrient requirement**s are expressed on a dry matter (DM) basis.



Giant tiger prawn. Photo courtesy of CSIRO. Licensed under CC BY 3.0.

Protein and amino acids

Based on growth performance and feed efficiency, the requirement of prawns for dietary **protein** is 30–40% during the post-larvae and juvenile stages (Li *et al*., 2021). For larger prawns reared in ponds, less than 30% dietary protein may be sufficient. Dietary protein, digestible **carbohydrates** and **lipids** are utilized as **energy source**s in prawns. The use of dietary protein as an energy source can be substantially reduced (spared) by non-protein energy sources (lipids and **starch**). Therefore, it is important to balance the ratio of protein and energy in the diet.

Among all proteinogenic **amino acid**s, ten of them (**arginine**, **histidine**, **isoleucine**, **leucine**, **lysine**, **methionine**, **phenylalanine**, threonine, **tryptophan** and **valine**) are classified as nutritionally indispensable, because they are not synthesized *de novo* (Li *et al*., 2021). Fish meal and other animal-

sourced feedstuffs provide prawns with adequate amounts of these amino acids. Many plant-sourced feedstuffs (e.g. **soybean** meal, **corn** meal and **coconut oil** cake) can be included at appropriate levels in the diets of prawns. The requirements of these aquatic animals for all amino acids, including those that are synthesized *de novo*, should be satisfied for maximum growth and optimum health. Because the quantitative requirements of all species of prawns for different amino acids have not been well determined, the profiles of these nutrients in prawn's **skeletal muscle** are often used to provide guidelines in **feed formulation**. However, it should be recognized that the digestive tract of prawns catabolizes many amino acids (particularly **glutamate**, **glutamine** and aspartate) at different rates and, therefore, modifies the patterns of dietary amino acids that enter the **blood** circulation. Many amino acids serve as precursors for the synthesis of **glucose**, **lipids**, **nitric oxide** (NO), H_2S, **creatine**, **glutathione**, **polyamine**s and other low-molecular-weight molecules with enormous biological importance (such as maintaining **mucosa**l integrity, **immunity** and **antioxidant** defences) in prawns.

Lipids

The requirements of freshwater prawns for lipids are dependent on dietary levels of **essential fatty acid**s (D'Abramo and New, 2010). It is generally accepted that freshwater prawns cannot tolerate more than 10% of dietary lipids (D'Abramo, 1998; Soberanes-Yepiz *et al*., 2018). Due to inefficient biosynthesis, most freshwater prawns appear to require the dietary provision of some C_{18}, C_{20}

and C_{22} **polyunsaturated fatty acid**s (e.g. 18:2, n-6; 18:3, n-3; 20:4, n-6; 20:5, n-3; and 22:6 n-3). Dietary **sterols** (mainly as **cholesterol**) and **phospholipid**s are necessary for the **growth**, **maintenance**, cell integrity and proper functioning of prawns (Nesara and Paturi, 2018). The requirement of prawns for dietary cholesterol is approximately 0.3–0.6%. Dietary phytosterols are equally as effective as cholesterol for juvenile *M. rosenbergii* (D'Abramo, 1998; Mukhopadhyay *et al*., 2003). About 1–2% of dietary phospholipids are required for *M. rosenbergii*, depending on life stages and feed formulation (Hien *et al*., 2005; D'Abramo and New, 2010).

Carbohydrates

Digestible carbohydrates are important and low-cost energy sources for prawns. These animals have a limited ability to digest **dietary fibre**. The efficiency of utilization of starch by prawns is less than that of terrestrial omnivores. Regardless of source, the appropriate level of digestible carbohydrates in prawn diets is 20–30% (Wang *et al*., 2016). Compared with marine **shrimp** species, the juvenile *M. rosenbergii* prawn has a much higher α-**amylase** activity in the midgut gland, intestine and **stomach** (Nesara and Paturi, 2018). In the presence of exogenous **cellulase**, dietary **cellulose** can be used as a source of energy in prawns.

Vitamins and minerals

The requirements of prawns for vitamins are similar to those of other aquatic species. Vitamins serve as **coenzyme**s in metabolic pathways and as antioxidants. Several vitamins (such as **vitamin C**, **vitamin E** and folic acid) have been recommended for inclusion

in prawn diets. However, the requirements of prawns for other vitamins have not been established. Microorganisms in the water system are a good source of vitamins for prawns (Ballester *et al*., 2018).

Nutritionally essential macro-minerals for prawns are **sodium** (Na), **potassium** (K), chlorine (Cl), **calcium** (Ca), **phosphorus** (P), **sulphur** (S) and **magnesium** (Mg). Nutritionally essential micro-minerals for these animals are **iron** (Fe), **copper** (Cu), **cobalt** (Co), **manganese** (Mn), **zinc** (Zn), **iodine** (I), **selenium** (Se), **molybdenum** (Mo) and **fluorine** (F). **Chromium** (Cr), tin (Sn), **vanadium** (V), **silicon** (Si), **nickel** (Ni), **boron** (B) and bromine (Br) may be needed by prawns. Investigations addressing quantitative mineral requirements of *M. rosenbergii* are lacking. Some minerals (e.g. Ca, P, Na and Fe) in the water can be absorbed by prawns, and many of them can also be derived from natural organisms such as the microbiota. Several minerals (e.g. Ca, P, Mg and Fe) have been recommended for inclusion in prawn diets. Additional minerals and vitamins in formulated rations may not be needed under some culture conditions if prawns have free access to natural foods and obtain enough of these nutrients from water (Ballester *et al*., 2018).

Larval nutrition

Larvae of prawns, like other crustaceans, have limitations in **feed intake** and **digestion**; therefore, the forms of their feeds are different from those at older life stages. The feeding of larval prawn relies on a live food source that is highly digestible and may provide exogenous prey **enzymes**. Brine shrimp (*Artemia*) is

commonly used as the preferred initial live food for larval prawns. Larvae have higher requirements for protein and lipids than at later, post-larval, stages (New and Valenti, 2000). Brine shrimp may be fed to larval prawns to meet their nutrient requirements. (XL)

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Prebiotic

A non-digestible food ingredient that beneficially affects the host by selectively stimulating the growth or activity of one or a limited number of bacteria in the digestive tract that have the potential to improve host health. Examples include **oligosaccharide**s, **resistant starch** and specific **non-starch polysaccharide**s. (SB)

See also: Probiotics

Predation

The taking of an animal with the intention of ingesting it. If it is of the same species, it is termed **cannibalism**. The various stages of predation include encounter, detect, recognize, attack, capture and consume. The strategies adopted by predators include active hunting, ambush, deception, luring of prey and use of mimicry. Predators have often exceptional sensory apparatus to detect prey. Prey respond to these strategies by limiting exposure of weak individuals by concentrating birth into a narrow time period, group living, camouflage and rapid escape. The presence of large numbers of vulnerable **herbivore**s in modern husbandry systems can lure predators to the site. Protection may be offered by guardian animals, such as dogs and llamas. (CJCP)



Lions are apex predators, usually hunting in packs on African grasslands. Photo courtesy of jcsogo. Licensed under CC BY 2.0.

Pregnancy:

see Cow pregnancy; Ewe pregnancy

Preservation

The process of storing food in a state designed to control or prevent

the development of undesirable bacteria and moulds, and which ensures minimal losses of nutrients during storage. Common methods of preservation are drying and ensiling. (JMW)

Preservative
Material used to control or prevent the development of undesirable bacteria or moulds in animal feeds. Preservatives include **ammonia**, **propionic acid**, **formic acid**, **lactic acid** bacteria (in inoculants for **silage**) and **antioxidant**s. (JMW)

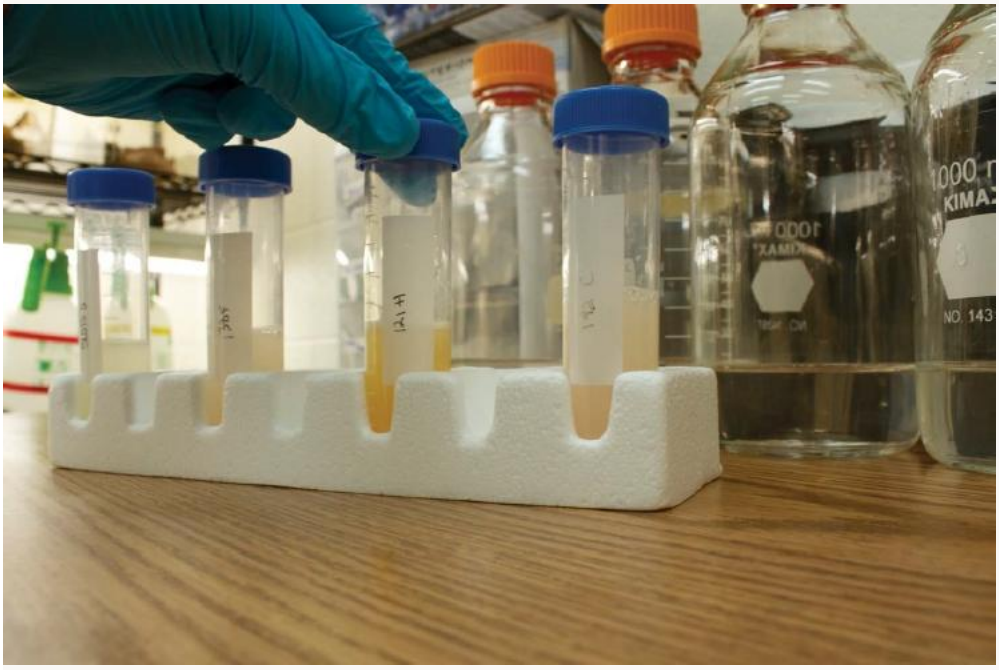
Pressing
The act of squeezing a feed mechanically to remove a liquid component, which may be water or **oil**. (JMW)
See also: Extraction, oil; Fractionation, green-crop

Prey size
The mouth size of the predator dictates the size of prey that can be ingested. Optimal prey size for **fish larva**e is often presented as a proportion of mouth diameter. Prey organisms that are too large may take an inordinate amount of time to consume. Prey that is too small may require a high energy investment for capture or handling with little reward. (DN)

Probiotics
A probiotic has been defined as 'a preparation or a product containing viable, defined microorganisms in sufficient number, which alter the microflora (by implantation or colonization) in a compartment of the host, and by that, exert beneficial health effects on the host' (Roselli *et al*., 2005; Bajagai *et al*., 2016; Blair, 2018).

The description implies that probiotics should be able to survive exposure to the digestive juices and that an adequate dose is necessary to have beneficial effects. The rationale for probiotic use is that they are able to restore normal gut microflora. The mechanisms by which probiotics (and prebiotics) produce beneficial effects on the gut have not yet been fully elucidated. However, at least three mechanisms of action have been proposed: (i) antibacterial agents produced by probiotic organisms may have an inhibitory effect on pathogenic microbes; (ii) immune responses may be enhanced to suppress potential pathogens; and (iii) **competition** in the gut epithelium may allow **lactic acid** bacteria and bifidobacteria to supplant pathogenic organisms. The effect of probiotics is well documented in the literature (Blair, 2018), showing that a live caecal culture from salmonella-free poultry reduced salmonella colonization in chicks. Gram-positive bacteria, including those of *Lactobacillus*, *Enterococcus*, *Pediococcus*, *Bacillus* spp. and bifidobacteria, and fungi such as *Saccharomyces* (**yeast**), are often fed after antibiotic therapy as a means of reintroducing a beneficial microflora to the gut of affected animals (Burel and Valat, 2009). Tayeri *et al*. (2018) showed that there were significant performance and health benefits of using prebiotics, probiotics and synbiotics for broilers, rather than antibiotics. Probiotics appear to act by enhancement of competitive exclusion of the **gastrointestinal microflora** against exogenous pathogenic microorganisms in the gut, allowing lactobacilli and bifidobacteria to multiply and reduce the pathogenic bacterial population by simple competition. Probiotics have also been shown

to have some effectiveness as anti-coccidial agents.



Probiotic stock solution in the laboratory. These anti-fungal bacteria are first tested on frogs. Photo courtesy of Brian Gratwicke. Licensed under CC BY 2.0.

In ruminants, they are more effective in controlling the diseases of the **gastrointestinal tract** of young animals, as there is no complication of the **rumen** microflora. They must be able to pass the **stomach–duodenum** barrier and multiply at the desired site. Colonization of the intestine by benign bacteria may confer protection against pathogenic bacteria. This is not only by competitive exclusion; they can also limit the adhesion of some bacteria to the intestinal wall and most improve the immunocompetence of the host animal. Some probiotics, particularly the lactobacilli, can neutralize ***Escherichia coli*** enterotoxins; others, notably *Lactobacillus acidophilus*, produce large quantities of lactic acid that reduce pH and prevent the growth of some pH-sensitive bacterial strains.

The initial colonization of the **small intestine** is from the dam's microflora and the immediate surroundings, and usually includes streptococci, *E. coli* and *Clostridium welchii*. When **milk** feeding commences, the lactobacilli become the predominant bacteria present. Calf probiotics contain benign lactobacilli or streptococci and are likely to be valuable only when given to calves that have suffered stress or have been treated with antibiotics that have destroyed the natural microflora. Addition of probiotics to the diet produces variable benefit, depending on whether the animals are in poor health. It is also difficult to determine which bacterial species would be beneficial in any given circumstance. In adult ruminants, yeasts may be used as probiotics to improve rumen **fermentation**.

Probiotics have sometimes been found to be beneficial in protecting pigs from infectious diseases. Lactic acid bacteria isolated from the gastrointestinal tract of pigs, such as *Enterococcus faecium* and *L. acidophilus*, can inhibit enteric **indicator** strains, such as *Salmonella enteritidis*, *S. cholera suis*, *S. typhimurium* and *Yersinia enterocolitica*. Dry yeast (*Saccharomyces cerevisiae*) has the advantage over bacterial probiotics that it is more tolerant of extreme pH and environmental conditions.

Probiotic use is subject to extensive legislation designed to protect farm animals and consumers. A current problem with probiotics, at least in North America, is that commercial veterinary probiotic preparations are not accurately represented by label claims (Weese, 2002). (RB; CJCP)

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Procarboxypeptidase:

see Carboxypeptidase

Processing:

see Coating; Crushing; Extraction, oil; Extrusion; Grinders; Heat treatment; Pelleting; Toasting; Wafering

Production efficiency factor

Production efficiency factors have been devised to calculate the efficiency of **broiler chicken** enterprises. They generally incorporate measures of **feed conversion** efficiency with measures of the survivability of birds within a flock. The European poultry efficiency factor (EPEF) calculation is shown here. (SPR)

$$EPEF = \frac{\text{Mean bird slaughter weight (kg)} \times \frac{\text{Total weight of birds sold (kg)}}{\text{Number of chicks housed}}}{\text{Age of birds at slaughter (days)}} \times 10{,}000 \times \frac{\text{Total feed used by flock (kg)}}{\text{Number of birds sold at slaughter}}$$

Proelastase:

see Elastase

Progesterone

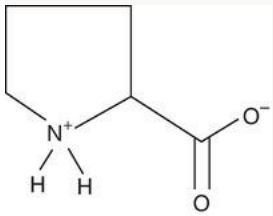
A steroid hormone produced by the corpus luteum, the placenta, or both. Progesterone production peaks during the luteal phase of the **oestrous cycle** and its production is maintained throughout pregnancy until just prior to parturition. Progesterone-releasing intravaginal devices (PRIDs) can be used in animals as a means of synchronizing the oestrous cycle to facilitate natural and artificial insemination programmes. (JRS)

Prolactin

A **peptide hormone** produced by the anterior pituitary and involved in mammogenesis and the stimulation of **milk** synthesis. Inhibition of prolactin secretion results in a decrease in milk yield. (JRS)

Proline

An **amino acid** ($C_4H_8N{\cdot}COOH$, molecular weight 115.1) found in **protein**. In many mammals, including pigs, humans and rats, it is synthesized in the body from either glutamate or **ornithine**. However, birds cannot convert **glutamate** into proline, due to the lack of pyrroline-5-carboxylate synthetase. Proline, together with its hydroxylated product **hydroxyproline**, accounts for about one-third of the **amino acid** residues in **collagen**. Although some of the proline contained in protein can be hydroxylated directly to hydroxyproline, this pathway is not reversible. Thus, whereas proline **catabolism** gives rise to glutamate, hydroxyproline catabolism gives rise to **glycine**, **pyruvate** and glyoxylate. Both proline and hydroxyproline are therefore gluconeogenic amino acids. Consumption of diets with a high collagen content, such as those with significant quantities of **meat** and **bone meal**, result in large quantities of proline and hydroxyproline being consumed. If digested and absorbed, most of these two compounds are catabolized and used for either ATP, **glucose** production, or the synthesis of glutamate and related amino acids. (DHB; GW)

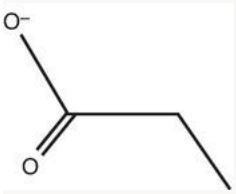


Pronase

A proprietary name for a bacterial non-specific protease (EC 3.4.24.31) from *Streptomyces griseus*. (SB)

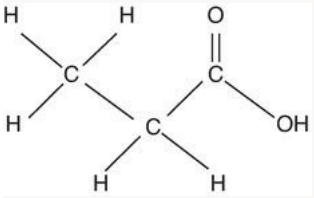
Propionate

A three-carbon **fatty acid**, $CH_3{\cdot}CH_2{\cdot}COO^-$, one of the steam-volatile fatty acids. It is produced in anaerobic **fermentation**, together with two other **volatile fatty acid**s, **acetate** ($CH_3{\cdot}COO^-$) and **butyrate** ($CH_3{\cdot}CH_2{\cdot}CH_2{\cdot}COO^-$). In the **liver**, propionate is converted to succinyl-CoA and is thus a source of carbon for **gluconeogenesis**. (NJB)



Propionic acid

Common name for propanoic acid. In common with most of the short-chain carboxylic acids, its use as a preservative in animal feedstuffs rests with its antimicrobial properties. It is listed in EU legislation as 'E280, Propionic acid, $C_3H_6O_2$, suitable for use in all feeding stuffs'.



Propionic acid is a colourless, slightly oily, corrosive liquid with a slightly sweet odour. It is a weak acid and so does not have a dramatic effect on pH but it has good antimicrobial properties in respect of clostridia, **fungi** and **yeasts**. Its main use is in the preservation of moist **grain** (typically 18–25% moisture). Evenly distributed throughout the grain at an appropriate concentration

(0.8–1.2%, depending on moisture) it will kill around 90% of common spoilage organisms and restrict the growth of others. Propionic acid has also been used alone and in mixtures with other acids or substances such as **formaldehyde** as an aid to **silage** making and as a **hay** preservative. It is a natural product of **rumen fermentation** and so is absorbed and used as an **energy source** when present in feeding stuffs given to ruminants(CRL)

Prostacyclin:
see Prostaglandins

Prostaglandins
Members of a large group of **lipid**-derived signalling molecules known as **eicosanoid**s. These molecules are synthesized in the plasma membrane and released to the cell exterior, where they act in an autocrine or paracrine mechanism to alter the function of the same cell or surrounding cells. Synthesis begins with the **hydrolysis** and release of (mainly) **arachidonic acid**, a 20-carbon ω-6 **polyunsaturated fatty acid**, from membrane **phospholipid** via the activation of **phospholipase** A_2. Arachidonic acid is acted on by either a cyclo-oxygenase or a lipo-oxygenase **enzyme**. The cyclo-oxygenase-dependent pathway leads to the production of **prostaglandin**s, prostacyclins and thromboxanes. Alternatively the lipo-oxygenase-dependent pathway produces **leukotriene**s. Collectively these molecules, including arachadonic acid itself, regulate a variety of physiological processes, including uterine contraction, **blood flow**, gastric acid secretion, platelet aggregation and much of the inflammatory

response that accompanies cell injury. These pathways are the targets of a number of therapeutic agents, including the non-steroidal anti-inflammatory drugs aspirin and ibuprofen, which inhibit the cyclo-oxygenase enzyme. Corticosteroid **hormone**s inhibit phospholipase A_2 in the first step of the pathway and are effective in treating non-infectious inflammatory disorders. Prostaglandins as a group are composed of a 20-carbon fatty acid that contains a five-membered carbon ring. The diverse number of molecular forms comprising each eicosanoid species underscores the wide range of cellular effects elicited by these agents. (GG)

Prosthetic group
A chemical complex, such as the metal-porphyrin in **haemoglobin**, with a **protein**, allowing the protein to function. It can also be a **coenzyme** (such as NAD, NADP or FAD) which, when associated with an enzyme protein, allows the enzyme to catalyse a specific reaction. (NJB)

Protease inhibitors
Chemical compounds that inhibit the activity of proteases by forming a strong complex with their active proteolytic site. Protease inhibitors in the seeds and storage organs of plants specifically inhibit the activity of one or more of the digestive enzymes in non-ruminant animals; for example, the Kunitz and Bowman-Birk inhibitors in **soybean**s inhibit both **trypsin** and **chymotrypsin** and may seriously affect **digestion** if the soybeans are not effectively heat-treated by toasting. A potent trypsin **inhibitor** in the **pancreas** protects the pancreatic tissue from

autodigestion by spontaneously activated trypsin. (SB)

Proteases
Enzymes that degrade proteins by hydrolysing **peptide** bonds (R·CHNH·CO·R), yielding smaller **amino acid** chains called peptides. In **digestion**, peptides produced by intestinal proteases are further degraded by **endopeptidase**s, **aminopeptidase**s and **carboxypeptidase**s to yield di- and tripeptides that may in turn be further hydrolysed to free amino acids. (NJB)

Protected fat
Fat treated for use in ruminant feed either to minimize biohydrogenation of **unsaturated fatty acid**s in the **rumen** or to permit addition of fat to ruminant diets without adversely affecting fibre degradation in the rumen. Protection can be achieved in a number of ways, for example encapsulation of small fat droplets in **casein**, which is then sprayed with **formaldehyde** to crosslink the proteins, making it undegradable in the rumen. Alternatively, non-esterified **fatty acid**s can be converted to their **calcium salts**, which are insoluble in **rumen fluid**. (JRS)

Protected protein
Proteins may be protected from digestion in the **rumen** by heating or by reaction with chemicals such as **formaldehyde**. Total **digestibility** is reduced by overheating, which denatures the proteins. (JMW)

Protein
A polymer of **amino acid**s joined together by **peptide** bonds and

containing the elements carbon, **hydrogen**, **oxygen**, **nitrogen** and **sulphur**. Some proteins contain **selenium** in the form of **selenocysteine** or selenomethionine. **Crude protein**, generally used to describe the protein content of diets, is defined as **nitrogen** × 6.25. (DHB)

Protein absorption
The absorption of intact proteins, e.g. immunoglobulins from colostrum, can occur up to 24 h after birth by specialized intestinal epithelia capable of **pinocytosis**, i.e. engulfing soluble proteins intact, transferring them from the intestinal lumen into the cell, from whence they are transferred to the **blood**. (SB)

Protein concentrate
A feed material that is relatively high in protein, often used in the production of **compound feed**s. Protein concentrates include **oilseed** meals and cakes and, where permitted, animal **by-product**s such as fish meal. (JMW)
See also: Bovine spongiform encephalopathy

Protein deficiency
A lack of protein may be due to underfeeding, with a shortage of all nutrients, or to a diet of low protein content. In growing animals, protein deficiency causes slow growth; in mature animals it results in mobilization of body protein. Initially this has little impact on body functions but eventually it threatens essential pathways and structures, resulting in muscular weakness, thin and easily damaged skin and impairment of the immune system, with

reduced ability to respond to disease.

Ruminants can obtain much of their protein supply from **rumen** microbes, which synthesize it from non-protein sources of **nitrogen** (NPN), but non-ruminants require all the indispensable **amino acid**s as well as either dispensable amino acids or other sources of nitrogen from which the dispensable amino acids can be synthesized.

Protein supply is most likely to be deficient in rapidly growing animals, where the **appetite** is not fully developed, or highly lactating cows or goats. Such ruminants will require supplementary protein that is not degraded in the rumen but is digested by the host's **enzymes** post-ruminally. The requirements of dairy cows are particularly high in early **lactation**. Preparing the cow by feeding rumen-undegraded protein before she calves will help to ensure adequate protein in early lactation. (JMF)

Protein degradation

The degradation of protein in living cells can be both part of normal **protein turnover** and a response to tissue damage. It can be by **digestion** in lysosomes or by a targeted system involving a small 8.5 kDa protein called **ubiquitin**. Protein **catabolism** (breakdown) is difficult to measure, because of isotope reincorporation. To measure degradation, the protein or tissue is labelled and the rate at which the specific activity of the protein or tissue declines is used to estimate a half-life ($t_{1/2}$) which is the time it takes for the specific activity tracer/non-tracer atom (e.g. ^{3}H or $^{2}H/H$, or ^{14}C or $^{13}C/^{12}C$) to decrease by half. The specific activity of

the protein can only change when both synthesis and degradation are occurring simultaneously. The labelled **amino acid**s released from protein degradation make up about 80% of the amino supply for **protein synthesis**, thus reincorporation of tracer decreases the decline in specific activity and increases the half-life. Rate constants for the degradation of single proteins can be estimated by isolating them and measuring the rate at which the specific activity of the labelled amino declines. The semilog plot of specific activity vs. time is linear, but still has the problem of tracer reincorporation. The decline in specific activity is curved with tissue proteins because of the different half-lives and amounts of the many proteins in a bulk (e.g. liver) sample.

Another approach to estimate the rate constant for protein breakdown (K_d) has been to use the difference between the rate constants for synthesis (K_s) and growth (K_g). The basis for this approach is that growth is the difference between synthesis and degradation (i.e. $K_g = K_s - K_d$). Again this can be difficult to measure because the measurement of interest is the difference between two independent estimates, each with its own inherent error. If the interval between the two estimates is small, the estimated value based on a difference may vary from plus infinity to minus infinity.

In general the half-lives ($t_{1/2}$) of individual proteins are thought to be a function of the structure of the protein and thus have a tendency to have a repeatable value but can be altered by **substrate**, **coenzyme**s and ions. Another approach used to estimate the rate constant for protein breakdown (K_d) in animals

has been to measure urinary excretion of 3-**methylhistidine**. This unique amino acid is the result of protein-bound **histidine** being methylated by ***S*-adenosylmethionine**. It is found in **actin** and **myosin** in **muscle** but significant amounts are also found in skin and intestine. When the protein is degraded to its constituent amino acids, 3-**methylhistidine** is released and partially or quantitatively excreted in **urine**. In rats and humans, 3-methylhistidine is quantitatively excreted, hence estimates of protein catabolism can be made. This method has not been uniformly productive in its use in food animals (pig, sheep and chicken) because of incomplete recovery of known amounts of injected 3-methylhistidine. (NJB)

Protein digestibility

A measure of the extent to which ingested protein is digested and absorbed from the intestine. It commonly refers to **crude protein**, i.e. N × 6.25. Protein digestibility is indicative of the digestibility of individual **amino acid**s in the protein but, for a correct evaluation, individual values for all essential amino acids are needed.

Crude protein digestibility by the whole digestive tract in non-ruminants may be determined by analysis of faeces but, because of extensive microbial activity in the **large intestine**, faecal amino acid analysis does not accurately reflect the extent to which dietary amino acids have been absorbed. For this reason, amino acid digestibility is commonly estimated from analysis of **digesta** collected at the terminal **ileum**. Ileal digesta can be obtained from cannulated animals or by a slaughter technique in which the animal is anaesthetized whilst the digesta are sampled, in order to avoid

the shedding of mucosal cells into the lumen that may occur at death. Digestibility may be estimated by measurement of the total flow of digesta (or the total excretion of faeces). It may also be estimated from the increase in concentration of an indigestible **marker**, added to the diet, in relation to the concentration of N (or amino acid). Among a large number of possible markers, **chromium** oxide is commonly used.

Values of protein digestibility are most often higher at the faecal level than at the ileal level. This is mainly due to absorption of **ammonia** occurring from the microbial activity in the large intestine by which undigested dietary protein and non-reabsorbed endogenous protein are also converted to **microbial protein**. The presence of easily fermentable dietary **carbohydrates**, i.e. water-soluble **dietary fibre** and, in adult non-ruminants, also **lactose**, may considerably increase the microbial utilization of ammonia for **protein synthesis** and, consequently, reduce the **intestinal absorption**. Protein digestibility measured at the ileal level is therefore a better **indicator** of the proportion of the dietary amino acids that is available to the animal.

Apparent digestibility

is so called because it is a simple measure of the difference between dietary protein intake and protein in the analysed digesta, which also includes endogenous protein secreted into the gut during digestion. Apparent digestibility can be measured directly in low-protein feeds fed alone, or in protein-rich foodstuffs diluted with a semi-synthetic N-free mixture. In the latter case, endogenous ileal protein flow is induced by both the **protein**

source and the N-free mixture. Apparent digestibility does not include a correction for the endogenous contribution.

Net digestibility is a measure of apparent protein digestibility relating directly to the foodstuff itself rather than to a test diet. Thus, for low-protein foodstuffs which can be analysed directly, net digestibility may be identical to apparent digestibility. For protein-rich foodstuffs, which need to be diluted with a protein-free mixture to obtain a suitable protein level in the test diet, net digestibility must be determined by extrapolation to the pure foodstuff according to a theoretical 100% level of inclusion.

True digestibility

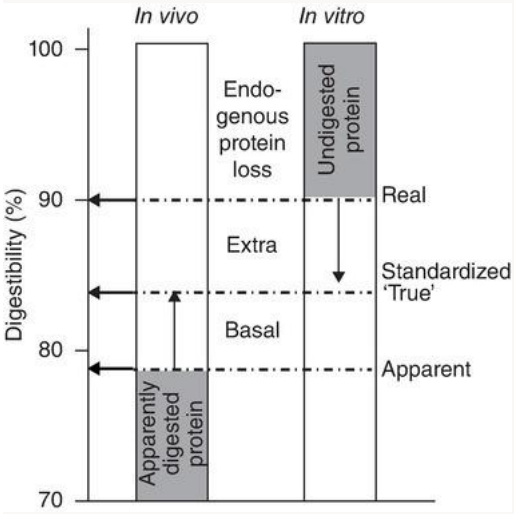
is a measure of protein digestibility in which a correction is made for the flow of undigested protein by using an estimate of the basal **endogenous protein** flow determined by feeding either an easily digestible nitrogen-free diet or a diet containing a 100% digestible protein. This endogenous loss is considered to correspond to the minimal (basal) protein loss for the digestive processes.

Standardized digestibility refers to tabulated values of true digestibility calculated from estimates of basal endogenous losses determined at well-defined and standardized conditions (see figure and table).

Real digestibility

is a measure of protein digestibility relating directly to the foodstuff itself. This can be performed by a ^{15}N isotope-dilution technique after **labelling** the experimental animal with ^{15}N and

measuring the dilution of $^{15}N/^{14}N$ in the digesta compared with the $^{15}N/^{14}N$ in the **blood**. In this value, a correction is made for all components of the endogenous ileal protein flow, i.e. nonspecific basal losses and extra losses specifically induced by the particular diet. The extra losses are primarily related to dietary fibre and various **antinutritional factor**s and they may be considerably higher than the basal losses.



Standardized (or true) digestibility of protein calculated from either *in vivo* or *in vitro* measurements.

Ileal standardized digestibility of crude protein (CP) and essential amino acids in common feedstuffs for pigs.[a]

Obs.[b]	**CP (%)**	**CPS**	**LYSR**	**THRT**	**MEYS**	**CYRP**	**TRLE**	**ILEU**	**LEAL**	**VAIS**	**HISE**	**PHYR**	**TYRG**

	Obs.[b]	CP (%)	CPP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Barley	13	10.9	800	775	754	849	791	813	830	801	814	833			
Barley brewers' grains	12	20.9	530	501	311	612	421	219	599	421	612	523	538		

	Obs.[b]	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Barley distillers' grains[c]	1	21.5	83	73	84	89	87	86	90	90	86	87	92	93	93

	Obs. b	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Beet pulp, dehydrated	1	11.1	53	50	31	61	22	41	59	59	42	61	52	53	58

	Obs.[b]	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Blood meal	8	85.4	82	86	85	85	77	88	86	84	44	82	86	86	86
Bone meal	2	38.4	81	86	85	89	66	–	85	86	84	86	86	85	84

	Obs.[b]	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Cottonseed meal, decorticated	8	40.4	77	63	71	73	76	68	74	76	76	76	83	81	90

Cotton	**Obs.** b	**CP** § %)	**CP**	**LYS**	**THR**	**MET**	**CYS**	**TRP**	**ILE**	**LEU**	**VAL**	**HIS**	**PHE**	**TYR**	**ARG**
seed meal, part. decorticated															

	Obs.[b]	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Fababean	6	27.6	84	88	82	83	77	81	85	87	82	87	87	84	91
Feather meal	3	80.5	77	65	78	71	70	72	86	83	83	71	86	76	84

	Obs.[b]	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Fish meal	15	65.55	89	93	92	93	86	89	93	94	92	89	92	92	94
Fish soluubles	1	80.2	93	96	96	96	84	–	97	98	96	95	98	98	99
Grea ves	1	82.99	82	84	80	85	79	79	88	88	88	85	90	88	92

Obs. b	**CP** (%)	**CPP**	**LYS**	**THR**	**MET**	**CYS**	**TRP**	**ILE**	**LEU**	**VAL**	**HIS**	**PHE**	**TYR**	**ARG**

	Obs. b	CP (%)	CPP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Ground nutmeal, detoxified	1	50.3	707	611	711	745	752	783	866	881	–	900	901

	Obs.[b]	CCP (%)	CCP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Ground nutmeal, not detoxifie	2	47.3	90	88	89	92	88	–	92	94	92	90	95	95	97

dLuce	**Obs.** b	**CP (%)**	**CP** o	**LYS**	**THR**	**MET**	**CYS**	**TRP**	**ILE**	**LEU**	**VAL**	**HIS**	**PHE**	**TYR**	**ARG**
rne, dehydrated															
Lupin	3	31.11	885	886	881	883	883	–	888	887	890	909	898	898	893
Maize	15	8.96	860	803	891	919	908	908	893	879	887	910	901	901	911

	Obs.b	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
distillers	1	23.6	62	58	62	76	59	28	72	78	66	59	79	76	76

	Obs.b	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Maizegermmeal, starchby-pr	1	27.5	68	61	71	81	67	71	74	76	72	84	81	78	84

product	**Obs.**	**CP** (%)	**CPP**	**LYS**	**THR**	**MET**	**CYS**	**TRP**	**ILE**	**LEU**	**VAL**	**HIS**	**PHE**	**TYR**	**ARG**
gluten feed	1	2	6	6	7	8	6	6	7	8	7	7	8	8	8
gluten meal	2	0.2	9	6	0	4	9	6	8	4	5	0	4	3	6
gluten meal	5	6	9	8	9	9	9	8	9	9	9	9	9	9	9
		0.4	0	9	2	5	2	7	2	5	1	2	4	4	5

	Obs. b	CP (%)	CPP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Maizehominyfeed	1	15.3	72	65	65	86	67	60	75	83	73	74	84	88	86

	Obs.b	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Meat and bone meal	17	51.1	81	84	82	86	67	80	84	85	83	79	85	82	86

	Obs.b	CCP (%)	CCP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Meat and bone meal, low digestibil	5	54.7	66	72	64	76	46	78	72	70	68	71	72	70	75

it	**O**	**C**	**C**	**L**	**T**	**M**	**C**	**T**	**I**	**L**	**V**	**H**	**P**	**T**	**A**
y	**b**	**P**	**P**	**Y**	**H**	**E**	**Y**	**R**	**L**	**E**	**A**	**I**	**H**	**Y**	**R**
M	**s**	**§**	8	**S**	**R**	**T**	**S**	**P**	**E**	**U**	**L**	**S**	**E**	**R**	**G**
il	**.**	**%**	9	7	1	7	4		8	6	9	5	8	7	6
k	b	**8**													

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	Obs. b	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Milk powder, whole	1	33.8	90	89	94	96	95	97	89	97	92	97	98	98	88

	Obs.	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Milk protein concentrate	1	48.7	90	94	86	89	86	90	91	93	90	95	92	89	94
Oats	10	10.5	76	73	69	84	75	78	79	81	77	73	84	80	88

	Obs.[b]	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Oats, decorticated	1	14.7	79	79	80	85	85	82	83	83	81	83	83	85	86

	Obs. b	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Palmkernelmeal, expeller	5	16.0	54	37	52	68	47	52	60	70	66	61	75	67	78
Pea	39	21.4	80	83	76	80	72	73	79	80	74	74	80	81	89

	Obs.[b]	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Pea, extruded	2	23.3	90	93	90	86	88	89	91	92	89	94	93	94	94

	Obs. b	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Potato protein concentrate	2	78.77	87	89	90	91	78	75	89	91	99	89	91	89	92

	Obs.b	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Poultryoffalmeal	5	57.0	76	77	76	80	68	69	81	80	77	70	81	78	85

	Obs. b	CP (%)	CPP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Rapeseedmeal	18	35.2	76	75	75	87	81	80	78	82	77	84	83	80	87

	Obs.	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Rapeseed, full-fat	2	19.99	72	78	71	81	80	73	68	71	70	73	73	74	81

	Obs. b	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Rapeseed, full-fat, treated	2	20.0	73	81	72	85	81	75	73	75	73	82	75	72	84

	Obs.b	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Rice bran	4	14.42	70	75	68	78	68	74	72	72	71	84	74	80	86
Rye	8	8.4	77	72	71	81	84	76	77	78	75	79	82	77	80

	Obs.b	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Sesame meal, solvent extracte	1	40.5	91	87	89	94	94	–	91	92	90	92	94	92	96

Sorghum soybean concentrate	Obs.	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
	1	65.4	94	95	94	93	94	94	94	95	94	97	96	96	99

	Obs. b	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Soybeanhulls	1	11.6	57	60	61	71	63	63	68	70	61	58	72	64	84

	Obs.b	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Soybeanmeal, crudefibre<5	13	47.1	89	92	88	93	89	92	91	90	90	92	91	92	95

% Soybean meal, crude fibre > 5 %	**Obs.**	**CP (%)**	**CP**	**LYS**	**THR**	**MET**	**CYS**	**TRP**	**ILE**	**LEU**	**VAL**	**HIS**	**PHE**	**TYR**	**ARG**
	b	46	7												

	Obs. b	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Soybean meal, extruded	3	47.4	87	89	86	88	85	86	87	88	87	90	89	88	95

	Obs.b	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Soybean, full-fat, treated	5	35.8	78	82	79	81	77	80	78	79	78	84	81	82	86

	Obs.[b]	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Sunflower meal, not decortic at	2	27.2	81	80	82	92	81	85	86	87	84	86	90	92	95

O	**C**	**C**	**L**	**T**	**M**	**C**	**T**	**I**	**L**	**V**	**H**	**P**	**T**	**A**
b	**P**	**P**	**Y**	**H**	**E**	**Y**	**R**	**L**	**E**	**A**	**I**	**H**	**Y**	**R**
s	**§**	8	**S**	**R**	**T**	**S**	**P**	**E**	**U**	**L**	**S**	**E**	**R**	**G**
.	**%**	2	2	1	2	2	4	5	5	3	4	7	9	3
b	**)**													

flowermeal, partially decortic at

edTritical scale	**Obs** 12b	**CP (%)** 12.3	**CPS** 87320187869001	**LYS** 3	**THR** 2	**MET** 0	**CYS** 1	**TRP** 8	**ILE** 7	**LEU** 8	**VAL** 6	**HIS** 9	**PHE** 0	**TYR** 0	**ARG** 1
Wheat	17	12.83	88139189	8	8	8	9	8	8	9	8	9	9	9	8
Wheatbran	10	15.4	72299687	7	6	7	7	7	7	7	7	8	8	8	8

	Obs.[b]	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Wheat distillers' grains[c]	1	27.4	82	66	80	86	82	81	83	85	80	80	90	88	88

	Obs.	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Wheat feed flour	4	13.37	93	90	90	94	94	92	93	95	91	96	96	95	96

	Obs.[b]	CP (%)	CPP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Wheat germ meal	2	27.0	85	89	82	90	81	81	86	88	85	90	88	87	94
Wheat gluten	1	81.0	89	64	78	89	95	79	91	93	89	–	95	94	87

	Obs.	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Wheat gluten feed	3	14.0	68	57	67	72	72	66	70	73	66	73	78	78	80

	Obs.b	CP (%)	CPP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Wheat middlings	15	15.57	84	84	80	88	83	86	86	87	74	89	89	88	91

	Obs.[b]	CCP (%)	CCP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Whey, acid, dehydrated	2	10.5	70	83	70	74	66	79	80	77	69	80	82	78	51

	Obs.b	CP (%)	CPP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Yeast, brewers’	1	47.4	69	74	66	69	49	55	72	73	66	77	66	64	78

	Obs.[b]	CP (%)	CP	LYS	THR	MET	CYS	TRP	ILE	LEU	VAL	HIS	PHE	TYR	ARG
Yeast, brewers', high protein	1	69.0	59	52	58	51	32	40	54	55	64	52	53	54	61

[a] Adapted from AmiPig (2000).

[b] Number of observations.

[c] Ethanol by-product.

Protein and amino acid digestibility in foodstuffs and diets can be predicted from *in vitro* **incubation**s of the diet with suitable enzyme preparations that simulate the digestion in the **stomach** and **small intestine**. Values of *in vitro* digestibility are not influenced by endogenous losses and thus correspond to **real digestibility**. The prediction of protein digestibility from *in vitro* analyses is therefore dependent on proper correction for the endogenous losses. (SB)

See also: Endogenous protein; Protein digestion

Further reading

Sauer, W.C., Fan, M.Z., Mosenthin, R. and Drochner, W. (2000) Methods for measuring ileal amino acid digestibility in pigs. In: D'Mello, J.P.F. (ed.) *Farm Animal Metabolism and Nutrition*. CAB International, Wallingford, UK, pp. 279–306.

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Protein digestion

The digestion of protein is a complex process, because proteins generally consist of some 20 different **amino acid**s and can contain more than 3000 amino acid residues. This means that a large number of proteolytic **enzymes** (proteases and peptidases) with different specificities are needed to complete the **hydrolysis** of proteins to amino acids.

Protein digestion begins in the **stomach**, where **hydrochloric acid** (HCl) denatures the proteins, i.e. destroys their three-dimensional structure, which make the **peptide** bonds susceptible to enzymatic hydrolysis. **Pepsins** secreted from the gastric mucosal cells initiate protein digestion by cleaving some of the peptide linkages. Pepsins are secreted in the form of inactive precursors, called pepsinogens, which are activated by gastric hydrochloric acid and previously activated pepsin. Pepsins are most active from pH 1.5 to 3 and hydrolyse the peptide bonds between aromatic amino acids such as **phenylalanine** or **tyrosine** and a second amino acid. Chymosin, a **milk**-clotting enzyme, also called **rennin**, is found in the stomach of young animals.

In avian species, pepsin is ready for secretion at the time of hatching and is at a high level from the first meal, which can be of the same composition as that eaten by adults and is digested efficiently. The site of gastric secretory glands (HCl and pepsin) in birds is the **proventriculus**; peptic hydrolysis occurs in the **gizzard**, which is also responsible for grinding food particles.

In ruminants, most of the dietary protein is utilized by the microbial flora in the **rumen**; consequently the proteins of the rumen flora are the major source of protein for ruminants. Processing can render some proteins indigestible in the rumen (bypass protein) but the protein can be digested better post-ruminally. This is particularly important in fast-growing animals and high-yielding dairy cows, in which essential amino acids may be limiting for growth or milk synthesis.

In the **small intestine** of ruminants and non-ruminants alike, the polypeptides resulting from **digestion** in the stomach are further degraded by the proteolytic enzymes of the **pancreas** and **intestinal mucosa**. The pH is about 6.5.

Enterokinase is found only in **enterocyte**s and is released from the apical membrane by the detergent action of **bile salts** secreted from the liver. The activity of enterokinase is stimulated by **trypsinogen**, which is its only **substrate**. Enterokinase is responsible for initiating the luminal phase of pancreatic protein digestion by cleaving a peptide from the amino terminus of trypsinogen, producing **trypsin**. The activated trypsin then activates the other pancreatic proenzymes.
Trypsin, **chymotrypsin** and **elastase** are closely related in their molecular structure, in particular in their active catalytic site around the hydroxy group of **serine**; they are therefore called serine proteases. Because they all cleave interior peptide bonds in the peptide molecules, they are called **endopeptidase**s. Trypsin cleaves the bonds on the carboxyl side of the basic amino acids (**lysine** and **arginine**); chymotrypsin those on the carboxyl side of the aromatic amino acids (tyrosine, phenylalanine, **tryptophan**); and elastase on the carboxyl side of aliphatic amino acids (e.g. **alanine**, **glycine**, **leucine**, **isoleucine**, **valine**).

Carboxypeptidases act on peptide bonds at the carboxyl end of polypeptides, releasing free amino acids or **oligopeptide**s of two to six residues. Carboxypeptidase A cleaves all peptide bonds except at the basic amino acids, lysine and arginine, whereas

carboxypeptidase B cleaves only peptide bonds at these amino acids.

The proteolytic actions of gastric and pancreatic enzymes result in a mixture of free amino acids (40%) and peptides (60%) in the intestinal lumen. Some of the di- and tripeptides are absorbed intact by active transport systems but the completion of digestion of the major fraction of peptides requires a large number of specific peptidases. These are mostly **metalloenzyme**s found in the apical membrane or within the enterocytes.

Most **brush border** peptidases belong to one of four classes: endopeptidases, **aminopeptidase**s, **carboxypeptidase**s and dipeptidases. The carboxypeptidases of the pancreas and the aminopeptidases of the brush border are **exopeptidase**s that hydrolyse the amino acids at the carboxy and amino ends of the polypeptides. Some amino acids are liberated in the intestinal lumen; others are liberated at the surface by the aminopeptidases and dipeptidases in the brush border of the mucosal cells. Some di- and tripeptides are actively transported into the intestinal cells and hydrolysed by intracellular peptidases, with the amino acids entering the bloodstream. Thus, the final digestion to amino acids occurs in three locations: the intestinal lumen; the brush border; and the cytoplasm of the mucosal cells.

Dipeptides containing the secondary amino acid **proline** cannot be hydrolysed by pancreatic carboxypeptidases. Enterocytes release prolidases I and II, which hydrolyse peptide bonds from proline or **hydroxyproline**, respectively.

Most dietary protein digestion and amino acid **absorption**

occurs in the first 60% of the **small intestine**. Protein in the distal segment of the small intestine is to a large extent of endogenous origin.

In most animals, bacterial proteases in the **large intestine** have generally little influence on amino acid utilization. However, liberated **ammonia** can be absorbed and utilized by the host animal for synthesis of **non-essential amino acid**s. In some herbivorous animals with a sacculated **caecum** or **colon**, e.g. the horse, amino acids may be absorbed in the large intestine; in coprophagous or caecotrophic animals, such as the rabbit, bacterial protein can also be utilized. Finally, backflow of **digesta** from the large intestine to the small intestine may provide non-ruminants with **microbial protein**. (SB; GW)

See also: Intestinal absorption; Metabolizable protein; individual enzymes

Key reference

Wu, G. (2018) *Principles of Animal Nutrition*. CRC Press, Boca Raton, Florida.

Protein efficiency ratio (PER)

A system used to evaluate the quality of dietary proteins. Groups of animals (usually laboratory rats or chicks) are fed diets containing 10% **crude protein** from the source to be evaluated. PER is calculated as the weight gain in grams divided by the grams of protein consumed over 4 weeks. In theory, the more closely the pattern of **amino acid**s in the protein matches the pattern of amino acids the animal requires, the higher the quality. A high-quality protein has a high PER because a smaller quantity can meet

an animal's needs. (NJB)

Reference

Hackler, L.R., Bodwell, C.E., Happich, M.L., Phillips, J.G., Derse, P.H., Elliott, J.G., Hartnagel, R.E. Jr et al. (1984) Protein efficiency ratio: AACC/ASTM Collaborative Study. *Journal of the Association of Official Analytical Chemists* 67, 66–77.

Protein:energy ratio

The ratio of protein to energy in a feed or diet. It may be expressed as the ratio of digestible protein to **digestible energy**, as the ratio of **metabolizable protein** to **metabolizable energy**, or as the ratio of effective **rumen**-degradable protein to fermentable metabolizable energy. (JMW)

Protein extraction

The process of extracting a pure protein from a mixture of other components, e.g. the extraction of **casein** from **milk** to produce casein isolate. (JMW)

Protein isolate

A feed ingredient that is very high in protein, or which is pure protein, produced by extracting the protein component from the feed. (JMW)

Protein metabolism

Animals do not have a dietary protein requirement per se. Historically, animals have been considered to require each of the nutritionally indispensable (nutritionally essential) **amino acid**s at the required amount, plus sufficient **amino nitrogen**, generally in

the form of excess essential amino acids or dispensable (nutritionally non-essential) amino acids. More recently, it has been recognized that amino acids previously considered to be 'non-essential' play roles in optimum animal performance, health and epigenetic regulation. Protein metabolism in animals involves ingestion and **digestion** of dietary protein with the **absorption** of the resulting small peptides and amino acids. It involves cell-based synthesis of protein to meet the cells' own needs for maintenance of cellular membrane and subcellular organelle structure and function. Protein metabolism also involves changes in the amount of specific proteins such as **enzymes**, transporters or **hormone**s that are required to support and control the functional capacity of the cells and tissues. It also involves secretion of proteins from **liver** cells into **blood** for maintenance of osmoregulation, proteins involved in blood coagulation, and proteins from the **pancreas** for extracellular digestion of foodstuffs in the intestinal lumen. Within the body, there is simultaneously a breakdown of cellular proteins in addition to synthesis; the balance between these two processes is called protein balance, and is expressed as a net degradation or net synthesis. The continuous synthesis and breakdown of proteins provides animals with the potential for repair and the potential for altering capacity to carry out a function. The processes discussed above aid in maintenance of **homeostasis** at a cellular and whole-body level.

Following the consumption of a protein-containing meal, proteolytic enzymes are produced by the **stomach**, pancreas and intestinal **brush border**. These enzymes cleave **peptide** bonds

within the polypeptide chain (**endopeptidase**s), at the carboxy terminus (**carboxypeptidase**s) or amino terminus (**aminopeptidase**s). Except for a brief duration in the neonatal period, intact proteins are too large to be transported into the **enterocyte**. The free amino acids and di- and tri-peptides released by the proteolytic enzymes in the lumen of the digestive tract can be transported into the enterocyte. Approximately 85% of **protein digestion** occurs in the upper one-half of the **small intestine**. Both di- and tripeptides are absorbed by the enterocyte and hydrolysed prior to being transferred to the bloodstream as amino acids. Transport of amino acids as di- and tripeptides can represent a substantial proportion of the total **absorption** of individual amino acids. In pigs and rats, the intestine degrades many specific amino acids such as **glutamate**, **glutamine**, aspartate, **arginine** and branched-chain amino acids, thus substantially changing the amino acid profile leaving the small intestine relative to that consumed. The **liver** can use the **nitrogen** of some amino acids and carbon skeletons produced in the metabolism of **carbohydrates** and amino acids to produce the dispensable amino acids. The liver also utilizes amino acids in the synthesis of products involved in the metabolism of the animal, including components of protein and non-protein hormones, as well as metabolic intermediates and precursors. A partial list is shown in the table.

Products derived from amino acids.

Amino acid[a]	**Product(s)**

Amino acid[a]	Product(s)
Arginine	Nitric oxide, citrulline, ornithine, creatine
Cyst(e)ine	Taurine, glutathione, SO_4
Glutamate	γ-Aminobutyric acid
Glycine	Creatine, glutathione, purine(s)
Histidine	Histamine, carnosine, anserine, balenine, 3-methylhistidine
Isoleucine	None known
Leucine	None known
Lysine	Cadaverine (polyamine), carnitine, trimethyllysine
Methionine	Cysteine, (Ado-Met) *S*-adenosyl-methionine (the source of methyl groups for methylations), choline, creatine, polyamines (spermine and spermidine) via decarboxylated Ado-Met
Ornithine	Citrulline (essential in urea cycle), putrescine (polyamine)
Phenylalanine	Tyrosine, melanin
Threonine	None known

Amino acid[a]	Product(s)
Tyrosine	Dopa (3,4 dihydroxyphenylalanine), dopamine, norepinephrine, epinephrine, melanin, triiodothyronine (T_3), thyroxine (tetraiodothyronine, T_4)
Serine	Phosphatidyl-serine, phosphatidyl-ethanolamine
Tryptophan	Niacin, serotonin, tryptamine
Valine	None known

[a] Indispensable amino acids for mammals are shown in **bold**.

The **catabolism** of amino acids yields ammonium and a carbon skeleton. Ammonium is highly toxic and must be rapidly excreted or converted to less toxic substances. Ammonotelic animals (e.g. bony fish, larval amphibians) excrete ammonium; the unlimited access to water in their environment can accommodate the large amount of water needed to excrete ammonium. Ureotelic animals (e.g. cartilaginous fish, adult amphibians and mammals) convert ammonium to urea via the **urea cycle**; urea requires much less water per gram of nitrogen excreted than ammonia. Uricotelic animals (e.g. birds, reptiles and many insects) convert the ammonium to uric acid through an energetically costly process; however, there is a substantial reduction in the amount of water

required per gram of nitrogen excreted.

Another aspect of protein metabolism is that of **protein synthesis** and **protein degradation**, both of which are involved in growth and restructuring tissue architecture. The restructuring of tissue is due to the two processes, synthesis and degradation, which contribute to **protein turnover**. This process occurs in cells and can vary with diet and time of day. The mature erythrocytes of mammals lack nuclei and rough endoplasmic **reticulum**, as well as mitochondria, and therefore do not synthesize protein in cytoplasm or mitochondria. (DRK)

Key references

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Protein quality

A term used to describe the relative values of dietary proteins. In concept it is an estimate of how well the **amino acid** (AA) pattern of a dietary protein or combination of dietary proteins matches the pattern of the amino acids an animal requires. In application, less of a high-quality protein (or a mixture of proteins with a high quality) will be needed to meet an animal's requirement than when proteins of lower quality are used. Estimates of protein quality can be made by calculation of the **chemical score** (mg AA g^{-1} N) of the protein relative to the calculated pattern (mg AA g^{-1} N) from the requirement of the animal. Chemical scores have percentage values such as 70%, etc. The chemical score is estimated from the amino acid content of the protein: it does not involve an animal assay. These estimates are the least accurate, because they do not involve consumption, **digestion** and **absorption** of the dietary amino acids by the animal in question.

The simplest animal experiment to estimate the quality of dietary protein is **protein efficiency ratio** (PER), which is the animal's weight gain (in grams) per gram of protein consumed. To remove variation in different laboratory estimates, PER values can be corrected by using a standard **casein** PER value determined at the same time. A problem with this estimate is that no value is given for meeting the **maintenance** requirement for protein. If an animal does not grow, PER is zero, even though the protein has provided its maintenance needs.

Two other similar animal growth assays have been used to

estimate protein quality. **Net protein ratio** (NPR) takes into account the value of the protein in meeting the animal's maintenance requirement by adding to the weight gain of the test group the weight loss of a similar group of animals given a protein-free diet. Net **protein utilization** (NPU) is a similar assay based on the gain of body N, rather than weight. In principle, both these methods give value to the dietary protein for providing for maintenance. These estimates also take account of protein intake and **digestibility**, which is appropriate as animals have to eat, digest and absorb the amino acids released from the protein in order for it to be of value to them.

Another assay of protein quality is **biological value** (BV). This method also requires an animal feeding experiment. A diet is fed containing the protein or protein mixture in question and measurement is taken of total faecal N corrected for endogenous N loss and total urinary N corrected for endogenous loss, i.e. BV is the percentage of absorbed N retained. While the equation suggests a linear response, the amount of protein in the diet affects the BV (Bressani, 1974a,b).

Another estimate of protein quality is the slope ratio assay (Hegsted, 1974). In this approach animals are fed diets with graded amounts of the proteins to be compared and the slope of the response over the linear portion of the response curve is compared with that of the response to a standard high-quality purified protein such as lactalbumin, which is given a value of 100. These values are dependent on the animal's response to lactalbumin. In this test proteins are always compared against a standard protein.

The response can be the gain of weight, of N or of an amino acid over a specific time. Values are generally < 100 because lactalbumin is a very high-quality protein for growing animals. Others (Finke *et al.*, 1987) used the slope ratio assay to estimate protein quality but did not compare values in the linear portion of the response curve because of strong evidence of curvature at responses that were < 50% of the maximum response. Because a continuous curve could be generated, the relative value of proteins could be estimated at maintenance (zero growth) or at various fractions of the maximum response. These studies revealed that the relative values of proteins vary over the response curve such that no protein or mixture of proteins has a constant predictable value. Thus, while the idea of assessing the relative values of proteins is an important one from a nutritionist's point of view, one must recognize that the relative values of proteins vary with level in the diet and for the purpose for which they are used. (NJB)

See also: Protein utilization

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Protein requirements of ruminants

The protein requirement of the ruminant animal is generally considered in terms of the main activities of the body – the **maintenance** of essential functions (Table 1), **lactation** (Table 2), pregnancy (Table 3) and weight change (Table 4). The requirement is calculated as net protein and is converted from net protein to **metabolizable protein** (MP), which takes account of the variable efficiency with which metabolizable protein is utilized.

The requirement for MP for lactation is quantitatively the most important, varying with **milk** yield and, to a lesser extent, with the protein concentration in the milk (Table 2).

Table 1. Requirements for metabolizable protein (MP) for maintenance.

	Cattle		**Sheep**
Liveweight (kg)	**MP required** (g per day)	**Liveweight** (kg)	**MP required** (g per day)
100	105	20	23
200	140	30	31
300	178	40	39
400	216	50	46
500	256	60	52

	Cattle		Sheep
Liveweight (kg)	**MP required** (g per day)	**Liveweight** (kg)	**MP required** (g per day)
600	293	70	59
700	329	80	65

Table 2. Requirements for metabolizable protein (MP) for lactation.

	Cattle		Sheep
Milk yield (kg per day) at 32 g protein kg^{-1}	**MP** (g per day)	**Milk yield** (kg per day) at 82 g protein l^{-1}	**MP** (g per day)
10	456	1	106
15	684	2	212
20	912	3	317
25	1140	4	423
30	1382	5	529
35	1660	6	635
40	1967		
45	2339		
50	2780		

Table 3. Requirements for metabolizable protein (MP) for pregnancy.

	Cattle		Sheep
Month of gestation	**MP** (g per day)	**Month of gestation**	**MP** (g per day)
1	1	1	0.2
3	7	2	1
5	22	3	3
7	63	4	10
8	114	5	22
9	160		

Table 4. Requirements for metabolizable protein (MP) for weight change.

	Dairy cattle		Sheep	
Weight change (kg per day)	**MP** (g per day)	**Weight** (kg)	**MP** for 200 g per day weight gain	**MP** for 400 g per day weight gain
−1.5	−197	20	48	95
−1.0	−131	30	46	86
−0.5	−66	40	42	83
0	0	50	40	81
0.5	122			
1.0	245			

	Dairy cattle		Sheep	
Weight change (kg per day)	**MP** (g per day)	**Weight** (kg)	**MP** for 200 g per day weight gain	**MP** for 400 g per day weight gain
1.5	367			

The requirement for metabolizable protein to support fetal **growth** in pregnancy is very low in the early stages and only becomes significant in cattle in the final 2 months of gestation, and in the final month in sheep (Table 3).

The total requirement for metabolizable protein is calculated as the sum of the requirements for the appropriate bodily functions. Thus, for a dairy cow weighing 600 kg **liveweight**, yielding 25 l milk, in her third month of pregnancy and gaining 0.5 kg liveweight per day, the total requirement is 293 g (maintenance) + 1140 g (lactation) + 7 g (pregnancy) + 122 (weight gain) = 1562 g MP per day.

In some situations the protein requirement is expressed as a recommended **crude protein** concentration in the total diet **dry matter** (DM) This may appear to be an oversimplification, but if the degradability characteristics of the protein in some dietary ingredients are not known, and if there is uncertainty about the actual **animal production level**, diets should be formulated as crude protein, according to Table 5.

The metabolizable protein system for dairy cows works reasonably well at low and medium levels of milk yield (20–30 l

per day), but at higher levels of production the MP required is underestimated. This implies that the efficiency of utilization of MP for milk production is not constant at 0.68, but that it decreases at increased levels of output. The values given in Table 2 for MP requirement for lactation have been adjusted upwards to take account of the decrease in efficiency of utilization of MP for milk production above a milk yield of 25 l per day. Other systems of assessing protein supply and requirements, for example the French PDI system, also take account of the relatively greater requirement for MP of the high-yielding cow. (JMW)

See also: Metabolizable protein

References and further reading

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Table 5.Indicative protein requirements of ruminants.

Animal type	W (kg)	MY (kg/d)	LWG (g/d)	DMI (kg/d)	CP (% DM)	RDP (% DM)
Sheep (wool breed)						
Dry ewe	60	–	0	1.05	7.5	6.9
Wether, wool producing	30	–	200	1.24	11.6	11.5
Lactating ewe, single lamb	60	0.87	–17	1.77	11.9	6.9
Dairy cattle (Friesian)						
Heifer, growing, non-pregnant	350	–	500	7.7	10.2	8.9

Animal type	W (kg)	MY (kg/d)	LWG (g/d)	DMI (kg/d)	CP (% DM)	RDP (% DM)
Lactating cow, peak lactation	680	25	800	20.3	15.0	9.9
Beef cattle (*Bos taurus*)						
Growing steer, grazing good pasture	300	–	1000	7.0	11.3	9.0

Animal type	W (kg)	MY (kg/d)	LWG (g/d)	DMI (kg/d)	CP (% DM)	RDP (% DM)
Lactating cow, peak lactation	450	13.6		12.6	12.9	

W, liveweight; MY, milk yield; LWG, liveweight gain; DMI, dry matter intake; CP, crude protein; RDP, ruminally degradable protein

Protein retention
A value derived from **nitrogen balance** experiments in which the amount of N retained in the body is estimated. **Crude protein** retention is calculated by multiplying the N retained by 6.25. (NJB)

Protein source
A feed included in diets primarily for the protein it supplies (in contrast to **energy source**s). The major sources of protein in animal feeds are pasture **grasses**, **forage** legumes, **legume** seeds, **oilseed** meals and cakes, and fish meal. (JMW)

Protein-sparing effect
In many animals a high lipid content can be used to support **energy requirement**s, ensuring that protein in the diet is used

for **growth** and essential metabolic functions. For example, in **fish** species, a lipid content of up to 20% of the dry weight of the diet allows protein to be effectively utilized for growth in many fish species without depositing excessive lipid in the tissues. High-lipid diets have become increasingly popular for this reason in **aquaculture**, but can have consequences for **lipid metabolism** and product quality. (QS; CJCP)

Protein supplement

A feed, which may be a mixture of ingredients, used to add protein to a diet. The major protein supplements in animal feeds are **legume** seeds, **oilseed** meals and cakes, and fish meal. (JMW)

Protein synthesis

Proteins are essential to life. In both animals and microbes, DNA is transcribed to form rRNA, mRNA and tRNA in the nucleus by RNA polymerases I, II and III, respectively, as well as various other types of RNA (such as signal recognition particle RNA, small nuclear RNA and microRNA). Eukaryotic mRNA precursors are processed by 5′ capping, 3′ cleavage and polyadenylation, and RNA splicing to remove introns before being transported to the cytoplasm, where protein synthesis from AAs on the mRNA template occurs on the ribosomes in the rough endoplasmic **reticulum**. The mitochondria also contain DNAs and the needed machinery to synthesize a limited number of proteins. The process of cytosolic and mitochondria protein synthesis consists of five stages: activation of **amino acid**s (catalysed by aminoacyl-tRNA synthase); initiation of polypeptide synthesis (formation of 80S

ribosome from 40S and 60S subunits); elongation of polypeptide; termination (recognized by the terminating signal on the mRNA); and post-translational modifications of peptides. The protein synthetic pathway requires a number of eukaryotic initiation factors (e.g. eIF1, eIF2, eIF2B, eIF3, eIF4A, eIF4E, eIF4G and eIF5), elongation factors (e.g. eEF1A, eEF1B and eEF2) and release factors. Translation initiation also depends on the **phosphorylation** of several regulatory proteins, including mechanistic target of rapamycin (MTOR), eIF4E-**binding protein** 1 and RPS6 kinase-1.

After the newly synthesized proteins are released from the ribosome, they undergo post-translational modifications (for example limited cleavage, acetylation, disulphide linkage formation, **methylation**, phosphorylation, and/or ubiquitination) to become biologically active. Protein synthesis requires a relatively large amount of **energy** (~15% of dietary **energy intake**) but fulfils important physiological functions, including regulating intracellular concentrations of proteins, promoting cell proliferation and supporting cell replacement. Specifically, 5 mol of high-energy phosphate bonds (equivalent to 5 ATP → 5 ADP + 5 Pi) are required to incorporate 1 mol of amino acids into the protein (e.g. 100 g of **animal protein**). The transport of some AAs by cells also requires ATP (e.g. 0.5 mol ATP mol^{-1} AA on average).

Tracer methodologies involving stable (e.g. ^{15}N-**leucine** and ^{13}C-**phenylalanine**) and radioactive (e.g. ^{14}C-leucine and ^{13}C-phenylalanine) isotopes have been developed to determine both *in vitro* and *in vivo* rates of protein synthesis in cells, tissues and the

whole body. The most common *in vivo* methods are the flooding dose technique and the constant infusion of a tracer amino acid. In addition, $^{2}H_2O$ has been used to determine protein synthesis in the whole body and specific tissues of humans and other animals. Each of these methods has advantages and disadvantages and should be chosen according to the objectives of studies.

Fractional rates of protein synthesis (% per day) are relatively high in the liver, **pancreas**, **small intestine**, lungs, spleen, **stomach**, kidney and **colon**, but relatively low in **skeletal muscles**. The absolute rate of whole-body protein synthesis in a healthy 70 kg adult person has been estimated to be 300 g per day (or 4.3 g kg^{-1} body weight per day), with the rate of **albumin** released from the liver being ~15 g per day. In all species of mammals and birds, the absolute or fractional rates of whole-body protein synthesis decrease with an increase in age and are affected by nutritional and hormonal states, as well as physical activity, **environmental temperature** and diseases. For example, some amino acids (e.g. **arginine**, **glutamine**, **glycine**, **leucine** and **tryptophan**) activate the mechanistic target of rapamycin (MTOR), and increasing dietary intake of amino acids stimulates protein synthesis and inhibits intracellular **protein degradation** in tissues (including the small intestine, liver, heart, kidney and skeletal muscle). In addition, anabolic **hormone**s (e.g. **insulin**, **growth hormone** and **insulin-like growth factor**-1) primarily promote protein synthesis, whereas catabolic hormones (**glucocorticoids**), metabolic acidosis and inflammatory **cytokines** activate proteolysis. Furthermore, by stimulating

protein synthesis and inhibiting protein degradation, feeding adequate amounts of high-quality protein is the most attractive way to promote protein deposition in the whole body. Finally, a lack of muscle contraction reduces protein synthesis and possibly has no effect on proteolysis in skeletal muscle cells, as occurring during bed rest and space flight, leading to muscle atrophy (such as loss of muscle mass and strength). (GW)

Protein turnover

The turnover of protein refers to the continuous processes of **protein synthesis** and degradation in cells. This metabolic cycle occurs in nearly all cell types as an essential physiological event. Intracellular **protein degradation** is catalysed by **exopeptidase**s and **endopeptidase**s. Based on the catalytic sites, proteases are classified as **serine**, **cysteine**, aspartate and metallo proteinases. According to the location of proteases, proteolytic systems are classified as lysosomal (optimal pH 3 to 5) and non-lysosomal (optimal pH 7 to 8) systems. Lysosomal proteases consist of cathepsins B, H, L and D and are responsible mainly for degradation of organelles and membranes, long-lived intracellular proteins, endocytosed proteins, partly myofibrillar proteins and proteins under conditions of nutrient deprivation and stress, as well as oxidized and misfolded proteins. Autophagy plays a crucial role in this process. Non-lysosomal proteases include calpains, caspases, ATP-dependent but **ubiquitin**-independent proteases and the ATP- and ubiquitin-dependent 26S proteasome, and are responsible for degradation of both short-lived and long-lived proteins, abnormal and denatured proteins, oxidized and

misfolded proteins and newly synthesized collagens. Recently much attention has been directed to the structure and functions of the complex 26S proteasome, which contains one 20S core and two 19S regulatory caps. This multi-unit protease is highly conserved among eukaryotic cells and responsible for most protein degradation in the cells. Thus, the 26S proteasome functions as a universal degradation machine for a wide variety of **protein substrates**. Intracellular protein degradation requires a large amount of **energy** (~2 ATP molecules for **hydrolysis** of each **peptide** bond) but is essential for regulation of many cellular processes, including the cell cycle, gene expression, processing of **antigen**s in the immune system and responses to oxidative stress. The energetic cost of intracellular protein turnover is about 7 mol ATP mol^{-1} peptide bond. Intracellular protein turnover accounts for about 20% of whole-body **energy expenditure** in humans and other animals. To understand the regulatory mechanism of **protein homeostasis**, both tracer and non-tracer methods, including pulse labelling, ^{13}C- or ^{14}C-**leucine oxidation**, the release of an **indicator amino acid** (e.g. 3-**methylhistidine** and 4-**hydroxyproline**) from a tissue and urinary excretion of 3-methylhistidine (e.g. cats, cattle, chickens, deer, frogs, humans, rats and rabbits) have been developed to determine the rates of intracellular protein turnover and extracellular proteolysis *in vitro* and *in vivo*. Choice of the methods should be dictated by scientific questions to be asked. In healthy adults gaining no protein, the rate of protein degradation is equal to the rate of protein synthesis in the whole body and tissues. (GW)

See also: Protein metabolism; Turnover

Key reference

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Protein utilization

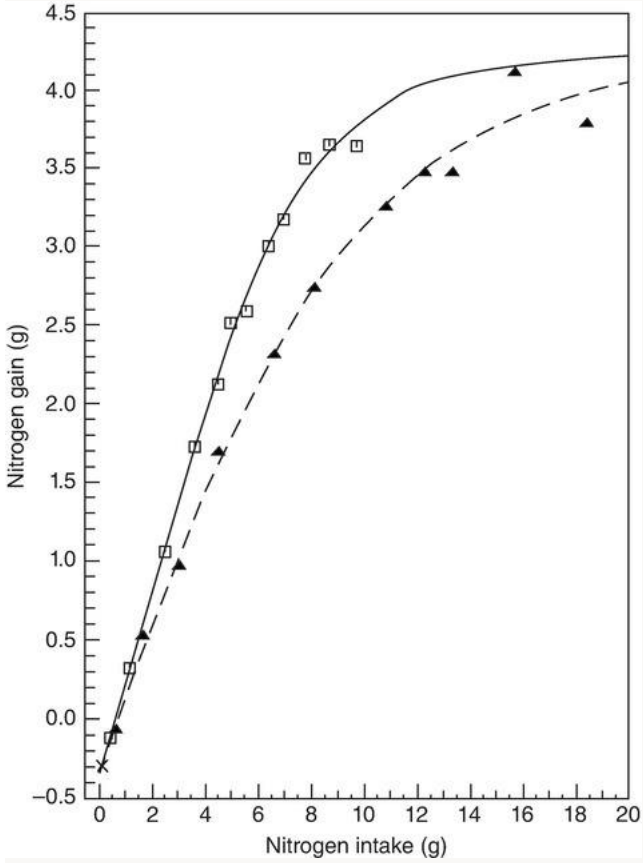
The utilization of protein depends on not only the **amino acid** content of dietary proteins, but also the **digestion** and **absorption** of the amino acids in the protein. The rate of digestion of proteins in the diet can affect the pattern of amino acids available for **protein synthesis** (*see* Amino acid metabolism). This is most obvious when limiting amino acids are added in free form to a diet. The rate of **growth** may not be the same as when a similar amino acid pattern is provided to the animal as part of a protein. Apparently the time at which an amino acid is available for protein synthesis affects the utilization of the amino acids for protein synthesis, probably because of the concomitant destruction of amino acids that could have been used to support growth. Components of the diet that decrease the rate and extent of digestion, such as **lignin** and other fibrous materials, or **antinutritional factor**s, such as **trypsin inhibitor**s, decrease the nutritional value of the **protein source**.

The amino acid content of the proteins can have an effect on dietary protein utilization, because a full spectrum of the eight to ten indispensable amino acids plus the dispensable amino acid produced by the animal is required for the animal to utilize the dietary amino acids for protein synthesis. The spectrum of amino

acids available for protein synthesis is a mixture of dietary amino acids and those available at **protein turnover** in the animal. In general, about 80% of the amino acids available for tissue protein synthesis is derived from cellular protein turnover and 20% from the diet. From the point of view of indispensable amino acids available for protein synthesis, it is common to use mixtures of plant proteins and/or **animal protein**s to improve overall protein utilization. The pattern of dietary amino acids is improved when **soybean** is added to **maize** (maize is low in **lysine** and **soybean** is low in **sulphur** amino acids), because these two proteins complement each other's amino acid pattern deficit. With respect to dispensable amino acids (e.g. **alanine**, **serine**, **glycine**, **arginine**, aspartate, **glutamate**, **proline**), the **liver** plays an essential role in their biosynthesis from intermediates of **carbohydrate** (**glucose** and related **sugars**) degradation and from intermediates (**pyruvate**, **oxaloacetate** and α-ketoglutarate) of amino acid **catabolism**.

The efficiency of amino acid (i.e. protein) utilization is directly dependent on the energy content of the diet. When the **energy requirement** of the animal is not met fully, amino acids (protein) are used as a source of energy and thus the resulting growth or **nitrogen retention** increments are less than expected. The efficiency of amino acid utilization is not constant, in that the response to increased equal dietary increments decreases with additional increments (a diminishing returns response). The figure shows the change in N gain over a range of N intakes of Mormon cricket meal without or with supplemental L-**methionine**. An

indication of a decrease in protein utilization is evident from a decrease in N gain per unit of N intake with higher N intakes. Relative to zero gain (i.e. **maintenance**) the amount of N intake required to reach 50% of maximum is 6 and 9 times more N (supplemented vs. unsupplemented), while that required for 95% of maximum is 17 and 27 times more, showing markedly less response as level of response approaches the maximum. Furthermore, the response to identical increments of N from the two N sources is different. The relative value of the unsupplemented protein changes with the level of N intake. Setting the value of the supplemented protein at 100, that of the unsupplemented protein at 0, 50 or 95% of the response maximum is at 0, 90%, 50, 74% and 95, 62%. These comparisons show that the utilization of protein varies with level and that the relative values of protein change with level of intake. (NJB)



Changes in N gain with N intake from Mormon cricket meal.

Key references

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Proteinase:

see Proteases

Proteinase inhibitors:

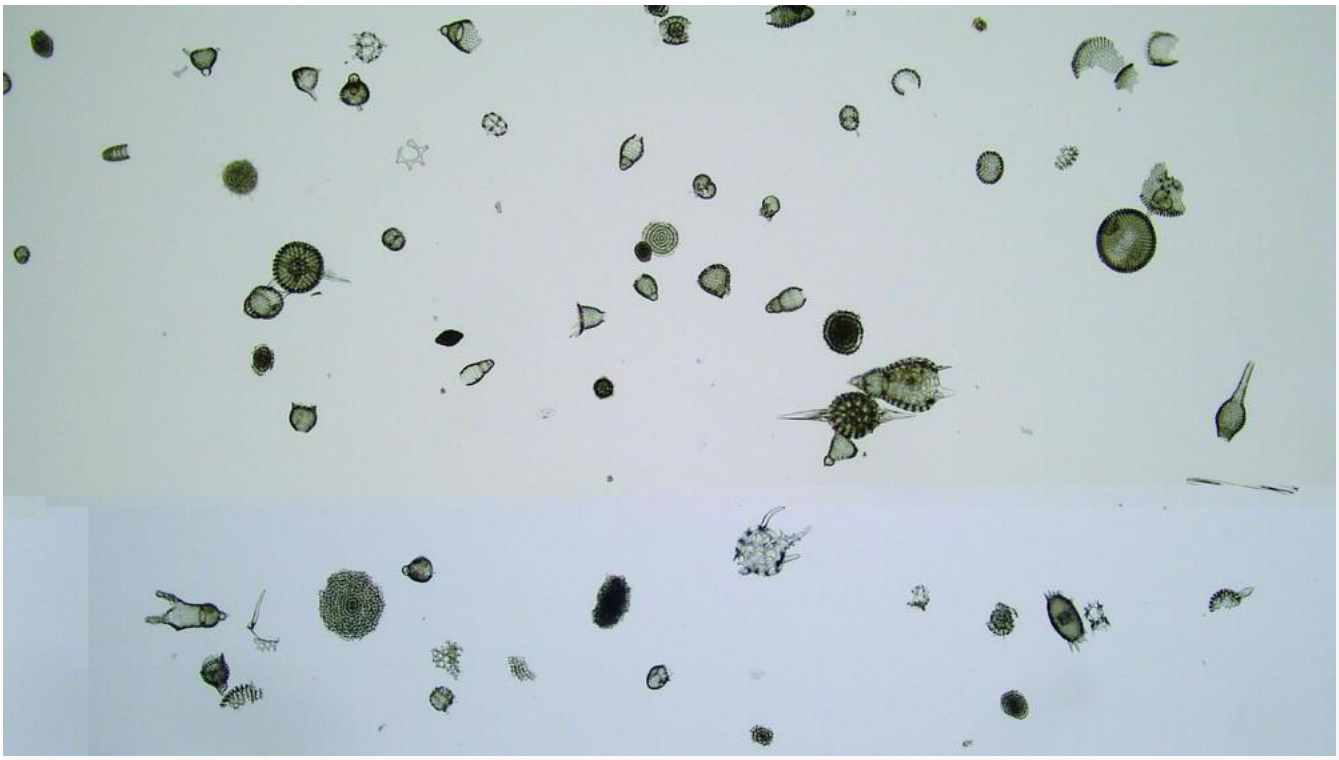
see Protease inhibitors

Proteolysis:

see Protein degradation

Protozoa

Protozoa (mobile, asymmetrical, single-celled organisms) are important inhabitants of the **gastrointestinal tract** of ruminants. Although rarely exceeding 10^6 ml^{-1} **rumen fluid**, because of their size (50–170 μm) they comprise a substantial portion of the rumen microbial biomass. While a number of flagellate species are present, the ciliated oligotrich and holotrich protozoa predominate.



Radiolaria, flagellated protozoa. Photo courtesy of Berkshire Community College. No copyright.

Their ability to take up both soluble **substrates** and feed particles (including bacteria) by engulfment markedly influences the rumen environment, population dynamics and the rate, site and extent of **fermentation**. Protozoa, unlike bacteria, are not vital for the development and survival of the ruminant host, and their elimination (defaunation), although producing a less stable rumen environment, has been found to reduce gaseous carbon and nitrogen losses. (FLM)

See also: Gastrointestinal microflora; Rumen microorganisms

Proventriculus

The anterior part of the glandular **stomach** in birds. The proventriculus can be found above the liver and between the oesophagus and **gizzard**. It is a spindle-shaped, thick-walled organ with a secretory function of gastric **enzyme** and **hydrochloric**

acid release in preparation for the **digestion** of food prior to passage to the gizzard. (MMax)

Proximate analysis

The basic requirement in defining the **nutritive value** of a food is information on its contents of the major **nutrients**, viz. **carbohydrate**, **lipid** and **protein**. 'Proximate analysis' is the term given to the separate analyses necessary to quantitate these components. From data on these components the **energy** content of the food may also be calculated. Besides the major nutrients, proximate analysis also includes measurements of moisture and **ash** levels. The ash component can be used for **mineral** analyses and the lipid component can be further analysed for **cholesterol** and **fatty acid**s.

Proximate analysis is best initiated by determining the moisture content of the food. A **sample** of the food is dried to constant weight at 103°C and the loss on drying is ascertained.

Proximate analysis of the carbohydrates attempted to divide them into two groups: those well digested (named **nitrogen-free extract**) and those less well digested (called **crude fibre**). The method used was designed at the Weende experimental station in Germany over 100 years ago. Crude fibre was the residue remaining after all soluble components had been removed by boiling a sample of the food successively in weak acid followed by weak alkali. Nitrogen-free extract was obtained by difference, being the value obtained when all other measured components (crude fibre, lipid, protein, ash and moisture) were subtracted from the whole. Because this scheme did not always separate carbohydrates

into readily digestible and indigestible fractions, another method of partitioning food carbohydrate has since been developed. This utilizes detergents which complex with protein, rendering it soluble. Boiling the sample with a neutral detergent removes soluble carbohydrates, protein, **organic acid**s and so on, leaving a residue (neutral detergent fraction) comprising **hemicellulose**, **cellulose** and **lignin**. Boiling this residue with an acid detergent hydrolyses hemicellulose, leaving cellulose and lignin as acid detergent fibre.

The lipid content of a food is normally measured gravimetrically after quantitative extraction with diethyl ether in a Soxhlet apparatus. The lipid residue is weighed after evaporation of the ether. Alternatively, an acid extraction procedure, employing a Monjonnier extraction flask, has been used. A sample of the food under test is digested with ethanolic HCl at 70–80°C for 45 min. After cooling, the digest is quantitatively transferred to a Monjonnier **fat** extraction apparatus and quantitatively extracted with three separate portions of diethyl ether followed by a single portion of light petroleum. The combined **ether extract**s are evaporated to constant weight.

Proximate analysis of protein is carried out by quantitative measurement of the **nitrogen** content of the food under test. Nitrogen is usually measured by a **Kjeldahl** procedure and the **crude protein** content of the food is obtained by multiplying the value so obtained by the factor 6.25. This factor is based on the fact that, on average, proteins contain 16% N. Proximate analysis of protein is referred to as ‘crude protein’ because: (i) not all the N in

foods is protein N (a variable amount occurs as free **amino acid**s, **amide**s, **purines**, **pyrimidine**s and so on); and (ii) the protein in the food may not contain precisely 16% N.

The amount of ash in a food is measured gravimetrically after burning off the **organic matter** in a muffle furnace at 600°C for 18 h. During this process ('ashing'), the organic matter in the food is oxidized. (CBC)

See also: Dry matter; Ether extract; Feed composition table and analysis; Weende analysis

Pseudostem:

see Banana

Pseudovitamins

Compounds similar in structure to vitamins but without vitamin activity. Some pseudovitamins have the same empirical formula as the true vitamin but not the correct stearic configuration and hence have no biological activity. For example, L-**biotin** has none of the activity of the active form D-biotin. Pseudo-**pyridoxine** (pyridoxamine or pyridoxal) does not support the growth of rats. Similar structural variations have been noted with vitamin B_{12}-related compounds, of which some are designated pseudovitamin B_{12}. (NJB)

Pteroylglutamic acid

Folic acid, a water-soluble B vitamin. It is a compound of 2-amino-4-oxo-6-methylene pteridine, *para*-aminobenzoic acid and L-glutamic acid. Folic acid as such is not functional in cells but must

first be converted to tetrahydrofolatemonoglutamate ($PteGlu_1$). In the cell as many as seven L-glutamates are added ($Pte_{1–7}$) with five (Pte_5) being the most common. These **polyglutamate** forms of **tetrahydrofolate** are involved in cell **metabolism** as **substrates** in one-carbon transfer and can be found with the **oxidation** of carbon varying from $-CH_3$, $-CH_2-$, -CHO. (NJB)

Ptyalin α-amylase
(1,4-α-D-glucan-glucanohydrolase; EC 3.2.1.1), found in the **saliva** of omnivorous animals. It hydrolyses α(1→4) glucosidic bonds in **starch** and **glycogen**, producing **maltose**, **isomaltose** and limit dextrins. (SB)

Puberty
The stage in the life of an animal when the sex glands become functional and ovulation or semen production is initiated. Puberty is generally delayed by **undernutrition** and is only attained when a threshold weight is reached. In seasonal breeders, the month of birth may also affect age at sexual maturity. (PJHB)
See also: Sexual maturity

Puffer fish
Includes two families of fish: balloonfish and the spiny burrfish or porcupine fish. These fish swallow water to enlarge their body size to discourage predation. An additional deterrent to predators is the spines of the puffers. The skin and organs of these fish contain tetrodotoxin, which is lethal when consumed by humans and other **aquatic organisms**. The flesh of puffer fish is considered a

delicacy in Japan and is prepared after specially trained chefs remove this toxin from certain parts of the fish's body. (SPL)

Pumpkin (*Cucurbita* spp.)

Creeping plant, often intercropped at low density with **maize**. As a sole crop, a yield of 30–40 t ha^{-1} is often achieved in higher rainfall areas on fertile soils. Pumpkins have a high moisture content; cattle and pigs find them succulent and highly palatable, especially during the **dry season**. As a result of the low dry matter content, they have a low **nutritive value**. Care should be taken when feeding pumpkins to pigs, because the carcass may contain soft fat if the intake is too high. (LR)

Typical composition of pumpkins (% dry matter).

	DM (%)	CP	CF	Ash	EE	NFE	Ca	P
Fresh pumpkins	7.6	14.5	13.2	7.9	2.6	61.8	0.39	0.26

CF, crude fibre; CP, crude protein; DM, dry matter; EE, ether extract; NFE, nitrogen-free extract.

Typical digestibility (%) and ME content of pumpkins.

	CP	CF	EE	NFE	ME (MJ kg^{-1})
Ruminant					
Fresh pumpkins	90.0	80.0	83.0	95.0	13.58

ME, metabolizable energy.

Further reading

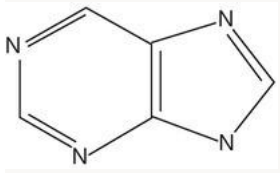
Yadav, M., Jain, S., Tomar, R., Prasad, G.B.K.S. and Yadav, H. (2010) Medicinal and biological potential of pumpkin: an updated review. *Nutrition Research Reviews* 23, 184–190.

Pup

A young **rabbit** (also kit, or kitling) from birth to **weaning**. (PC)

Purines

Bicyclic nine-member heterocyclic rings with the general formula $C_5H_4N_4$.



The following purines are designated as **nucleic acid**s: **adenine** (A), $C_5H_5N_5$; and **guanine** (G), $C_5H_5N_5O$. When ribose (in **ribonucleic acid**, RNA) or deoxyribose (in **deoxyribonucleic acid**, DNA) is added to A or G, the resulting

compounds are nucleosides: when the **sugars** are phosphorylated the compounds are designated as the **nucleotides** adenosine monophosphate (AMP) and guanosine monophosphate (GMP). Inosine monophosphate (IMP) is the source of both AMP and GMP. In DNA the purine adenosine (A) is always paired with the **pyrimidine** thymine (T), $C_5H_6N_2O_2$, and the purine guanosine (G) is always paired with the pyrimidine **cytosine** (C), $C_4H_5N_3O$. The A–T and G–C pairings in DNA are the basis of its three-dimensional structure and its replication, because the coding strand of DNA is the basis for the template strand. In the synthesis of RNA, G always binds to C but A, instead of binding to T, binds to **uracil** (U), $C_4H_4N_2O_2$. In DNA replication, A in the coding strand always results in T in the template strand. In the production of RNA from DNA, T always gives rise to A but A always gives rise to U. Other purines of importance in animal **metabolism** are **hypoxanthine**, an intermediate in the **catabolism** of adenosine, and precursor of xanthine, an intermediate in the catabolism of adenosine, inosine and guanosine. The excretory end-product of purine catabolism is uric acid, which is also the urinary excretion product of N metabolism in uricotelic animals. (NJB)

Putrescine

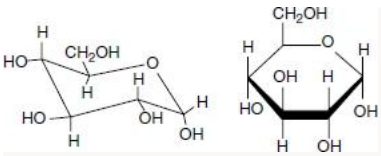
1,4, diaminobutane, $NH_2{\cdot}(CH_2)_4{\cdot}NH_2$, a precursor of the **polyamine**s spermidine and spermine in the non-agmatine pathway. The initial step in polyamine synthesis is the formation of putrescine from L-**ornithine** by ornithine decarboxylase. Some mammalian tissues express agmatinase for converting **arginine**-

derived agmatine into putrescine and **urea**. Polyamines are associated with the polyanions DNA and RNA and are involved in stabilization and packaging of DNA. (NJB; GW)

Pylloquinone
Alternative to phylloquinone, 2-Me-3-phytyl-1,4-**naphthoquinone** is the form of **vitamin K** produced by plants. (JS)

Pyranose
Six-member ring structure of a **monosaccharide** created by the reaction of the alcoholic hydroxyl group on carbon 5 with the aldehydic group at carbon 1 or the reaction of the **oxygen** of the hydroxyl group on carbon 6 with the carbonyl group on carbon 2. This term is used as it indicates that the six-member ring compound is a derivative of pyran.

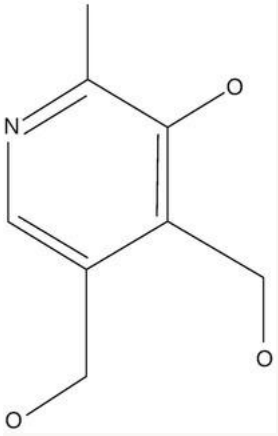
Structures of pyranoses and **furanose**s are more meaningfully depicted as hexagons and pentagons. **Glucose** is used in this example to depict the three-dimensional orientation of a carbohydrate molecule by the conformational (on the left) and Haworth formulations. With the Haworth convention, the plane of the ring is shown as perpendicular to the plane of the paper, and this is emphasized by shading those bonds that are indicated to be nearer the reader. In the alpha form, the hydroxyl group on the anomeric carbon is below the plane of the paper, which is thus indicated by placing the hydroxyl below the bond. The conformational representation of alpha-D-glucose is useful in interpreting the reactivity of the hydroxyl groups. (JAM)



See also: Carbohydrates; Galactose; Mannose

Pyridoxine

$CH_3C_5HN(OH)(CH_2OH)_2$, **vitamin** B_6, one of the water-soluble B vitamins. It is synthesized commercially and available as pyridoxine HCl.



Pyridoxine is synthesized by bacteria in the **rumen** and is thus not required in the diets of ruminants. It is also synthesized by bacteria in the intestine of non-ruminants, but this takes place lower down the gut than the sites where the vitamin is digested and absorbed so that for these animals a dietary supply is essential. In addition to the normal forms of the vitamin, many plant sources contain variable amounts of pyridoxine as a **glucoside** (this may be a storage form) in which **glucose** is linked to the 5′-position (5′-*O*-(β-D-glucopyranosyl) pyridoxine). Three phosphorylated forms of pyridoxine are found in animal and plant tissue. They are pyridoxine 5′-phosphate (PNP), pyridoxal 5′-phosphate (PLP) and

pyridoxamine 5′-phosphate (PMP). In **laboratory animal**s and humans, the vitamin is associated with the enzyme **glycogen** phosphorylase in **muscle**: as much as 70–80% of the total body pool of vitamin B_6 may be associated with this muscle enzyme in the laboratory rat.

Because pyridoxine in **coenzyme** form is intimately associated with **amino acid metabolism**, it is widely distributed in nature and found in numerous animal and plant products. At the concentrations found in foodstuffs, PNP, PLP and PMP are digested and absorbed as the free vitamin pyridoxine and as pyridoxal and pyridoxamine. When supra-physiological levels of PNP, PLP and PMP are used, the phosphorylated forms of the vitamin are taken up. The three forms of the vitamin, PN, PL and PM, are phosphorylated in the 5′-position by the same enzyme, pyridoxal kinase: they can be interconverted but all must be changed to pyridoxal (PL) for the production of 4-pyridoxic acid, which is the form in which pyridoxine is excreted in the **urine**. In animal metabolism, PLP and PMP are the coenzyme forms associated with enzymatic **transamination**, **decarboxylation**, side-chain cleavage, dehydratase reactions, and D–L interconversion of amino acids. Some of these reactions are critical to the synthesis of dispensable amino acids from carbon sources such as α-**keto acid**s (**pyruvate**, **oxaloacetate**, α-ketoglutarate) derived from glucose and other **carbohydrates**.

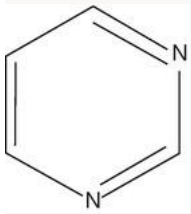
A deficiency of pyridoxine can be assessed by an oral load test of the amino acids **tryptophan** or **methionine** and measuring urinary excretion of xanthuranic acid or cystathionine, respectively.

As a deficiency progresses, the urinary excretion of these products increases. Another approach to identifying a deficiency of pyridoxine is that of measuring the activity of the erythrocyte enzyme aspartate **aminotransferase**, which requires PLP as a co-factor. This assay is most meaningful when it is tested with and without the addition of the enzyme co-factor PLP. As a deficiency progresses, the amount of cellular co-factor available to support the activity of the enzyme decreases and the activity of the enzyme declines. In the laboratory test, direct addition of the co-factor (PLP) to the *in vitro* test results in a greater stimulation or recovery of **enzyme activity**. Thus, a greater stimulation of enzyme activity due to supplemental PLP is an indication of a deficiency. Requirements for this vitamin are in the range of mg kg^{-1} diet. (NJB)

Pyrimidines

Six-membered heterocyclic unsaturated ring compounds with the general formula $C_4H_4N_2$. The B vitamin **thiamine** is a pyrimidine derivative and the pyrimidine-based compounds alloxan and thiouracil are important in medicine. The following pyrimidines are designated as **nucleic acid**s: **uracil** (U), $C_4H_5N_3O$; thymine (T), $C_5H_6N_2O_2$; and **cytosine** (C), $C_4H_5N_3O$. Small amounts of the pyrimidine 5-methylcytosine ($C_5H_6N_3O$) are found in bacterial and human DNA while the pyrimidine 5-hydroxymethylcytosine ($C_5H_6N_3O_2$) is found in the DNA of bacteria and viruses. When ribose is added to C or U or deoxyribose is added to C or T, they become nucleosides; and when the **sugars** are phosphorylated,

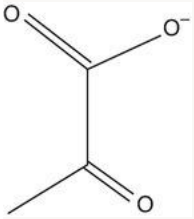
they become the **nucleotides** uridine monophosphate (UMP), cytidine monophosphate (CMP) and thymidine monophosphate (TMP). RNA contains C and U but DNA contains C and T. In DNA, the **purine** adenosine (A) is always paired with the pyrimidine thymidine (T) and the purine guanosine (G) is always paired with the pyrimidine cytosine (C). The A—T and G—C pairings in DNA are the basis of its three-dimensional structure and its replication, because the coding strand of DNA is the basis of the template strand. In the synthesis of RNA, G always binds to C but now A, instead of binding to T, binds to U. In DNA replication, A in the coding strand always results in T in the template strand. In the production of RNA from DNA, T always gives rise to A but A always gives rise to U. (NJB)



Pyruvate

The anion of pyruvic acid, $CH_3{\cdot}CO{\cdot}COOH$, a key **substrate** in intermediary **energy metabolism**. Pyruvate is produced from **glucose** and related three-carbon compounds (triose phosphates, i.e. 3-phosphoglycerate in the process of **glycolysis**, Embden-Meyerhof pathway) and is in equilibrium with L-**lactate**, $CH_3{\cdot}HCOH{\cdot}COO^-$. It is also produced in the **catabolism** of three-carbon **amino acid**s such as L-**alanine**, L-**serine** and L-**cysteine**. Pyruvate $CH_3{\cdot}CO{\cdot}COO^-$ in **muscle** takes up ammonium **nitrogen**

(NH_4^+) to become **alanine** $CH_3{\cdot}HCNH_3^+{\cdot}COO^-$ for disposal of N in the liver as **urea**. This is referred to as the pyruvate–alanine shuttle. (NJB)



Pyruvic acid:
see Pyruvate

Q

Quality control in feed mills
Quality control standards within the modern feed mill are set by central governments.



A large-scale feed mill in Belarus that manufactures dry dog food. Photo courtesy of SDS2004. Licensed under CC BY-SA 3.0.

However, mills supplying feed for livestock that are entering the supermarket retail business normally work to higher standards laid out by retail quality assurance schemes. As part of these, all raw materials entering the feed mill must come from an approved supplier or be part of a farm quality-assured production system. All materials must adhere to predetermined quality criteria. They are then mixed according to a known formula and the amount of each raw material is recorded against a batch number, so that there is full traceability of all feeds produced. To avoid any cross-contamination from one feed to another, feeds can only be manufactured in a specific order, with particular reference to the scheduling of any feed that may contain some form of medication. Mills are required to have written standard operating procedures (SOPs) for the whole process and to have a hazard analysis by critical control points (HACCP) programme in place. There is usually a legislative requirement to monitor and control production

by the chemical analysis of the finished feed. (KF)
See also: Compound feed; Feed mixing

Quinolines
Aromatic bicyclic unsaturated six-member ringed compounds, C_9H_7N. Quinolines are organic bases. They have a penetrating odour approaching that of pyridine. They are used to preserve tissue samples, as an anti-malarial and in the manufacture of the B vitamin **niacin**. (NJB)

Quinones
Six-member unsaturated ring compounds, $C_6H_5O_2$. They have a penetrating odour resembling chlorine and are toxic by ingestion or inhalation and an irritant to the skin, eyes and mucous membranes. (NJB)

R

Rabbit
Small herbivore that has an enlarged hindgut (**caecum** and **colon**), facilitating utilization of forages and other fibrous feeds. The rabbit's digestive strategy is to separate and rapidly excrete

fibre and to retain non-fibre material in the caecum, where it is subjected to microbial **digestion**. Selective excretion of fibre and retention of non-fibre components are accomplished by muscular activities of the colon. At regular daily intervals, the caecum is evacuated and the animal consumes the caecal contents (caecotropes, soft faeces, night faeces) directly from the anus (caecotrophy). The nutritional benefits of caecotrophy are mainly that microbially synthesized **water-soluble vitamins** (**B-complex**) are obtained independently of a dietary source. A secondary benefit is the utilization of caecally synthesized **microbial protein**. Although there is some microbial **protein synthesis** in the caecum, the rabbit has a very limited ability to utilize dietary sources of **non-protein nitrogen** such as **urea**. Because of the selective and rapid excretion of fibre as a major component of the hard faeces, the **digestibility** of **crude fibre** in the rabbit is much lower than in horses and ruminants.



Rabbits are mammalian herbivores but do not ruminate, instead using caecatrophy to achieve adequate digestion of the herbage. Photo courtesy of C. Watts. Licensed under CC BY 2.0.

The microbiology of the rabbit caecum is unique. The dominant

organisms are *Bacteroides* spp. Lactobacilli and ***Escherichia coli*** are generally absent from the rabbit digestive tract. The major **volatile fatty acid**s (VFAs) produced in caecal **fermentation** are acetic and butyric acids.

Calcium is absorbed very efficiently in the rabbit, in contrast to other animals in which calcium absorption is regulated according to need by **vitamin D**. High dietary calcium levels result in elevated plasma calcium and the excretion of excess calcium in the **urine**. The urine often contains high levels of calcium carbonate as a white precipitate. **Urolithiasis** is common in older rabbits (especially pets) that are chronically exposed to high calcium intakes.

Rabbits are susceptible to both deficiencies and toxicities of **vitamin A**. Because most rabbit diets contain **lucerne** or other forages, there is generally an adequate quantity of β-carotene in the diet. Addition of synthetic vitamin A to diets rich in carotene may cause vitamin A toxicity. Levels in excess of 40,000 IU vitamin A kg^{-1} may cause severe reproductive effects, including fetal **resorption**, **abortion**, small litters, hydrocephalus and low neonatal viability. Vitamin A deficiency produces similar signs. A dietary level of 10,000 IU vitamin A kg^{-1} diet will prevent both deficiencies and toxicities. Little information is available on **vitamin E** requirements of the rabbit. Deficiency causes muscular dystrophy, paralysis of hindlegs and reproductive failure. Vitamin D toxicity has been observed in rabbits, due to errors in diet formulation. Signs include progressive emaciation and weakness,

anorexia, **diarrhoea**, intense thirst, **ataxia**, and paralysis leading to death. Extensive soft tissue (liver, kidney, artery walls, muscle) calcification occurs.

Compared with other animals, rabbits have a high water requirement. Water intake is about 120 ml kg^{-1} body weight per day. Rabbit urine is usually alkaline, is often pigmented red or yellow, and may be turbid because of precipitates of calcium carbonate. (PC)

Rabbit, essential nutrients

The rabbit (*Oryctolagus cuniculus*) was domesticated some 2000 years ago. It frequently escaped and was universally common in England by the 16th century. It was increasingly regarded as a pest and the wild population in the UK is increasing rapidly despite a collapse in numbers through myxomatosis. Its role as a pet has been from around the middle of the 19th century. The number of pet rabbits in the UK is estimated to be between 1 and 1.7 million (PDSA, 2021) and approximately 2.2 million in the USA (AVMA, 2023).

The basic physiology of the rabbit is that it is a true non-ruminant land-based **herbivore**. Its digestive **enzyme** system is similar to other non-ruminants and it cannot digest plant fibre in the **small intestine**. It has two pairs of upper incisor **teeth**, therefore it is not a rodent (which only has one pair). It has a large **stomach** (pH < 2) and **caecum**. It is a frequent feeder (30 meals per day, for 4–6 min each, around 2–8 g per meal). It has a low gut **retention time**. The health and function of the hind gut is vital to its overall well-being. Here there is **fermentation** of plant fibres

to **energy**-yielding **volatile fatty acid**s. Accordingly the rabbit has a requirement for fermentable plant fibre. The practice of caecotrophy (deliberate consumption of soft pellets following voiding from the anus) is a crucial element of this process.

As far as **carbohydrates** are concerned, there are two main categories: cell contents and cell walls. The former (**starch**, which is usually well digested except in the very young, and simple **sugars**) are digested by endogenous **enzymes**, with the main enzyme being α-**amylase** and with **glucose** being the main product. The usual site of action is the **duodenum**, as the gastric pH is too low (< 2) to allow significant activity except following caecotrophy (pH 3.5). Starch overload in the caecum may encourage excessive bacterial proliferation, therefore it is very important that less well-digested starch (following heating of diets) is kept to a minimum. For the latter, there are no endogenous enzymes present. Cell walls (often referred to as **non-starch polysaccharide**s) (NSPs) are a very diverse range of compounds. Patterns of hind-gut fermentation in the caecum are promoted by readily fermentable NSPs but not by highly cellulosic or lignified compounds, which should be avoided. **Obesity** is becoming an increasing problem with pets (not just rabbits); therefore **energy requirement**s should be sufficient to promote adequate **growth** in the young animal but, for adults, should be limited essentially to **maintenance** requirements, except for pregnant or lactating does.

With respect to the **protein** requirement of rabbits, it is conventional to refer to the **amino acid** content in their diets.

Caecotrophy is usually considered in the context of volatile fatty acids, but it can also be a significant contributor of amino acids. It is common to consider energy:protein ratios in dietary formulations. At present, little is known about quantitative dietary requirements of rabbits for amino acids that are synthesizable *de novo* in animal cells.

Lipids are considered important in the context of provision of **essential fatty acid**s. As with other pets, rabbits need a range of **minerals** and **vitamins**. Water is often described as the 'forgotten nutrient' in nutrition. Its provision is essential. At birth the rabbit obtains its water via **milk**, in common with other mammals. Milk intake starts to decline around 15 days of age, at which point water must be provided and its intake increases rapidly. Water must be of good quality, free of contaminants ranging from particles to bacterial contamination. Overall guidelines for nutrient provision for rabbits are presented in Table 1. (JW)

Table 1. Suggested nutrient provision for pet rabbit diets (Lowe, 2020)

Component and nutrient (g kg^{-1})	Range	Nutrient (mg kg^{-1})	Typical range
Protein	120–170	Vitamin A (IU kg^{-1})[d]	5,000–12,000
Crude fibre[a]	140–200	Vitamin D (IU kg^{-1})	800–1,200
ADF	170–n/a	Vitamin E	40–70

Component and nutrient (g kg^{-1})	Range	Nutrient (mg kg^{-1})	Typical range
NDF	300–450	Vitamin K	1–2
Starch[b]	0–140	Copper	5–10
Fat	20–50	Vitamin B_1	1–10
Digestible energy (MJ kg^{-1})	9–10.5	Vitamin B_2	3–10
Lysine	5–n/a	Vitamin B_6	2–15
Methionine and cysteine	5.5–n/a	Vitamin B_{12}	0.01–0.02
Threonine	6.0	Co if B_{12} limited	0.25
Calcium[c]	5–10	Folic acid	0.2–1.0
Phosphorus[c]	5–8	Pantothenic acid	3–20
Magnesium	0.3–3	Niacin	30–60
Zinc	50–100	Biotin	0.05–0.20
Potassium	6–7	Choline	300–1,500
Sodium chloride	3.5–7.0		

ADF, acid detergent fibre; n/a, not applicable.

[a] A more appropriate estimate for minimum fibre inclusion is 310 g neutral detergent fibre (NDF) kg^{-1} and 190 g ADF kg^{-1} for the young

rabbit and 270 g NDF kg^{-1} and 170 g ADF kg^{-1} for the adult (Gidenne, 2003).

[b] The starch maximum only applies to diets for the very young rabbit. For the young adult pet, a 140–200 g kg^{-1} maximum constraint for the mature adult may be considered, provided the fibre constraints are exceeded.

[c] These levels allow for the fact that the pet rabbit may be used for breeding. Adult maintenance can be satisfied with levels in the region of 4 g phosphorus kg^{-1} and 6 g calcium kg^{-1}. Also note that >10 g kg^{-1} may be unpalatable to the rabbit (NRC, 1977).

[d] It may be necessary to include higher levels of some vitamins to allow for losses during manufacture. These will be specific to the raw materials and production processes used and must be taken into account when designing the supplementary additions.

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Rabbit feeding

Appropriate feeding of rabbits necessitates appreciation of some unique features of their digestive tract physiology. Having evolved as a **herbivore**, the rabbit has a feeding strategy of consuming feeds high in fibre but also has ileo-caecal-colonic mechanisms for separation and rapid excretion of fibre. It requires a fibrous diet for maintaining health of the digestive tract but also ample concentrations of high-quality sources of energy and protein. The **crude protein** requirement for **growth** is lower than the requirement for optimal reproductive performance. A dietary concentration of 16% crude protein is adequate for maximum growth, while for lactating females 18–19% dietary protein is optimal. Precise values for **amino acid** requirements have not been established. Provisional requirements of growing rabbits are 0.75% **lysine**, 0.65% **sulphur** amino acids and 0.64% threonine.

Feeding excess dietary protein may increase caecal **ammonia** and pH, leading to increased incidence of enteritis. Excretion of excess **nitrogen** in the faeces and urine results in elevated environmental ammonia concentrations, which may provoke increased **respiratory disease**. The highest **energy requirement**s of rabbits are for **lactation**: does in early lactation are typically in negative **energy balance**. High-energy diets containing added **fat** may be beneficial during lactation.

Dietary fibre levels are important, with optimal levels of 10–15% **crude fibre** for growing rabbits. Lower concentrations may result in reduced growth rate, fur **chewing**, with formation of gastric hairballs (trichobezoars), and an increased incidence of enteritis. With Angora rabbits, in which the occurrence of trichobezoars is a major problem, feeding long **hay** or **straw** as a **supplement** to a pelleted diet may be beneficial. Administration of a source of proteolytic **enzymes**, such as raw **pineapple** or papaya juice or enzyme tablets (papain, bromelain), is effective in breaking down trichobezoars and facilitating passage of **hair** from the **stomach**. The **digestibility** of crude fibre in rabbits is variable, being less than 15% for feeds high in **lignin** and **cellulose** (e.g. **lucerne** meal) but as high as 60% in nonlignified fibre sources such as beet pulp.

Major feedstuffs for rabbit production include dried forages such as lucerne meal, cereal **grain by-product**s such as **wheat bran**, and plant **protein supplement**s (e.g. **soybean** meal). **Molasses** and fats are used as **energy supplement**s.

Ideally, a series of different diets (e.g. starter, grower, finisher and lactation diets) would be used. However, under most practical conditions of rabbit production, only one diet is used. Allowances for differences in requirements can be made to some extent by adjusting the amount of feed offered. Gestating females and the males are usually fed restricted amounts of feed, while lactating females and growing–finishing rabbits are fed *ad libitum*.

There is little information on breed differences in nutritional requirements. Dwarf breeds require higher-energy diets, while

giant breeds have the greatest ability to utilize high-fibre diets. (PC)

Raffinose

A trisaccharide, $C_{18}H_{32}O_{16}$, molecular weight 504, consisting of one **galactose** residue and one **sucrose** molecule. It is found in **sugarbeet**, **legumes** and **cottonseed**. It is converted by invertase into **fructose** and **melibiose**. Other names: melitose, melitriose, gossypose. (JAM)

See also: Carbohydrates; Fructans; Glucofructans; Lychnose; Oligosaccharides

Ragwort poisoning

Ragwort is the common name for several species of *Senecio* that contain pyrrolizidine **alkaloid**s. Although pyrrolizidine alkaloids have been identified in over 100 *Senecio* species, only about a dozen poison livestock.



Ragwort is potentially poisonous to livestock, but they can learn to avoid

this toxic weed. Photo courtesy of Markles55. Licensed under CC by SA 2.0.

Most livestock **poisoning** is caused by the widely distributed and highly toxic tansy ragwort (*Senecio jacobaea*). Relatively non-toxic pyrrolizidine alkaloids are bioactivated by liver mono-oxygenase **enzymes** into toxic pyrroles. Pyrroles are potent electrophiles that bind and form adducts with cellular **nucleic acid**s and proteins, resulting in liver necrosis, proliferation of **bile** duct epithelium and fibrosis (similar to **cirrhosis**). Pyrroles also alter cell growth and division, resulting in large liver cells (megalocytosis). High doses cause immediate liver failure. Low dose exposures result in prolonged disease that becomes fatal when the animal cannot compensate for the progressive liver damage. Plants containing pyrrolizidine alkaloids have worldwide distribution. Though they are generally not palatable, they often contaminate feeds and food, resulting in animal and human poisoning. As animals often do not develop clinical symptoms until months after exposure, identifying the contaminating seeds or plants is often impossible. (BLS)

Rainbow trout (*Oncorhynchus mykiss* Smith & Stearley)
A salmonid endemic to western North America from southern Alaska to Mexico. It has been introduced to eastern North America, Asia, Africa, Australasia, Europe and South America.



Rainbow trout yearling (*Oncorhynchus mykiss*). Photo courtesy of Robert Posse. Licensed under CC BY 2.0.

There are at least three forms of **trout** recognized: the anadromous 'steelhead' form, the lake-dwelling 'Kamloops' form and the stream-dwelling rainbow. Both marine steelheads and freshwater rainbows are extensively cultured around the world, with production in 2019 totalling over 950,000 t, mostly (90%) in **fresh water**. (RHP; QS)

Rainy season

Many regions, including much of the tropics and subtropics, have defined rainy seasons. These are usually in the summer, as in the tropics, but occasionally in winter (e.g. Mediterranean area). In the tropics, agricultural production and food security depend on the amount and distribution of rainfall in the rainy seasons. (TS)
See also: Wet season

Ram

The mature entire (uncastrated) male of any species of sheep. The term is usually applied after the animal has reached sexual maturity, although young males may be referred to as ram lambs. The primary function of the ram is to produce spermatozoa and

introduce them into the female reproductive tract at oestrus in order to fertilize any ova that are shed some hours after the end of oestrus. The ram's reproductive tract consists of primary, secondary and accessory sex organs. These are similar to those of the bull, except that the testes are much larger in relation to overall body size. Also, in the ram, the glans penis is equipped with a filiform appendage, which rotates rapidly during ejaculation and sprays semen around the outer opening of the cervix. There is no prostate body in the ram. After **puberty**, semen production is essentially a continuous process in the ram, but there are seasonal fluctuations in the quantity and quality of semen produced as well as in libido, and rams tend to be most fertile during the ewe's breeding season. This seasonality is more pronounced in some breeds than in others and is timed to ensure that lambs are born in the spring, when there is fresh forage to feed the lactating ewe and subsequently the weaned lambs. (PJHB)

Rancidity

The occurrence of undesirable flavours (usually characterized as bitter or metallic) in **lipid**-containing foods. Lipolytic rancidity is due to unesterified **fatty acid**s derived from endogenous lipolytic activity (a frequent occurrence in **milk fat**). Oxidative rancidity is due to the **oxidation** of unsaturated lipids. Oxidation is initiated by interaction of a **free radical** with the methylene carbon allylic to double bonds, resulting in abstraction of a proton and generation of an unstable bond which undergoes further reactions and generation of more free radicals; thus a chain reaction occurs. Peroxidized molecules are vulnerable to scission, generating a

multitude of products. Some products are quite volatile; **aldehyde**s are generated, which have low **taste** thresholds and contribute greatly to the rancid flavour. Methylene groups between double bonds are most susceptible to free radical attack; thus **polyunsaturated fatty acid**s have the greatest potential for peroxidation. **Antioxidant**s, such as lipid-soluble **vitamin E**, function by quenching free radicals that are generated during **metabolism** or oxidative insult. (NJB)

Randle cycle

A control mechanism by which **glucose** utilization is decreased when **fatty acid**s are available (especially to **muscle**). It functions through a hormone-sensitive **lipase** and is thought to vary the activity of the mitochondrial enzyme **pyruvate dehydrogenase** (PDH). Glucose **oxidation** is dependent on the activity of PDH. The rate of fatty acid oxidation can alter the ratios of **metabolite**s in the mitochondria (acetyl CoA:CoA; $NADH+H^+$:NAD; ATP:ADP) and alter the proportion of PDH in the active form. A decrease in PDH can alter glucose oxidation. (NJB)

Rangeland

Natural **grazing** used for extensive livestock production, containing many species of grasses, forbs, shrubs or bushes and trees. Best usage is from mixed livestock species, both grazers and browsers (e.g. goats and cattle, or wildlife and cattle). Amounts of land needed per livestock unit are relatively large. Rangeland also supplies thatching grass and wood for fuel and construction. (TS)

Rape

A member of the genus ***Brassica***, rape is in the **mustard** family (Brassicaceae). Alternative common names include rapeseed, **oilseed** rape, summer **turnip**, field mustard and canola (some cultivars specifically). Rape is grown throughout China, the Indian subcontinent, northern Europe and Canada. There is not a single species of oilseed rape: the two commonly cultivated species are *Brassica campestris*, a spring annual, and *Brassica napus*, a winter annual, though both species include varieties that are both spring and winter crops; other species are *Brassica carinata* (Ethiopian mustard) and *Brassica juncea* (Indian mustard). They are all closely related to the species *Brassica nigra* (black mustard) and *Brassica oleracea* (the **cabbage**s).

Rape grows from 1 m to 1.5 m tall; it has a deep taproot and a bright yellow inflorescence of four-petalled flowers, producing small, spherical seeds that are brown, yellow or black. The lighter-coloured seeds, with their thinner husks and consequent reduced fibre content, are considered more valuable. Rape is tolerant of cool temperatures but can be sensitive to high temperatures.



Oilseed rape flower. Photo courtesy of Anthony Cranney. Licensed under CC BY-NC 2.0.

The uses of rape are primarily the **oil** (the seeds containing 40–44% oil) and the meal, which is a high-protein (35–40%) feed for both ruminant and non-ruminant livestock. These include poultry and fish species, the latter principally benefitting from the provision of **lipid** rather than protein. The composition of rapeseed protein and oil have been much manipulated through breeding. In general, rapeseed protein is high in **sulphur**-containing **amino acid**s and deficient in **lysine**. The **fatty acid** composition of rapeseed oil varies with maturity but in the mature seed comprises mainly **unsaturated fatty acid**s, with linoleate and oleate being the most significant. **Saturated fatty acid**s present include palmitate and stearate. Feeding rapeseed oil to

dairy cows has been shown to influence the fatty acid profile of **milk**. By thus increasing the oleate:palmitate proportion of milk, the value of milk can be increased (e.g. for producers of soft cheeses). Rape has also been used as a **forage** for both pigs and poultry.

Oilseed rape is the third most important source of edible vegetable **oil** globally, behind **soybean** and palm oils. Industrial uses of the oil have included soap production, lamp oil, high-temperature lubricating oils, the manufacture of plastics and a biofuel to power highspeed diesel engines.

Rape contains antinutritive substances, including erucic and eicosanoic acids, sulphur-containing **glucosinolate**s (which are responsible for the mustard flavour), **phytates**, **non-starch polysaccharide**s and aromatic **choline** esters. All of these limit the value of rape as a feed. Canola cultivars contain low levels of glucosinolates (in the meal) and **erucic acid** (in the oil), improving the **palatability** for both human and animal feed products. Further improvements in palatability and animal production have been achieved by both **heat treatment** and **enzyme** treatment of the rapeseed meal. Most of the rape varieties other than canola are used to produce oil for industrial purposes only.

In addition to the **nutritive value**, the lipids in rape meal can favourably affect the composition of the fat produced by the animal, improving profitability. Subcutaneous fat in pig carcasses contains higher concentrations of **polyunsaturated fatty acid**s (particularly **linoleic acid** and **linolenic acid**). Increased

concentrations of ***trans* fatty acid**s in milk fat from cows given rapeseed meal are associated with improved spreadability of the butter. However, high dietary concentrations of rapeseed meal can reduce **feed intake**s and **growth** in pigs and poultry, and impair **rumen** function in cows, resulting in reduced **digestibility** and intakes. (DA)

See also: Erucic acid

Further reading

Mejicanos, G., Sanjayan, N., Kim, I.H. and Nyachoti, C.M. (2016) Recent advances in canola meal utilization in swine nutrition. *Journal of Animal Science and Technology* 58, 7.

Paula, E.M., da Silva, L.G., Brandao, V.L.N., Dai, X. and Faciola, A.P. (2019) Feeding canola, camelina, and carinata meals to ruminants. *Animals* 9, 704.

Rapidly digestible starch

Starch that is rapidly digested *in vitro* and which is therefore expected to be effectively digested by animal **enzymes** in the **small intestine**. (SB)

Ration:

see Diet; Feed

Ratites

Ratites are classified as being a part of the order Struthioniformes and can be divided into the following families.

Table 1. Ratite families

Family	Species	Common name

Family	Species	Common name
Struthionidae	*Struthio camelus*	Ostrich
	Rhea americana	Greater rhea
	Pterocnemia pennata	Lesser rhea
Casuariidae	*Casuarius casuarius*	Double-wattled cassowary
	Casuarius unappendicualtus	Single-wattled cassowary
	Casuarius bennetti	Dwarf cassowary
Dromiceiidae	*Dromaius novaehollandiae*	Emu
Apeterygidae	*Apteryx australis*	Brown kiwi
	Apteryx hoastii	Great spotted kiwi
	Apteryx awenii	Little spotted kiwi

Although ratites have wings, their keel is not well developed and they cannot fly. In contrast, their legs are well developed and strong, which means they can run fast. The feathers on their body and tail can be described as decorative plumes and do not need to be oiled as in other bird species. **Ostrich**es weigh up to 130 kg, rheas 25 kg, cassowaries 55 kg, emus 41 kg and kiwis up to 2 kg.

The **gastrointestinal tract** differs from that in many other bird species, in particular because they do not possess a crop for storing food. Fibre storage takes place mainly in the **colon** in ostriches, while in emus the distal **ileum** serves as a

fermentation organ. Rheas have a relatively large caecum. These features require that the captive diet needs to be adapted to their specific **digestion** system.

Ratite nutrition: feeding ecology

The natural environment of ostriches in Africa varies from arid or semi-desert to grassland. They are natural plant eaters and live on grass, leaves of trees and shrubs, succulents, berries and seeds. An ostrich requires 5–6 kg fresh material (containing about 70 g water kg^{-1}) daily. The average composition of the food of free-ranging desert ostriches is 112 g protein kg^{-1}, 42 g fat kg^{-1} and 352 g fibre kg^{-1}. The intake of bones, **eggshells** and seashells ensures a sufficient **calcium** intake.

Cassowaries are natives of Australia and south-east Asia. They are obligate frugivores and eat mainly fallen fruit and occasionally fruit from branches. They will also eat dead rats, birds, skinks and other reptiles.



The southern cassowary is a frugivore that is a native of Australia. Photo

courtesy of Shankar S. Licensed under CC BY 2.0.

Emus live in semi-arid and arid areas in Australia. About 90% of their diet consists of green vegetation, 9% of seeds and 1% of fruit, invertebrates and vertebrates.

Kiwis are nocturnal. The typical diet for kiwis is not well understood, but the average diet in the wild is thought to consist of 40–45% earthworms, 40–45% other invertebrates and 10–15% plant materials (seeds and fruit).

Ratite feeding behaviour

Like most ratites, ostriches and rheas can not only pluck vegetation near ground level but can also consume during the process significant amounts of stones, straw and roots. This can result in impaction of the digestion system.

The caeca and colon are relatively large compared with those of other birds and serve as fermentation chambers, containing bacteria that can digest **hemicellulose** and **cellulose** to produce **volatile fatty acid**s. **Retention time** in the digestive tract in young ostriches varies from 21 to 76 h, compared with 5.5 h in emus and 3.3–26.9 h in cassowaries.

Feeding and diet

Ratite chicks are omnivorous/insectivorous. Chicks of ostriches can be reared by foster birds or artificially, in which case they can be moved outside in the daytime and inside at night, or remain totally in a housed facility. Providing chopped fresh grass or alfalfa and/or poking into the food will stimulate the chicks to start feeding. Food should be provided immediately after hatching. The chicks should be fed chicken pellets, initially a starter pellet, then after 6–12

weeks a grower diet, and after 6 months a maintenance diet.

Ostriches and other ratites, except the kiwi, can be reared for commercial purposes or in zoos and private institutions. When kept for commercial purposes the diet should be based on the specifications used with poultry for **meat** or **egg production**. The **maintenance energy requirement** (MJ) should be provided if they are fed daily 0.678 g kg^{-1} EBW (empty body weight).

The summarized nutrient specifications in the Table 2 were recommended by Ulrey and Ellen (1996) for ostriches, emus and rheas, and by Cilliers and Van Schalkwyk (1994) for ostriches. The recommendations by Janssens *et al.* (1997) for ostriches are on a dry matter basis.

Table 2. Nutrient specifications for ostriches, emus and rheas

			Janssens *et al.* (1997)	
Nutrient	Ullrey and Allen (1996)	Cilliers and Van Schalkwyk (1994)	**Minimum**	**Maximum**
Crude protein (g kg^{-1})	244	154	145	207
Methionine + cysteine (g kg^{-1})	8	–	5	7

Nutrient	Ullrey and Allen (1996)	Cilliers and Van Schalkwyk (1994)	Janssens *et al.* (1997)	
			Minimum	**Maximum**
Lysine (g kg^{-1})	13	9	7	9
Linoleic acid (g kg^{-1})	11	–	–	–
Crude fibre (g kg^{-1})	111	–	95	182
Calcium (g kg^{-1})	18	12.5–15	10	17
Phosphorus	11	–	6	11
Magnesium (g kg^{-1})	2	0.05	0.4	0.5
Iron (mg kg^{-1})	167	30	31	142
Copper (mg kg^{-1})	22	15	5	75

Nutrient	Ullrey and Allen (1996)	Cilliers and Van Schalkwyk (1994)	Janssens *et al.* (1997)	
			Minimum	**Maximum**
Zinc (mg kg^{-1})	133	73	80	123
Vitamin A (IU kg^{-1})	8889	12,000	9167	11,600
Vitamin D_3 (IU kg^{-1})	1778	383	775	1300
Vitamin E (IU kg^{-1})	278	27	–	–

Table 1. Digestive activities of rumen archaea and bacteria. Modified from Allison (1984).

Activity	**Species**	**Principal fermentation products**
Cellulolytic	*Fibrobacter succinogenes*	Acetate, formate, succinate
	Ruminococcus flavefaciens	Acetate, formate, succinate, H_2
	Ruminococcus albus	Acetate, formate, ethanol, H_2, CO_2

Activity	Species	Principal fermentation products
Hemicellulolytic	*Butyvibrio fibrisolvens*	Acetate, lactate, butyrate, formate, H_2, CO_2
	Prevotella ruminicola	Acetate, formate, succinate
	Ruminococcus spp.	Acetate, formate
Pectinolytic	*Butyvibrio fibrisolvens*	Acetate, butyrate, formate, lactate, H_2, CO_2
	Prevotella ruminicola	Acetate, propionate, formate, succinate
Amylolytic	*Bacteroides amylophilus*	Formate, acetate, succinate
	Streptococcus bovis	Lactate, acetate, formate
Ureolytic	*Selenomonas* spp.	Acetate, propionate, lactate, CO_2
	Bacteriodes ruminantium	
Methanogenic	*Methanobrevibacter ruminantium*	Methane
	Methanobacterium formicicum	

Activity	Species	Principal fermentation products
Sugar-utilizing	*Treponema bryantii*	
Acid-using	*Megasphaera elsdennii*	Acetate, propionate, butyrate, caproate, H_2, CO_2
	Selenomonas ruminantium	Acetate, propionate, lactate, H_2, CO_2
Proteolytic	*Bacteroides amylophilus*	Formate, acetate, succinate
	Prevotella ruminicola	Acetate, formate, propionate, succinate
	Butyvibrio fibrisolvens	Acetate, butyrate, lactate, formate, ethanol, H_2, CO_2
	Streptococcus bovis	Lactate, acetate, formate
Ammonia-producing	*Prevotella ruminicola*	Formate, acetate, propionate, succinate

Activity	Species	Principal fermentation products
	Megasphaera elsdennii	Acetate, propionate, butyrate, caproate, H_2, CO_2
Lipolytic	*Anaerovigrio lipolytica*	
	Butyvibrio fibrisolvens	Acetate, lactate, butyrate, formate, H_2, CO_2
	Eubacterium spp.	Acetate, butyrate, formate, CO_2



Emu in Western Australia typically inhabit rough grazing land. Photo courtesy of Red Moon Sanctuary. Licensed under CC BY-ND 2.0.

The basic diet for ostriches, emus and cassowaries in zoos should consist of a commercial diet using the recommendations in

the table. In addition, each bird should receive 1–4 heads of lettuce or comparable amounts of other green produce daily. It is advised also that cassowaries should receive some fruit, for example three apples or a similar amount of other fruit. For behavioural **enrichment** and for stimulating the digestive tract, some alfalfa can be offered also.

Kiwis usually receive a diet more based on fat-free **animal protein**, for example ox heart, together with a specific **supplement** designed for kiwis. Also, live invertebrates (earthworms, crickets, mealworms, locusts, etc.) should be provided.

All ratites require that the calcium content of the diet is sufficient, especially for young birds up to 4 months of age, in order to prevent leg problems such as rickets. A higher level of calcium is required for egg production.

To stimulate food intake, ratites should always have access to **fresh water**. It is suggested that fibre in the form of grass or **lucerne** (alfalfa) be added to the diet, so that the diet contains approximately 15% fibre, depending on the ratite species. By feeding grass or lucerne, some behavioural enrichment will be achieved. (JN)

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Real digestibility
A value of digestibility that relates solely to the dietary material, generally **protein** and **amino acid**s, and is thus not directly influenced by endogenous losses or microbial **metabolism**. Estimates of the real digestibility of protein and amino acids can be made by the ^{15}N isotope dilution method in which dietary N in the **digesta** can be distinguished from endogenous N. (SB)
See also: Protein digestibility

Rearing techniques:
see Artificial rearing of mammals

Rectum
The terminal section of the **large intestine**, between the **colon** and the anus. (SB)
See also: Gastrointestinal tract

Recycling:
see Nitrogen recycling

Red drum (*Sciaenops ocellatus*)
A euryhaline **marine fish** of the family Sciaenidae, native to the Gulf of Mexico and Atlantic Ocean, also called redfish or channel bass. Red drum, *Sciaenops ocellatus*, is a well-established species for **aquaculture** that naturally occurs from Tuxpan (Mexico) in the Gulf of Mexico to Massachusetts (USA) in the Atlantic Ocean. In

the early 1980s, the aggressive capture of the wild stocks by commercial fisheries led to restricted management regulations in the USA, including closure of the commercial fishery in the Gulf of Mexico and federally protecting it as a game species in 2007 (Watson *et al.*, 2014). Fortunately, the declining wild stocks of red drum prompted the development of technology for aquaculture purposes, such as optimizing **spawning** and fingerling production in captivity for enhancement of natural stocks as well as for fish farming.



Red drum fish. Photo courtesy of MyFWC Florida Fish and Wildlife. Licensed under CC BY-ND 2.0.

In its natural habitat, this species has a high-trophic-level feeding behaviour, preying mainly on arthropods, molluscs and other **fish** (Matlock, 1987). However, due to extensive research to determine various **nutrient requirement**s of this species, including all indispensable **amino acid**s (Gatlin, 2002; NRC, 2011) and development of practical diets, in captivity, this strict marine **carnivore** can consume manufactured diets containing relatively low levels of fish meal and/or high levels of plant-derived feedstuff (PDFs) (Rossi *et al.*, 2013, 2017; Denson *et al.*, 2018; Watson *et al.*,

2019). Another desirable characteristic for culturing red drum is its adaptation to wide variations in **water quality**. This euryhaline species can thrive in a wide range of water salinity (Watson *et al*., 2014), tolerate moderate levels of **ammonia** and **nitrite** (Wise *et al*., 1989), and survive the seasonal **temperature** fluctuations, as observed in their natural habitat.

Red drum undergo larval development after hatching from very small (~0.6 mm) buoyant **eggs** and primarily consume **zooplankton** such as **rotifers** and copepods until reaching a size of approximately 50 mm. Red drum juveniles naturally consume small benthic invertebrates such as **shrimp** and crabs along with small fish. They readily adapt to artificial prepared diets under aquacultural conditions in a variety of culture systems, including earthen ponds, recirculating raceways, cages and net pens.

Dietary requirements of red drum for many of the most critical nutrients have been determined. These carnivorous fish require between 35% and 45% **crude protein** in the diet with a **digestible energy** level of approximately 15 kJ g^{-1} diet, or 35–45 kJ energy g^{-1} protein for maximum weight gain and desirable **body composition**. Although red drum is a carnivorous fish in nature, it is not adversely affected by relatively high levels (~30%) of soluble **carbohydrate** in the diet, though at levels between 7% and 11% of diet the species uses **lipid** more efficiently than carbohydrate. **Marine oils** containing **highly unsaturated fatty acid**s of the **linolenic acid** (n-3) family are needed to satisfy the **essential fatty acid** requirements of red drum because of their limited ability to elongate and desaturate **short-chain fatty**

acids. Limited information is currently available on **mineral** and **vitamin** requirements of red drum. (DMG; QS)

See also: Fish larvae

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Red swamp crayfish (*Procambarus clarkii*)

A native of the southern USA. The red swamp crayfish (or crawfish) was introduced for consumption worldwide, assuming an important role in the trophic chain of colonized systems. Nowadays it is one of the most common crayfish species cultured commercially for human consumption (Liu *et al*., 2011; Gonçalves Loureiro *et al*., 2015), with a production of 1.71 million tonnes in the world in 2018. Due to our detailed knowledge of its biological characteristics and its ecological and economic importance, *P. clarkii* has been widely used as a model species for the assessment of contaminant effects in field and is considered as a

good model organism to study changes induced by pollutants too. (QS)

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Reducing sugars

Sugars that can reduce Fehling's solution (cupric **sulphate**, **sodium potassium** tartrate and sodium hydroxide, $NaKCuC_4H_2O_6$), which involves reduction of **copper** ($2CuO \rightarrow Cu_2O$) and is dependent on the presence of an **aldehyde** or **ketone** group in the **sugar** not attached to another atom in the form of **glycoside**. All the **monosaccharide**s are reducing sugars, as are the disaccharides **maltose**, **lactose** and cellobiose, but **sucrose** is not. (NJB)

Rehydration

The restoration of the fluid content of the body. This may involve more than merely an oral supply of water, for it may be necessary to administer **sodium chloride** as well, in order to maintain the plasma osmotic pressure. This can be achieved by parenteral administration of isotonic saline (0.9%). However, if there has been appreciable haemorrhage, then an intravenous infusion of **blood**, or of a plasma substitute such as dextran **polysaccharide**s of high

molecular weight (e.g. 70,000), may be required to maintain the plasma colloid osmotic pressure. (ADC)

Reindeer (*Rangifer tarandus*)

Reindeer inhabit a large area of northern circumpolar latitudes and have the greatest circumpolar distribution of any ungulate. Called caribou in North America and Greenland, a number of subspecies have been described based on anatomical differences that adapt them to different environments. Slight differences in the gastrointestinal system between reindeer allow them to adapt to regional variations in indigenous forage availability.

The dietary requirements of reindeer for many nutrients have not been specifically determined. Their natural diet exhibits a high degree of seasonal variation associated with their often migratory life. For example, the vegetation on which Svalbard reindeer feed ranges from rich tundra vegetation to areas with poor plant cover.



Svalbard or Arctic reindeer. Photo courtesy of Tips for Travellers. Licensed under CC BY 2.0.

New growth is selected by Svalbard reindeer during spring, while in summer reindeer feed selectively on a mixed diet of vascular plants, choosing plant items of high **digestibility** and high biomass within patches of forage. Some studies suggest that digestibility alone cannot explain **diet selection**; abundance of plant species and plant constituents (e.g. **protein** and secondary plant compounds) also seem important in determining **foraging** strategy. If nutritional resources are poor during early **lactation**, maternal **fat** reserves become exhausted, **milk** production declines and **calf growth** suffers as a consequence. During winter, **carbohydrate**-rich lichens and mosses form an important mainstay of the diet, together with fine twigs. Initial early winter weight loss appears to be primarily as a result of a decrease in gut fill, probably reflecting seasonal **inappetence**. Although the winter diet has a low **nitrogen** content, the **energy** content is generally adequate. Reindeer's feet are adapted to digging for food material through snow (as well as providing support on a snowy **substrate**). They may augment their diet with animal matter such as dead fish and dead lemmings and, like other deer, may gnaw the bones of dead animals. This is likely to be a response to a high demand for **minerals** during both lactation and antler growth (both male and female reindeer grow antlers). During antler growth, it may not be possible for males to meet their requirement for **calcium**. In addition, impaired calcium **homeostasis** may occur in **magnesium**-deficient animals.

It is common for reindeer herders to provide supplementary feed for 'managed' reindeer at critical times during the winter

when animals find access to lichens difficult, and several specialized diets have been developed. There are reports of problems with the introduction of diets with a high water content (e.g. some grass **silages**) to reindeer in a catabolic (winter) state. A syndrome known as 'wet belly' has been described in reindeer fed during the winter and has been associated with **starvation** or indigestion. While the cause remains unknown, supplementary feeding seems to be one of the factors involved (possibly related to kidney dysfunction) since the condition has not been observed in grazing reindeer. In addition, reindeer may be limited in their ability to digest rough, fibrous silage. Supplementary food offered to reindeer in an emergency situation must therefore be highly acceptable and not lead to digestive disturbances; if silage is fed it must be of high quality. (AJFR)

Renal failure:
see Kidney disease

Rendered animal-sourced feedstuffs
Animal-sourced feedstuffs generally provide higher-quality proteins (based on the quantity, ratios and digestibilities of proteinogenic **amino acid**s (AAs), including the AAs that are synthesizable *de novo* in animal cells (AASAs)), compared with plant-sourced feedstuffs, and have been used to feed many species of animals worldwide. Those animals include livestock (e.g. pigs, cattle, sheep and goats), poultry (e.g. chickens, turkeys and geese), fish, crustaceans (including shrimp, crayfish and crabs), fur-bearing animals (foxes, racoon dogs and mink), zoo animals and

companion animals (e.g. cats, dogs and ferrets). Animal-derived feedstuffs are particularly abundant in AASAs (including **glycine** and **proline**), which can reduce the energetic and precursor costs of AA synthesis in animals. In addition, these ingredients contain functional compounds, including **taurine**, **creatine**, **carnosine** and anserine (potent **antioxidant**s) that are all absent from plants. Adequate taurine, either as a synthetic AA or present in animal-sourced feedstuffs, must be provided to all domestic cats and some breeds of domestic dogs (for example golden retrievers fed protein-restricted diets, and Newfoundland dogs) with a limited ability to synthesize taurine from **cysteine**. Furthermore, animal plasma from bovine, porcine and poultry sources provides immunoglobulins to young mammals (e.g. piglets, calves, kittens and puppies) for boosting their **feed intake**, **immunity**, gastrointestinal health and overall **growth** performance. Egg products, marine animal-sourced feedstuffs and poultry meal contain **cholesterol** to meet the dietary requirements of crustaceans and enhance their growth, development and feed efficiency. Currently, the chemical definition and quantitative determination of functional components in a wide variety of animal-sourced feedstuffs are in their infancy. These ingredients also provide various animals with nutritionally essential minerals (including **calcium**, **phosphorus**, **magnesium**, **iron**, **manganese**, **zinc**, **copper** and **selenium**) with high digestibilities. Finally, **animal fat** products (e.g. tallow, **lard** and poultry fat) are potential sources of dietary energy for livestock and other farm animals to support their productivity at various

production stages (e.g. **lactation**, growing and **fattening**), particularly in hot and cold seasons. Using the database of typical composition of nutrients in a variety of feedstuffs rendered from terrestrial animals and fish (see table) is recommended to guide the formulation of diets for farm, companion, and zoo animals. For comparison, the composition of nutrients in **soybean** meal is also presented.

Cysteine and **histidine** are particularly abundant in **blood meal** and spray-dried poultry plasma. Although there is belief that blood meal has an undesirable AA balance for animal feeding, it may be used as a **protein supplement** in a compounded diet that usually contains a large amount of **isoleucine**. Of note, **arginine**, cysteine, **glycine**, 4-**hydroxyproline**, **leucine**, **proline**, **serine** and **valine** account for 62% of total AAs in **feather meal**. Thus, feather meal is a highly abundant source of all functional AAs for animal feeding, and may substitute certain crystalline AAs (e.g. arginine, cysteine, glycine and proline) for the diets of animals that have particularly high requirements for those AAs, such as piglets, poultry and fish. As an abundant source of **tyrosine**, black soldier fly larvae meal may be an important additive to the diets of dogs and cats that have high requirements for this AA to maintain adequate eumelanin in their hair. Animal-sourced feedstuffs can be supplemented to conventional diets alone or in combinations to bring about complementary nutritional effects and economic returns in animal agriculture, as well as optimum health and well-being in companion, fur-bearing, and zoo animals.

Agricultural **rendering** is the leading method for the disposal

of uneaten livestock and poultry tissues into useful feedstuffs in developed and many developing nations. These products are usually not intended for human consumption. Caution should be exercised about the risk of pathogen contamination during the rendering of animal products. Quality assurance programmes, such as the Food Safety Modernization Act legislation and regulations (effective since 2015) of the US Food and Drug Administration, are established to address the safety and quality of rendered animal-sourced feedstuffs. In addition, the use of animal-sourced feedstuffs should not replace the need for the balance and sufficiency of all essential nutrients in the diets of mammals, birds, insects, fish and crustaceans. In support of this notion, children and adolescents who have coeliac disease and consume supplements containing **gluten**-free rendered animal products may still exhibit deficiencies of **B-complex vitamins**, **vitamin D**, **phosphorus** and **magnesium**. (PL; GW)

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Content of nutrients in animal-sourced feedstuffs and soybean meal for feeding farm and companion animals[a]

Nutrient	**Bloodmeal**	BSFM	CBPM	CVD	**Feathermeal**	FM-M	FM-P	FM-SE	MBM	SDPM	PBM (PFG)	SDPP	SDEP	SBM
Dry matter	93.2	95.30	98.0	93.2	95.8	92.8	91.6	92.1	96.1	88.7	96.8	95.4	95.1	89.2
Crude protein b	89.6	42.0	68.1	67.2	91.3	62.4	68.8	64.7	52.0	55.2	70.2	69.8	48.9	46.3

Nutrient	**Blood meal**	BSFM	CBPM	CVD	**Feather meal**	FM-M	FM-P	FM-SE	MBM	SDPM	PBM (PFG)	SDPP	SDEP	SBM
Crude fat	0.82	33.5	13.4	8.57	3.52	11.1	7.32	5.07	9.21	4.63	11.5	4.02	35.0	0.94
Carbohydrate	0.40	13.6	4.20	5.44	0.15	0.38	0.37	0.39	0.89	9.14	3.91	3.35	6.34	36.2

Nutrient	**Bloodmeal**	BSFM	CBPM	CVD	**Feathermeal**	FM-M	FM-P	FM-SE	MBM	SDPM	PBM (PFG)	SDPP	SDEP	SBM
Gross energy[c]	4932	5975	5106	4656	5266	4431	4417	3986	3710	3790	5032	4283	6191	4075
Ash	2.35	6.22	12.4	12.0	0.87	18.9	15.1	21.9	34.0	19.8	11.2	18.3	4.88	5.68
Calcium	0.41	2.30	4.46	3.0	0.33	5.21	4.10	5.33	9.99	0.23	4.61	0.22	0.19	0.32

Nutrient	**Blood meal**	BSFM	CBPM	CVD	**Feather meal**	FM-M	FM-P	FM-SE	MBM	SDPM	PBM (PFG)	SDPP	SDEP	SBM
Phosphorus	0.30	0.87	2.41	1.7	0.50	3.04	2.46	3.41	4.98	0.80	2.59	1.07	0.84	0.65
Sodium	0.44	0.22	0.44	0.40	0.34	0.65	0.65	0.88	0.63	1.98	0.46	4.10	0.09	0.01

Nutrient	**Blood meal**	BSFM	CBPM	CVD	**Feather meal**	FM-M	FM-P	FM-SE	MBM	SDPM	PBM (PFG)	SDPP	SDEP	SBM
Chlorine	0.53	0.43	0.54	0.54	0.26	0.90	0.89	1.30	0.69	–	0.66	4.70	0.69	0.05
Potassium	0.15	1.12	0.53	0.55	0.19	1.15	1.16	1.52	0.65	2.00	0.69	0.13	0.56	1.96

Nutrient	Blood meal	BSFM	CBPM	CVD	Feather meal	FM-M	FM-P	FM-SE	MBM	SDPM	PBM (PFG)	SDPP	SDEP	SBM
Magnesium	0.11	0.43	0.18	0.22	0.20	0.16	0.24	0.25	0.41	–	0.15	0.038	0.043	0.27
Copper	8	9.5	10	14	10	11	9	7	11	–	10	26	2.7	20

Nutrient	**Blood meal**	BSFM	CBPM	CVD	**Feather meal**	FM-M	FM-P	FM-SE	MBM	SDPM	PBM (PFG)	SDPP	SDEP	SBM
Iron d	291 19	191 1	442	440	76	440	220	212	606	–	352	1782	78	202
Manganesed	6	191	9	11	10	37	10	23	17	–	9	3	1.5	29

Nutrient	**Bloodmeal**	BSFM	CBPM	CVD	**Feathermeal**	FM-M	FM-P	FM-SE	MBM	SDPM	PBM (PFG)	SDPP	SDEP	SBM
Selenium[d]	0.66	1.2	0.888	0.755	0.69	2.1	1.36	1.5	0.31	–	0.91	1.7	1.2	0.32
Zinc[d]	306	95	94	120	111	147	103	84	96	–	94	42	57	50
Alanine	7.82	3.14	4.54	4.12	4.12	3.63	4.74	4.59	4.78	3.51	3.98	4.98	3.43	1.97

Nutrient	**Bloodmeal**	BSFM	CBPM	CVD	**Feathermeal**	FM-M	FM-P	FM-SE	MBM	SDPM	PBM (PFG)	SDPP	SDEP	SBM
Arginine	4.91	2.64	4.75	4.02	5.83	3.67	3.58	4.15	3.67	3.59	4.15	4.94	3.82	3.20
Asparagine	4.67	1.93	2.61	2.50	1.79	2.26	2.28	2.60	2.21	1.52	2.56	2.57	2.69	2.10

Nutrient	**Blood meal**	BSFM	CBPM	CVD	**Feather meal**	FM-M	FM-P	FM-SE	MBM	SDPM	PBM (PFG)	SDPP	SDEP	SBM
Aspartate	6.20	3.04	3.93	3.66	3.07	3.33	3.41	3.87	3.08	3.72	3.86	5.17	3.60	3.12
Cysteine	1.92	0.69	1.07	1.22	4.17	0.67	0.72	0.69	0.49	0.99	1.04	2.65	1.37	0.70
Glutamine	4.32	2.51	3.88	3.73	2.91	3.60	3.39	3.96	2.81	2.78	3.41	4.49	2.90	3.78

Nutrient	**Bloodmeal**	BSFM	CBPM	CVD	**Feathermeal**	FM-M	FM-P	FM-SE	MBM	SDPM	PBM (PFG)	SDPP	SDEP	SBM
Glutamate	6.38	3.44	5.34	6.34	4.92	5.32	5.13	5.97	4.05	5.77	4.75	6.77	5.48	4.22
Glycine	3.86	2.91	5.94	8.25	8.97	4.26	5.09	5.87	8.67	4.95	6.86	3.40	2.45	2.30
Histidine	5.57	1.71	1.36	0.75	0.90	1.41	1.43	1.46	1.19	1.29	1.31	3.66	1.45	1.15

Nutrient	**Bloodmeal**	BSFM	CBPM	CVD	**Feathermeal**	FM-M	FM-P	FM-SE	MBM	SDPM	PBM (PFG)	SDPP	SDEP	SBM
Hyp	0.20	1.27	1.85	1.73	4.97	1.57	1.82	1.98	2.88	0.79	2.25	0.021	0.023	0.09
Isoleucine	2.54	2.02	2.72	3.84	3.78	2.42	2.75	2.79	1.92	2.44	2.38	2.77	2.97	2.03
Leucine	11.4	3.25	5.28	6.10	6.92	4.50	5.27	4.59	3.56	4.30	4.33	7.56	4.61	3.45

Nutrient	**Blood meal**	BSFM	CBPM	CVD	**Feather meal**	FM-M	FM-P	FM-SE	MBM	SDPM	PBM (PFG)	SDPP	SDEP	SBM
Lysine	8.25	3.21	4.52	5.02	2.15	4.46	5.25	4.57	3.13	4.07	3.54	6.85	4.09	2.81
Methionine	1.16	1.20	1.43	1.58	0.75	1.97	2.16	2.03	1.10	1.20	1.38	1.97	2.01	0.60

Nutrient	**Bloodmeal**	BSFM	CBPM	CVD	**Feathermeal**	FM-M	FM-P	FM-SE	MBM	SDPM	PBM (PFG)	SDPP	SDEP	SBM
Phenylalanine	5.83	2.18	2.70	3.70	3.96	2.31	2.31	2.65	1.85	2.33	2.32	4.74	3.04	2.20
Proline	6.29	2.92	4.30	5.53	11.6	3.72	4.27	4.80	5.86	16	5.07	4.32	3.39	2.44

Nutrient	**Blood meal**	BSFM	CBPM	CVD	**Feather meal**	FM-M	FM-P	FM-SE	MBM	SDPM	PBM (PFG)	SDPP	SDEP	SBM
Serine	4.49	2.34	3.05	6.45	8.992	2.52	2.91	3.28	2.08	3.37	2.62	4.99	5.39	2.14
Threonine	3.95	2.55	2.77	1.99	3.92	2.50	2.85	3.14	2.42	2.85	2.56	4.45	3.10	1.78

Nutrient	**Bloodmeal**	BSFM	CBPM	CVD	**Feathermeal**	FM-M	FM-P	FM-SE	MBM	SDPM	PBM (PFG)	SDPP	SDEP	SBM
Tryptophan	1.30	0.71	0.76	1.03	0.80	0.70	0.68	0.70	0.39	0.63	0.63	1.36	0.97	0.62
Tyrosine	2.86	3.85	2.29	2.56	2.14	1.89	2.01	2.36	1.45	2.24	1.88	3.51	2.61	1.68
Valine	8.21	2.87	3.32	5.57	5.81	3.02	3.65	3.25	2.23	3.05	2.91	4.96	3.57	2.08

Nutrient	**Bloodmeal**	BSFM	CBPM	CVD	**Feathermeal**	FM-M	FM-P	FM-SE	MBM	SDPM	PBM (PFG)	SDPP	SDEP	SBM
Taurine	0.152	0.009	0.210	0.132	0.014	0.409	0.749	0.986	0.188	0.164	0.388	0.246	0.033	0.000
TCr	0.007	0.041	0.154	0.166	0.014	0.539	1.17	0.658	0.160	0.419	0.201	0.014	0.020	0.000
Carnosine[d]	–	127	5506	136	2	125	665	366	0.152	955	545	1407	1.8	0.00

Nutrient	**Blood meal**	BSFM	CBPM	CVD	**Feather meal**	FM-M	FM-P	FM-SE	MBM	SDPM	PBM (PFG)	SDPP	SDEP	SBM
Anserined[a]	–	0.00	7966	48	6.7	0.00	0.00	0.00	0.054	67	1146	382	6.5	0.00
TPAd	126	181	1172	875	1117	2551	1990	1634	173	3322	1423	91	190	1532
TGSHd	14	154	113	20	0.71	35	24	225	6.6	175	73	48	34	174

[a] Unless indicated, values for all nutrients are expressed as % of feedstuff

on as-fed basis. Molecular weights of intact amino acids were used to calculate the content of AAs in feed ingredients. Dash (–) denotes that data are not available. Nutrient composition in feedstuffs may vary with their sources, manufacturers and storage.

[b] Calculated as N% × 6.25. The N-to-CP conversion factor of 6.25 may not be appropriate for all animal-sourced feedstuffs.

Except for energy content (kcal kg^{-1}), data are expressed as %.

[c] Expressed as kcal kg^{-1} of feedstuff (on as-fed basis).

[d] Expressed as mg kg^{-1} of feedstuff (on as-fed basis).BSFM, black soldier fly larvae meal; CBPM, chicken by-product meal; CF, crude fat; CH, carbohydrates; CP, crude protein; CVD, chicken visceral digest; DM, dry matter; FM-M, fish meal (United States Menhaden); FM-P, fish meal (Peruvian anchovy); FM-SE, fish meal (Southeast Asian miscellaneous marine fish); GE, gross energy; Hyp, 4-hydroxyproline; MBM, meat and bone meal; PBM (PFG), poultry by-product meal (pet-food grade); SBM, soybean meal; SDEP, spray-dried egg product; SDPM, spray-dried peptone from enzymes-treated porcine mucosal tissues; SDPP, spray-dried poultry plasma; TAAs, total amino acids; TCr, creatine + phosphocreatine + creatinine; TGSH, reduced glutathione + oxidized glutathione; TPA, total polyamines (putrescine + spermidine + spermine)

Rendering

The process that cooks raw animal tissues or restaurant grease at high temperatures (approximately 115–145°C) for 40–90 min, depending upon the type of system and materials. The rendering process destroys microorganisms, while separating fat, protein and water into usable nutritional components or chemical products by using a variety of equipment and control processes. Renderers, the professionals serving the rendering industry, have often been

called the original recyclers. Modern renderers carry out a practice that dates back thousands of years. The rendering operation was based on fat recovery for soap, glue and candle making materials. The earliest mention of soap production was from written texts from the Mesopotamians in the 2800 BC. In ad 77, Pliny the Elder mentioned soap production in *Historia Naturalis*. He described how soap was made from a combination of tallow and ashes. In the book *The Cattle on a Thousand Hills*, the author, Robert Glass Cleland, reported correspondence between two Western pioneers that translated to the sale of steers, fat and meat and showed the extreme importance of **animal fats** in the 19th century.

Over the years, as diets changed, less of the animal was consumed for food. Hence, the protein component not utilized during slaughter was left over. Originally this protein component was either thrown away or used as fertilizer. In Europe, the first prescribed use of animal **by-product**s in livestock feed was made by Liebig in 1865 where he advised feeding animal by-products to pigs. In the USA, research at Purdue University by Professor Plumb in the early 1900s showed that pigs fed protein residue from rendering fat along with corn grew much better than those fed corn alone. So began the feeding of rendered animal proteins to livestock because of the rich nutrient content and high **protein quality**. Intensification of the beef/pork packing industry and the poultry processing industry in the world prompted the development of the rendering industry, which generated animal proteins and fats on an industrial scale to support the global animal feed and pet food industry.

After research endeavours in improving equipment and processing management over past decades, today's renderers convert the leftover offal from livestock and poultry slaughter processes into protein-based feed ingredients (such as poultry by-product meal, meat and bone meal from various single animal species or mixed species, **blood meal**, **feather meal**) for animal feed, aquafeed and pet food industries. The fat component is used for feed and pet food, as well as biofuels and other industrial and commercial uses. Feathers and porcine hair are typically hydrolysed at high temperatures and high pressure to break down **keratin**'s **peptide** bonds inside feathers/hair and make the hydrolysates highly digestible in all animal species. Raw **blood** from **beef** or **pork** slaughtering is usually cooled and centrifuged at kill floors for the separation of plasma from blood cells. Blood cells are usually dried by ring dryer, flash dryer, or spray-dryer to produce blood meal. Liquid plasma is usually concentrated, refrigerated and sent to spray-dryer facilities to preserve its functionality and amino acids. Similar practice applies to other animal products, such as porcine peptone from hydrolysed mucosa tissues for heparin extraction, whole egg product, and enzyme-treated select organs for pet food, to ensure attractiveness and **palatability** to those companion animals. North American Renderers Association (NARA) and the affiliated Fats and Proteins Research Foundation (FPRF) have been determining the profiles, digestibilities and bioavailabilities of nutrients in various rendered products. These organizations and supporting member companies, mainly in the USA and Canada, have also optimized the uses of

their products in the diets of different animal species at various life stages to facilitate applications to animal agriculture, pet foods and zoos.

Rendering, by its very nature, contributes to the sustainability of animal industries. It is good for the environment as it takes leftovers from the **food chain** and diverts them from landfill to productive uses, thus decreasing carbon emissions. In addition, the protein from rendered products is a good source of **amino acid**s and other functional substances for aquatic feed manufacturers. This allows the **aquaculture** sector to expand and relieve pressure on feed ingredients (e.g. fish meal) that are increasingly limited in resource and production. Thus, rendering gives the feed and pet food industries a safe reliable source of **animal protein**s and highly **digestible energy**. Furthermore, the industry creates jobs, often in rural areas. The rendering industry has been operating for thousands of years and contributes to the sustainability of livestock production systems. (KJS)

See also: Rendered animal-sourced feedstuffs

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Rennin

A proteolytic **enzyme** (chymosin; EC 3.4.23.4) occurring in the gastric juice of newborn ruminants. When activated by HCl in the presence of Ca^{2+} it coagulates **milk** protein, which delays its passage, resulting in increased **digestion** in the **stomach**. (SB)
See also: Protein digestion

Reproduction

The production of a new generation of an animal by the fusion of the male sex cell, the spermatozoan, with its female counterpart, the oocyte. In mammals, the resulting zygote develops into an embryo and also contributes to the placenta. Placental invasion of the uterine wall accesses maternal nutrients for fetal growth and the birth of a new generation. In avian and also some fish species, the embryo is nourished by the lipids and proteins within the egg until hatching.



In seasonal breeders such as these goats in Yellowstone National Park, USA, mating is timed so that the young are born in time for the spring flush of grass. Photo courtesy of Yellowstone National Park. Licensed under Public Domain Mark 1.0.

Cattle

Puberty occurs around 10–12 months and 11–15 months of age in the main dairy and beef breeds, respectively. Nutrition, season of birth and **genotype** each influence the timing of puberty. For example, in zebus these factors interact to delay puberty until 18–24 months of age. The optimum calving intervals for all cattle genotypes is 1 year but this is seldom achieved on a herd basis, due to post-calving delays in the resumption of regular 21-day **oestrous cycle**s. Singleton calves are the norm, with surveys indicating a 2–3% incidence of twins, though this is environment and breed dependent and can be as high as 10% in some herds. On average the numbers of parities are four and seven for dairy and beef breeds, respectively, but in very high-yielding dairy herds the number is now closer to three.

Sheep and goats

For lambs and kids born in the spring and well nourished, puberty usually occurs in the autumn, i.e. at 5–7 months of age. Those whose growth is restricted and those born during the summer months usually do not achieve puberty until the autumn of the year following their birth, i.e. 15–20 months of age. Ewes and does of most breeds are seasonally polyoestrous short-day breeders, with oestrous cycle lengths of 17 and 21 days, respectively. Following

gestation lengths of approximately 150 days, both species normally produce one to three offspring (but occasionally four) at a single annual parturition. Some breeds (for example, those kept in equatorial environments and non-equatorial breeds such as the Dorset Horn, which tends to be non-seasonal in its breeding activity) can lamb every 8 months, provided that poor nutrition does not limit the expression of oestrus. Duration of breeding life varies with nutrition and genotype and is on average seven parities for both species.

Horses

Reproduction in mares is very variable. Some are truly polyoestrous but most are seasonally polyoestrous long-day breeders. Although puberty occurs from 12 to 24 months of age, in practice first mating is usually delayed until 3 years of age. The incidence of twin pregnancies is low (approximately 2%) and when it occurs manual intervention is used to eliminate one embryo so that only one foal is born. Mares breed once annually up to the age of 15–16 years, giving a total of 10–12 parities over their breeding life.

Pigs

Puberty in gilts occurs around 25 weeks of age. A 16-week gestation followed by abrupt **weaning** after 3 weeks of **lactation** results in oestrus about 1 week later and an average of 2.5 litters per year. The number of piglets per litter varies with genotype and nutrition, with an average of about ten. The number of parities per lifetime is about seven, with maternal oversize and a decline in reproductive performance being the main reasons for culling.

Rabbits

Commercial intensive production units achieve an average of 6.5 litters per doe per year with a mean litter size of 8.5–9.0. The reproductive lifespan of the doe is approximately 1 year.

Chickens

From a relatively short natural egg-laying period each year followed by broodiness and the hatching of the chicks after a 21-day **incubation** period, selective breeding, improved management and extended lighting regimens have produced strains with production approaching 300 **eggs** (250 chicks) in 50 weeks, followed by culling. Broiler or meat-type strains have a shorter laying period of about 40 weeks and produce about 180 eggs, followed by culling.

Ducks

Ducks reach sexual maturity at 6–7 months, i.e. approximately 1 month later than chickens, and have a 28-day incubation period. Modern layer and meat-type strains have first-year production of about 275 eggs (about 220 ducklings) in a 47-week laying period. Following an 8-week moult a second laying cycle, with 85–90% of the production of the first, is usually taken before culling.

Geese

Small and large types have 30-day and 33-day incubation periods, respectively, and reach sexual maturity at 9–10 and 10–12 months, respectively. Both types produce from 30 to 70 eggs (15–35 goslings) in their first laying year and have a breeding lifespan of 3–4 years.

Turkeys

Turkeys reach sexual maturity at 7–8 months of age, have an incubation period of 28 days, produce 110–120 eggs (about 85 chicks) in their first breeding season (duration 25–30 weeks) and are then culled.

Ostriches

Ostriches reach puberty at 2 years of age and have a breeding life which, in some individuals, can extend to 30 years. Peak egg production usually occurs around 9–10 years of age. Potential annual egg production is about 100 during a 7-month laying period. Of these, 50% should produce chicks after a 42-day incubation period. Currently many production systems fall short of these levels of egg laying and hatchability. Microbial contamination of eggs through poor nest structure is a major cause of reduced hatchability.

Fish

Atlantic salmon

(*Salmo salar*) and **rainbow trout** (*Oncorhynchus mykiss*) can achieve breeding status in their second year of life. Mature salmon females weigh 3–6 kg and produce about 1500 eggs kg^{-1} body weight. Fewer than 5% spawn a second time in the wild but with re-alimentation and good management some can spawn for a further 10 years in captivity. Female rainbow trout produce 2000–12,000 eggs, with up to 10% **spawning** the following year in the wild. Some can spawn for up to 5 successive years when nutrition and management are good. (JJR)

Reproductive disorders

Reproductive disorders are the most important veterinary causes of financial loss in farm animals and a major reason for veterinary attention. Nutrition is frequently blamed, though without good evidence. **Copper** deficiency or molybdenosis has been shown to reduce **fertility** in cattle by inhibiting release of **luteinizing hormone** (LH) (Phillippo *et al*., 1987). **Selenium** deficiency in cattle may be associated with retained fetal membranes, persistent metritis, reduced resistance to infection and reduced fertility (McClure *et al*., 1986). **Iodine** deficiency is commonly associated with stillbirths in cattle, with enlargement of the thyroid. **Phosphorus** deficiency is widely believed to be associated with reduced fertility but evidence for this as a separate entity is not convincing. **Energy** deficit is a major cause of reduced fertility in cattle, and increasing **milk** yields in dairy cattle is associated with a progressive reduction in pregnancy rate. **Overfeeding** of dairy cows in late **lactation** and in the dry period, leading to over-condition, results in reduced **appetite** in early lactation, **fat** mobilization syndrome (fatty liver) and reduced fertility. Excess protein in the diet is associated with reduced fertility in cattle but evidence that this occurs in the absence of energy deficit is controversial. In pigs, **biotin** deficiency is associated with reduced fertility. **Ergot poisoning** can cause small litters and small piglets. (WRW)

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Phillippo, M., Humphries, W.R., Atkinson, T., Henderson, G.D. and Garthwaite, P.H. (1987) The effect of dietary molybdenum and iron on copper status, puberty, fertility and anoestrous cycles in cattle. *Journal of Agricultural Science* 109, 321–336.

Requirement:
see Nutrient requirement

Resistant starch
Starch that is not degraded by enzymes during passage of the upper part of the digestive tract of non-ruminants. It has physiological effects that make it comparable to **dietary fibre**. Resistant starch (RS) occurs in such materials as partially milled **grain**s and seeds and in raw and cooled cooked **potato**es. RS is inaccessible to α-**amylase** because it is either physically entrapped or in starch granules. **Amylose**, but not **amylopectin**, may also become unavailable to α-amylase after technological treatments (heating, freezing, etc.) during which the physical structure of the starch is degraded and, with time, it recrystallizes, becoming retrograded starch. (SB)

Resorption
Synonymous with reabsorption. The **absorption** from the **gastrointestinal tract** of endogenous materials originating from secretions or cells that pass into the gastrointestinal tract. (SB)

Respiration chamber
The term respiration chamber is most commonly used in reference to methods of **indirect calorimetry** in which air is recirculated

by a fan round a closed system that includes an animal chamber and absorbers for **carbon dioxide** and water vapour. The method was first introduced 150 years ago by the French scientists Regnault and Reiset and has since been refined for use with farm animals, especially by Blaxter and his co-workers at the Hannah and Rowett Research Institutes in Scotland.

The animal chamber is a box of sheet metal with a cooling jacket which can be maintained at a temperature in the range −10°C to 40°C. The entrance door requires a good gasket, as the system must be completely free of leaks. The animal, which is trained to wear a harness with devices for collection of faeces and urine, stands in an inner cage of steel mesh. Lights, air-circulating fans, food hoppers and a drinking bowl are controlled from outside the chamber.

Air is drawn by a compressor from the chamber and then returned to it via three circuits, A, B and C, each controlled by a valve. Circuit A is a simple bypass and includes a gas-sampling loop. The main **absorption** loop, B, consists firstly of **silica** gel absorbers for removal of water; these are followed by caustic potash absorbers and more silica gel absorbers, whose combined weight gain represents carbon dioxide produced by the animal, and a flowmeter. Circuit C has further silica gel absorbers. Adjustment of the valves regulating the relative flow through B and C allows some degree of humidity control. **Oxygen** to replenish that consumed by the animal is provided from a calibrated reservoir called a spirometer. **Methane** produced by the animal builds up in the chamber over the period of measurement, which is normally 24

h. Gas samples taken from loop A at the start and end of the measurement period are analysed for calculation of methane produced plus any changes in oxygen and carbon dioxide content of the chamber. These values are used as corrections to the volume of oxygen supplied by the spirometer and the weight of carbon dioxide absorbed. Further corrections are made to allow for changes in atmospheric pressure, temperature and humidity during the measurement period. Food consumed and faeces and urine excreted are all collected, weighed, sampled and analysed.

The system makes possible the measurement of **oxygen consumption**, carbon dioxide and methane production and urinary **nitrogen** excretion. From these, **heat production** may be calculated and also carbon and nitrogen **turnover**. It has proved possible to demonstrate excellent agreement between **energy** retention measured from respiratory exchange and by the carbon and **nitrogen balance** technique (although the two estimations are not completely independent of one another). (JAMcL)

Further reading

McLean, J.A. and Tobin, G. (1987) Indirect calorimeters. In: *Animal and Human Calorimetry*. Cambridge University Press, Cambridge, UK, pp. 37–76.

Respiratory diseases

Respiratory diseases occur in all species of domestic animals and birds. A common cause is infection with a bacterial agent, such as *Pasteurella multocida* or *Bordetella bronchiseptica*. Respiratory disease is usually accompanied by nasal discharge and laboured

breathing. Viral infection may also be involved, especially in disorders such as bovine viral diarrhoea (BVD), which can cause bovine respiratory disease (BRD) and which involves a complex interaction of environment, pathogens and host factors. Environmental stressors include crowding, inadequate ventilation and airborne particles (dust). Shipping fever of cattle is similarly a result of complex interactions among nutritional, environmental and pathogen factors. Respiratory disease may result from inhalation of foreign objects (inhalation or aspiration pneumonia) such as **rumen** contents, fungal spores (farmer's lung disease) and toxic gases such as silo gases (nitrous oxide). Parasites such as lungworms cause signs of bronchitis and pneumonia. Acute bovine pulmonary emphysema is caused by rumen metabolism of **tryptophan** to 3-methyl **indole**, a pneumotoxic agent. Certain plants, such as purple mint (*Perilla frutescens*) and mouldy **sweet potato** (*Ipomoea batatus*), contain pneumotoxic furans. (PC)

Respiratory exchange ratio

The ratio (R) of the volume of **carbon dioxide** produced to the volume of **oxygen** consumed at any time whether or not equilibrium has been reached, as distinct from **respiratory quotient** (RQ), which is the ratio of carbon dioxide produced to oxygen consumed in the steady state. In the steady state, RQ is 1.0 if **carbohydrate** is being exclusively metabolized, because **hydrogen** and oxygen are present in carbohydrate in the same proportions as in water. The RQ for exclusive **fat** metabolism is 0.70, because extra oxygen is necessary for the formation of water. The RQ for **protein metabolism** is less straightforward, but it

has been calculated to be 0.82. (JAM)

Respiratory quotient (RQ)
The ratio of **carbon dioxide** production to **oxygen consumption**. The RQ for a food or food substance is the same gas ratio when the substance is metabolized. The RQ for **carbohydrates** is 1.00, that for **fat** is 0.70 and that for **protein** 0.82. The RQ of an animal can provide an indication of the type of nutrient being metabolized and how it is utilized. At **maintenance** on a carbohydrate diet RQ = 1; during **starvation**, when body reserves are being utilized, RQ drops towards 0.7; for a cow synthesizing milk fat from a mainly carbohydrate diet, RQ can be as high as 1.2. (JAMcL)
See also: Indirect calorimetry

Responses to dietary energy and nutrients
Responses are usually measured in terms of an increase in a given output (**meat**, **milk**, **eggs**, **wool** or **growth**) in relation to an increase in a particular input such as **energy** or **protein** (usually expressed in relation to body weight). The gross response varies throughout the input range, depending on a number of factors. These include, at the bottom of the range, the extent to which the needs for **maintenance** are met and, at the top of the range, whether the animal has sufficient genetic potential to respond to a further input. Responses are also affected by the age and weight of the animal, its gender and **genotype**, and its health status.

A key feature of modern animal husbandry is to seek to provide nutrients in appropriate amounts so that performance and

efficiency can be optimized. Although this can be done empirically, as it is in many traditional production systems, there is an increasing need to develop models that allow responses to be predicted. Modelling responses is especially relevant when feeding systems and **feed mixing** are semi-automated. In the future this could allow an individual animal to be offered an optimized diet and feed allocation on a daily basis.

When responses are graphically represented, it is usual to assign the input variable to the *x* axis and the output to the *y* axis. At their simplest, responses so represented may appear as two straight lines, one ascending and the other a plateau. The slope of the ascending limb can indicate the net efficiency of utilization of the nutrient and the horizontal line the limit of responsiveness. This 'broken stick' presentation has been much used in modelling and the intersection of the two lines is often taken to represent the 'requirement' for a particular nutrient. In a simple example, the nutrient input might be **ideal protein** and the output might be **nitrogen retention** or **muscle growth**. The point of intersection gives the requirement for ideal protein. The same principle, with an appropriate measure of response, can be applied to any nutrient. Although such simply defined responses work well for individual animals, a more complex response curve is required for populations of animals. This is because, as the input increases, individuals run out of responsiveness at different points along the input axis. Some evaluations of energy and **protein source**s are determined by slope ratio assays. It is important that the slopes are compared well within the responsive range.

Responses to dietary protein can be considered either as a response to the limiting **amino acid** in the diet, which for pigs and poultry is usually **lysine**, or as a response to an increment of ideal protein. An ideal protein is one in which the balance of the essential amino acids required for a productive purpose cannot be improved by the addition or subtraction of any one of them. Responses to **supplement**s of individual amino acids usually reflect the extent to which the available protein is moved towards the ideal balance by the addition. Provided that the supplementary amino acid remains limiting, additional increments will have the effect of increasing the available ideal protein. Eventually further additions will have no further benefit because either some other amino acid becomes limiting or the total ideal protein is adequate.

The strategy for modelling and defining responses is affected by whether the species is a ruminant or a non-ruminant. Predicting the responses to nutrients that must pass through a functioning **rumen** requires an understanding of what controls the **fermentation** process. Different dietary **substrates** may change the ratio of **volatile fatty acid**s produced in the rumen and this can have a profound influence on voluntary intake and, for example, the yield of butter fat in **milk**. A further factor is the extent to which the protein supplied can pass through the rumen undegraded by the bacteria and still be digested in the **abomasum** and **small intestine**.

A major consideration in defining responses is to take proper account of the effect of change of input on **appetite** or daily **feed intake**. Ruminants can increase their daily intake of energy in

response to an improvement in the quality of the **roughage** in the diet. Pigs and poultry may modify their intake to balance changes in energy concentration of the diet so that the daily intake of **metabolizable energy** remains more or less constant. It is also possible that pigs and poultry compensate, on being offered a diet marginally deficient in a given nutrient, by increasing intake. Major deficiencies and excesses, however, reduce intake.

Because the daily intake of feed can vary, it is usual to fix one component of the diet, metabolizable energy for example, and express all other constituents as ratios to that. In the case of poultry nutrition, it is considered better to examine responses to changes in **energy**:**protein** ratio (E:P) rather than consider the two nutrients separately. In most normal circumstances the response to increases in **vitamins** and **minerals** is a reduction in signs of deficiency and in morbidity. Provided that the net requirements are comfortably met by the dietary supply and that there are no serious excesses, 'responses' as such are not usually considered important. An exception is in the case of vitamins such as **vitamin E** and **vitamin C** and the mineral **selenium**, which have interacting **antioxidant** roles. These may also promote or facilitate the activity of the immune system, particularly in young animals under stress. For these nutrients, it has proved difficult to define a precise requirement and for populations a 'response' approach may be more appropriate than an absolute requirement.

Of increasing concern is the danger that certain nutrients may be provided in excess and, consequent upon excretion, may damage the environment. These include **nitrogen**, **phosphorus**

compounds and **potassium**. Phosphorus particularly has been implicated in the eutrophication of water courses. Excesses of dietary protein result in **deamination** and the wasteful excretion of the nitrogen. In addition to faecal nitrogen, this excess is excreted in urine. Unless recaptured in a growing crop, **nitrogenous compound**s can be a pollutant of air and water.

The use of supplementary phosphorus and **calcium** raises a number of controversial issues. Although both minerals have a metabolic function, they have structural roles in **bone formation**. The problem is that neither is used very efficiently for bone formation. Maximum **bone density** and mineralization may only be achieved by high inputs at which the efficiency of retention of phosphorus is as low as 20%, whereas much lower inputs are required if a lower degree of mineralization is accepted as adequate, and the efficiencies can rise to two or three times this. This highlights the difference between maximizing output and optimizing utilization. In the final analysis, optimizing responses can only be achieved when true costs can be assigned to the nutrient inputs and true values to the outputs. (VRF)

Restricted feeding systems

Any regimen in which an animal's **feed intake** is limited to less than it would voluntarily consume. There are several contexts in which restricted feeding is, or has been, used in commercial animal production, usually when unrestricted feeding would lead to **metabolic disorder**s and **obesity**. Feed restriction does, however, represent a potential **welfare** concern in the context of the first of the UK Farm Animal Welfare Council's 'Five Freedoms'

(freedom from **hunger** and thirst).

The development of rapidly growing genotypes of farm animals, with the ability to grow rapidly when fed a high-quality diet, has led to the necessity to restrict the nutrient intake of breeding animals to avoid obesity and health problems. Thus **broiler breeder**s are fed restricted amounts of feed, especially during the rearing period. Between 8 and 16 weeks, intake will be restricted to 25–33% of *ad libitum* intake for this period. This has adverse effects on welfare and leads to abnormal behaviours, in particular stereotyped **pecking** at non-food items, polydipsia and pacing. Broiler breeders need a means of **foraging**, even if they cannot find an actual source of feed. Restriction of the feed leads to severe **competition** between birds, who can eat their daily ration in just 15 min. Ensuring adequate feeder space for all birds will help to prevent them damaging each other in their attempts to get to the feed. **Scatter feeding** can be used to increase **foraging behaviour**, reduce leg problems and increase feeding time. Spin feeders can automate the process, but the evidence that frustration and hunger is reduced by this method is so far not available. Skip-a-day feeding is commonly used within the industry and feeding on only five or six days per week allows the ration on those days to be increased. The impact on welfare is not clear. Reducing the energy density of the diet by increasing the fibre content has been shown in some, but not all, studies to reduce stereotyped pecking behaviour. Insoluble fibre may be better than soluble fibre for this purpose, encouraging dust bathing and other comfort behaviours. Appetent suppressants may be included in the feed to allow *ad*

libitum intake, but again the effects of welfare are not known.

Sheep

Sheep may be restricted in their feed intake during pregnancy, which usually causes them few problems, unless they are bearing multiple lambs. **Twin lamb disease** may ensue unless suitable **supplement**s are fed. Determining whether ewes are carrying single or multiple lambs early on in pregnancy will facilitate feeding according to needs.

Companion horses

Horses are often deliberately restricted in their intake because, as they are not growing or lactating, they easily become overweight if provided with too much **grain** or high-quality pasture. Nevertheless, there is a tendency to overfeed grain to stabled horses, because it is easier than providing **roughage** in the form of pasture or **hay**. This predisposes them to **colic**.

Growing layer pullets

In the past, various forms of mild food restriction were used to reduce body weight at point of lay, and thereby improve **egg production** and efficiency of food conversion. Restricted birds showed stereotyped pecking at non-food objects, characteristic of frustration of feeding motivation when their food supply was exhausted. Such practices are no longer used routinely with modern layer strains.

Adult layers

The most severe form of food restriction has been the total withdrawal of food for periods of several days imposed at the end of the first laying year, in order to induce a moult and a pause in

laying in hens being taken into a second laying cycle. This practice compromises bird welfare and it has been illegal in the UK since 1987; very few flocks in the UK are now taken into a second laying cycle.

Growing broilers

A period of reduced food or **energy intake** is sometimes imposed for a week or so early in the life of growing broilers, in order to reduce the incidence of skeletal and metabolic disease. The restriction can be achieved with short **photoperiods**, and is likely to benefit broiler welfare rather than compromise it.

Growing broiler breeders

All broiler breeders are fed on restricted rations during the growing period in order to limit body weight at sexual maturity and thereby improve health and reproductive performance. Male and female birds are reared separately and rations are usually provided once a day, or sometimes (as in the USA) on alternate days. Females fed on such (daily) rations typically eat them in < 10 min, eat only one-third as much as they would with free access to food, and are highly motivated to feed at all times. They are much more active than unrestricted birds and (unlike the latter) show abnormal pacing and oral behaviours characteristic of frustration of feeding. There is no evidence that welfare is improved, or that feeding motivational state is reduced, by using qualitative (e.g. low protein, diet dilution, appetite suppression) rather than quantitative restriction to limit growth rate.

Adult broiler breeders

Broiler breeders continue to be subjected to mild food restriction

throughout the breeding period, when some form of separate-sex feeding system is normally used, which allows the heavier males to receive a larger ration than females. There is a risk of injury to both sexes with some such systems and care is needed to ensure they operate efficiently.

Growing pigs

The practice of restricting the feed intake of pigs used to be common to limit fatness, particularly of castrated males, at traditional slaughter weights. It is now less usual, for several reasons. First, genetic improvement has resulted in pigs that can be fed *ad libitum* to slaughter without becoming excessively fat. Secondly, fewer male pigs are now castrated: intact males are less inclined to become over-fat. Thirdly, meat processing can more easily accommodate over-fat carcasses. Feeding of gilts being reared for breeding is restricted to prevent their becoming obese, which would compromise their lifetime reproductive performance.

Gilts

Gilts are also fed a restricted amount of feed (for example, only about 2 kg diet per day, compared with a normal feed intake of about 4 kg per day if they are fed *ad libitum*) during pregnancy. The goal of this restricted feeding is to reduce embryonic mortality and excessive maternal fat accumulation. The latter is a major factor impairing feed intake and milk production by lactating sows during the first week post-partum. A disadvantage of the restricted feeding is an inadequate provision of L-**arginine**, an amino acid that is necessary for optimum conceptus growth and survival.

Pregnant sows

Sows fed *ad libitum* on conventional foods during pregnancy become obese and suffer numerous problems, such as high piglet mortality and **lactation disorder**s. They are usually restricted to 2.0 kg of concentrated food per day, which is approximately two-thirds of the amount they would eat voluntarily. If allowed to compete in a group for this limited amount of food, there would be considerable inequality in the amount obtained by individuals. The use of equipment that rapidly delivers food to all animals simultaneously, or computer-controlled feeders to ration individual animals, has replaced individual stalls as a means of evenly rationing pregnant **sows**.

Adult boars

To preserve libido and semen quality, and to avoid their becoming obese and injuring sows during mating, working boars are normally given limited amounts of food.

Dairy cattle

Restricted concentrate feeding of dairy cattle is normal in most production systems. In the lactating cow, reduced **energy intake** from concentrates can be offset by increased **catabolism** of **body fat** reserves or by increasing forage intake, but protein reserves are less readily mobilized. Net **protein catabolism** during **lactation** is an **indicator** of reduced welfare in lactating cows, because it represents loss of an essential body tissue. Forage intake can be reduced for periods of about 3 weeks by up to 40% of *ad libitum* intake of the forage, but more than this will cause a reduction in milk production, in particular milk protein output, and considerable losses in body weight.

Dairy calves

Calves are fed restricted amounts of milk replacer, because of its high cost compared with solid feed, usually concentrated pellets. This can increase stereotyped **sucking** behaviour, but this can be abated by encouraging the calf to suck naturally through a teat rather than from a bucket. Feeding too much milk replacer makes **weaning** more stressful for calves. Dairy heifers may be restricted in their intake of pasture by keeping them on distant parts of dairy farms, with little return of **fertility** to the land in the form of manure and fertilizer. Adult cows are usually kept close to the milking units and may be fed restricted amounts of concentrates in the early part of lactation, compared with those fed according to their yield, which prevents them attaining a high peak yield too early, with the associated risk of metabolic diseases.

Bulls

Bulls kept predominantly indoors for semen production are prone to over-fatness and this is controlled by regular exercise, by a moderate restriction of food intake and by offering bulky forage foods. (JMF; MFF; CJCP; JSav; GW)

See also: Anorexia; Inappetence

Retention time

The time that food is retained in any compartment of the digestive tract, especially the stomach, rumen, caecum, etc. (MFF)

See also: Gastric emptying; Particle size

Retention, energy:

see Energy balance

Retention, nitrogen:
see Nitrogen retention

Retention, protein:
see Protein retention

Reticulum
The second compartment of the ruminant **stomach**. It communicates with the **rumen** through the wide ruminoreticular opening and with the **omasum** via the reticulo-omasal orifice. It is lined with a stratified squamous epithelium, which is raised into ridges around the numerous small reticular cells. It contracts first in the sequences of reticuloruminal contractions. (RNBK)



Honeycomb structure of the reticulum. Photo courtesy of Wiebe van der Worp. Licensed under CC BY-SA 2.0.

See also: Forestomach

Retinoic acid:
see Vitamin A

Retinoid

Retinoids are all compounds, natural or synthetic, that are structurally related to retinol (**vitamin A**). Retinol supports all known functions of the vitamin, including **growth** and cellular differentiation, **reproduction** and embryogenesis and vision. In contrast, not all retinoids exhibit vitamin A activity. (MC-D)
See also: Carotenoids

Retinoid-binding proteins
A number of cellular and serum proteins in addition to the nuclear retinoic acid receptors have been identified that bind to **vitamin A metabolite**s. Cellular retinol-**binding protein** (CRBP or CRBP type I) and CRBP type II bind to retinol and retinal but not retinoic acid. A newly described CRBP type III binds only to retinol **isomer**s. Cellular retinoic acid-binding protein (CRABP or CRABP type I) and CRABP type II bind to retinoic acid but not retinol or retinal. In addition to the cellular binding proteins, a serum retinal-binding protein (RBP) is responsible for transporting retinol from the liver storage site to the target tissues. (MC-D)
See also: Vitamin A

Retinol:
see Vitamin A

Retinyl acetate
Retinyl acetate is formed when retinol is esterified to the two-carbon acetic acid molecule. (MC-D)
See also: Vitamin A

Retinyl palmitate

Retinyl palmitate is formed when retinol is esterified to the fully saturated 16-carbon **long-chain fatty acid**, palmitic or hexadecanoic acid. This is the most common retinyl **ester** found in animal tissues. (MC-D)
See also: Vitamin A

Retrograded starch:
see **Resistant starch**

Rhamnogalactouronans
Heteropolysaccharides of **rhamnose** and galactouronic acid residues, also known as rhamnogalacturonans, frequently occurring as segments of the main chain in complex **pectic substance**s and thus commonly classed with pectins. (JAM)
See also: Carbohydrates; Dietary fibre; Galactouronans; Uronans

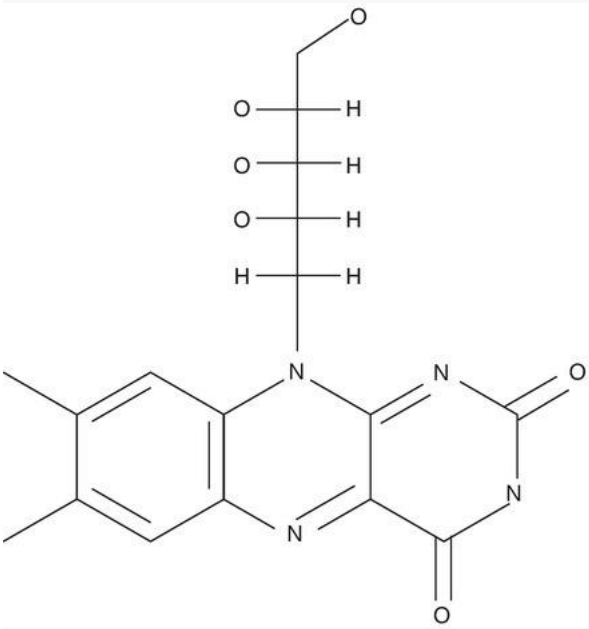
Rhamnose
A **deoxysugar** of **mannose**, $C_6H_{12}O_5$, molecular weight 164, in which the hydroxyl group on carbon 6 is replaced with a **hydrogen**, making it 6-deoxy-L-mannose. It is a constituent of glycoproteins, plant **glycoside**s, **storage polysaccharide**s and plant **gums**. (JAM)
See also: Carbohydrates; Dietary fibre; Gums; Pectic substances; Rhamnogalactouronans

Rhinitis
An upper respiratory tract disease caused by viral, bacterial, fungal or parasitic agents, and hypersensitivity reactions. It is characterized by exudates and erosion and ulceration of nasal

mucosa. Atrophic rhinitis in pigs results in severe ulceration and breakdown of the nasal turbinates, including distortion of the nasal septum and jaw deformity. Infectious agents (*Bordetella bronchiseptica*, *Pasteurella multocida*) and environmental factors (dust, **ammonia**) are involved. Sneezing, coughing and lacrimation are common signs. Antibiotic treatment and vaccination programmes are used to keep rhinitis under control. (PC)

Riboflavin

Vitamin B_2, one of the water-soluble B **vitamins**. Riboflavin is a heterocyclic three-ring compound (isoalloxazine, $C_{17}H_{20}N_4O_6$) attached to a five-carbon **sugar** alcohol, ribitol.



When the alcohol group of the ribitol is phosphorylated by ATP the vitamin becomes the co-factor flavine mononucleotide (FMN). FMN reacts with ATP, adding AMP to the **phosphorus** of FMN to form another riboflavin vitamin co-factor, flavine **adenine** dinucleotide (FAD). Both FMN and FAD are intimately involved in

lipid and **carbohydrate metabolism**. They are found in foods derived from both plant and animal products. **Digestion** and **absorption** of the food-derived **coenzyme** forms of riboflavin occur in the upper **small intestine**. After conversion of the coenzyme forms (FMN and FAD) to the vitamin, absorption is by a **sodium**- and ATP-dependent transport system. Riboflavin is transported through the bloodstream bound to proteins (**albumin** and **globulin**). It is excreted in the urine as free riboflavin. The vitamin co-factors of riboflavin are the **prosthetic group**s of oxidoreductase enzymes such as **amino acid** oxidase, **xanthine oxidase, glycerol**-3-phosphate **dehydrogenase** and **succinate dehydrogenase**, sarcosine dehydrogenase and as part of the electron-transferring flavoprotein in **fatty acid oxidation**.

Riboflavin is required for the **metabolism** of the vitamins, **pyridoxine**, **niacin** and folic acid, thus it is not surprising that a riboflavin deficiency can affect multiple components of metabolism and a deficiency of riboflavin gives rise to no specific symptom. Riboflavin deficiency may be due to limited riboflavin intake or inadequate conversion to the coenzyme forms, FMN and FAD. The reported deficiency symptoms are failure to grow, loss of hair, scaliness and incrustation of a red-brown material in skin, a normocytic **anaemia**, degenerative changes in the nervous system and impaired **reproduction**. The erythrocyte enzyme **glutathione** reductase is an FAD-requiring enzyme and is used to assess the degree of deficiency of riboflavin. Erythrocytes from deficient animals have lower concentrations of FAD and thus the enzyme glutathione reductase is less saturated with co-factor and

the activity measured *in vitro* declines. *In vitro* the activity can be stimulated by addition of FAD. Thus, as with other erythrocyte enzymes that require a B-vitamin co-factor, the activity of glutathione reductase can be measured without and with supplemental FAD and the degree of stimulation noted. An increase in the activity of 20% (an activity coefficient of 1.2) is expected in animals with adequate intakes of riboflavin. Activity coefficients of 1.4 or more reflect a deficiency state. Requirements for this vitamin are in the range of mg kg^{-1} diet. (NJB)

Key references

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Ribonuclease

A cellular enzyme that hydrolyses **ribonucleic acid**s. Ribonucleases cleave internal phosphodiester bonds of RNA to produce either 3′-hydroxyl and 5′-phosphoryl terminals or 5′-hydroxyl and 3′-phosphoryl terminals. They are classified as endonucleases. In the process of **digestion** of food, ribonuclease from the **pancreas** is involved in the digestion of the RNA in food. (NJB)

Ribonucleic acid (RNA)

A polymer of **purine** and **pyrimidine** ribonucleotides linked

together by 3′,5′-phosphodiester bridges. RNA is a single strand whereas DNA may have two strands. The two purines in RNA, **adenine** and **guanine**, are also found in DNA but of the two pyrimidines in RNA only **cytosine** is also found in DNA; the other, **uracil**, is not. The **sugar** in RNA is ribose whereas that in DNA is deoxyribose. In cells, RNA is found in three forms. Ribosomal RNA (rRNA) is associated with ribosomes, subcellular particles involved in **protein synthesis**. Messenger RNA (mRNA) is the RNA template that codes for the **amino acid** sequence of a protein being synthesized. Transfer RNA (tRNA) binds individual amino acids and associates with a specific triplet of ribonucleotide bases in mRNA, ensuring that amino acids are added to the developing polypeptide chain in the correct order. (NJB)

Rice

Rice (*Oryza sativa*) is a member of the **Gramineae** (**grass**) family and is the principal **cereal** crop of eastern and southern Asia. About 60% of all rice is grown and consumed in China and India. It is grown as an annual crop and requires a subtropical or warm temperate **climate**. Little rice is grown in Europe north of latitude 49°.

The seeds are firstly sown in prepared beds; once the seedlings are 25–50 days old, they are transplanted into paddy fields which are under 5–10 cm of water. The transplanted seedlings and subsequent rice crop are grown in water throughout the growing season, the crop reaching a final height of about 1.2 m. Additionally, rice may be grown on dry ground but this results in lower crop yields. The leaves are long and flattened, and its panicle,

or inflorescence, is made up of spikelets bearing flowers that produce the fruit, or rice **grain**.



Rice can be biofortified to enhance human intake of iron, selemium, iodine and zinc. Photo courtesy of the International Centre for Tropical Agriculture, CIAT. Licensed under CC BY-SA 2.0.

Rice grain is an important food product and the grain is also used in the manufacture of **starch**. As a result of processing rice grain for human food purposes, a number of **by-product**s are produced for livestock feeding. The harvested rice grain (kernel), also called paddy or rough rice, is enclosed in a fibrous outer hull and a layer of **bran**. The first stage of **milling** rice grain into white rice for human consumption involves the removal of the outer hull, which represents about 20% of the total grain weight. This process yields brown rice. Following hulling, the bran is removed together with the rice germ and part of the **aleurone** layer to produce white rice. The by-product of this process is called rice bran. To produce a glossy appearance, a **coating** of **glucose** and talc may

be applied to white rice, which is then called polished rice.

The by-products of rice grain processing are rice hulls, rice germ and rice bran. Rice hulls are rich in **crude fibre**, in the range of 470–550 g kg^{-1} dry matter (DM) and have a high **ash** content (180–270 g kg^{-1} DM) (see table). The **ash** fraction is mainly **silica** (170–250 g kg^{-1} DM). The **crude protein** (CP) content of rice hulls is very low (20–50 g kg^{-1} DM). Rice germ has a high protein content (210–230 g kg^{-1} DM) and the protein is of better quality than that of most other cereal grains. The **oil** content is high (210 g kg^{-1} DM) but the ash (90–100 g kg^{-1} DM) and crude fibre (30–70 g kg^{-1} DM) contents are low. Rice bran generally contains about 120–125 g CP kg^{-1} DM, 100–110 g ash kg^{-1} DM and 110–180 g oil kg^{-1} DM; this oil is rich in **unsaturated fatty acid**s.

Chemical composition of rice by-products (as g kg^{-1} DM unless stated otherwise). Source: MAFF, 1990.

By-product	**DM** (g kg^{-1})	**CP**	**Starch**	**EE**	**NDF**	**GE**[a]	**ME**[a]
Rice bran meal, expeller	902	128	302	90	370	18.9	11.0

By-product	DM (g kg^{-1})	CP	Starch	EE	NDF	GE[a]	ME[a]
Rice bran meal, extracted	896	154	236	7.3	451	16.7	7.1

[a] As MJ kg^{-1} DM.DM, dry matter; EE, ether extract; GE, gross energy; ME, metabolizable energy; NDF, neutral detergent fibre

The high oil levels present in both rice germ and rice bran mean that they share similar problems in terms of their use for animal feeding. Both are difficult to store, particularly during the summer, since the oil becomes rancid very quickly and reduces **digestibility**, the **availability** of **vitamin E** and the quality of deposited **fat** in growing animals. For these reasons the oil is generally removed by wet pressure (expelled rice bran meal) or by solvent extraction (extracted rice bran meal and rice germ meal). The expeller and extracted meals can be fed to cows at a level of 3 kg per head per day and represent about 20–30% of the concentrate portion of the feed. Rice bran meals can be fed to horses as a partial substitute for **oats** but they are not recommended for **fattening** pigs, due to their relatively high fibre and ash contents. In the preparation of starch from rice, a product known as rice sludge or rice slump is produced as a residue. This product, when dried, has a CP content of about 280 g kg^{-1} DM and

low levels of crude fibre and oil; it is suitable for feeding to both ruminants and pigs. (ED)

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Ricin

A toxic **lectin** isolated from castor beans and the first lectin to be isolated (by Stillmark in 1889). Like other lectins, it has the ability to agglutinate the red **blood** cells of humans and animals. (SEL)

See also: Phytotoxins

Rickets

A disease affecting the physeal region, or growth plate, of the bones of growing animals. Rickets is most commonly caused by a dietary deficiency of **vitamin D** or **phosphorus**. In some cases, dietary **calcium** deficiency induces a mild form of rickets. During vitamin D or phosphorus deficiency, the **cartilage** in the zone of hypertrophy within the physis fails to undergo mineralization. It seems that normal concentration of **blood** phosphorus (and to a lesser extent blood calcium) is needed before bone mineralization can proceed. As a result the cells of this zone continue to divide and proliferate, expanding the cartilaginous zone within the physis. In

severe cases this can result in bones that are bendable, with enlarged physes. This leads to pain, particularly at the joints. Costochondral junctions within the ribs are commonly greatly enlarged and readily palpable in animals with rickets. Vitamin D is a pro-**hormone** required for the production of the calcium-regulating hormone, 1,25-dihydroxycholecalciferol, without which dietary phosphorus and calcium are only poorly absorbed, which can lead to rickets. In addition, 1,25-dihydroxyvitamin D seems to have direct effects on the growth and **metabolism** of cartilage cells within the physis. (JPG)
See also: Hypophosphataemia

Roasting:
see Heat treatment

Rock phosphate
Naturally occurring, **phosphorus**-containing rock comprising mainly fluor- and chlor-apatites with the general formula $Ca_2(PO_4)_3^-$ (Cl, F). Besides **fluorine**, rock phosphates contain significant levels of other undesirable contaminants such as **cadmium** and **arsenic**. Without some form of decontamination, it does not meet feed grade standards. (CRL)
See also: Calcium phosphate; Diammonium phosphate; Dicalcium phosphate

Roho labeo (*Labeo rohita*)
One of the most popular freshwater **aquaculture** species in the Indian subcontinent. In 2017, more than 1.96 million tonnes of *L.*

rohita was produced, which accounted for approximately 3% of total global aquaculture finfish production (FAO, 2019). They are produced in a variety of different culture systems, for example polyculture with other carps such as **catla** (*Catla catla*), mrigal (*Cirrhinus mrigala*), silver barb (*Puntius gonionotus*), fringed-lipped peninsular carp (*Labeo fimbriatus*) and olive barb (*Puntius sarana*) (Das *et al*., 2019; Pradhan *et al*., 2019), mixed culture with other fish such as mola (*Amblypharyngodon mola*), punti (*Puntius sophore*), **tilapia** (*Oreochromis niloticus*) (Wahab *et al*., 2011, 2019) and freshwater prawn (*Macrobrachium rosenbergii*) (Hossain and Islam, 2006; Jana *et al*., 2019), and integrated culture with **rice** (Dey *et al*., 2019). (QS)

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Rolling

The process of **crushing** a feed, usually a cereal **grain** or other seed, between two rotating rollers, to break the **pericarp** and expose the embryo and **endosperm** so that they can be better digested by the animal when the seed is eaten. (JMW)

Rooting

Nosing of the ground by pigs in their search for food, such as roots. The damage caused to pasture may encourage farmers to place a

ring in the nose of their pigs to stop the rooting behaviour. (CJCP)

Roots:
see Carrot; Cassava; Fodder beet; Jerusalem artichoke; Potato; Sugarbeet; Swede; Sweet potato; Turnip; Yam

Rosemary (*Rosmarinus officinalis*)
A shrub of the Labiatae/Lamiaceae family, dense, evergreen and resistant to environmental stresses. It has woody stems 90–200 cm high and small needle-pointed leaves (2–4 cm). It contains aromatic substances such as essential **oils**. Rosemary is derived from the Latin *ros marinus*, which means the dew of the sea. It is also referred to as *anthos*, which in ancient Greek meant superior flower. Because of its pleasant smell, it was also referred to as *libanotis*. Rosemary is a food and medicinal additive with good **antioxidant** activity (Ogwuegbu *et al*., 2022). Bioactive compounds in rosemary include various flavonoids and phenolic diterpenes. Luteolin and genkwanin are two main flavonoids of rosemary extracts. The phenolic diterpenes of rosemary extracts include carnosic acid (14.7%), methylcarnosic acid (7.4%), carnosol (3.8%), rosmanol (1.4%) and epirosmanol methyl ether (0.8%). Also, the water-soluble extracts from rosemary contain rosmarinic acid (1.3%) and flavonoids (3%). Oxygenated monoterpenes (e.g. 1 and 8 cineol) and alcohols (e.g. borneol and alpha-terpineol) have also been reported in rosemary extracts (Faixova and Faix, 2008). However, the **chemical composition** of rosemary extracts depends on not only the geographical region but also weather conditions, soil type, plant organ, plant age and **harvesting** stage.

The antioxidant activity of carnosic acid is three times greater than carnosol and seven times greater than synthetic antioxidant supplements butylated hydroxyanisol and butylated hydroxytoluene (Richheimer *et al.*, 1996). Feeding domestic animals rosemary can enhance their antioxidant activity, especially under stressful conditions, as well as the quality and durability of products (**milk**, **meat** and **eggs**). Thus, rosemary can be considered as a phytogenic additive and an alternative to in-feed antibiotics (Gad and Sayd, 2015; Bianchin *et al.*, 2020; Seidavi *et al.*, 2021). (AS; BH-G; CJCP)



Rosemary about to be pollinated by a honey bee. Photo courtesy of Dave Nakayama. Licensed under CC BY 2.0.

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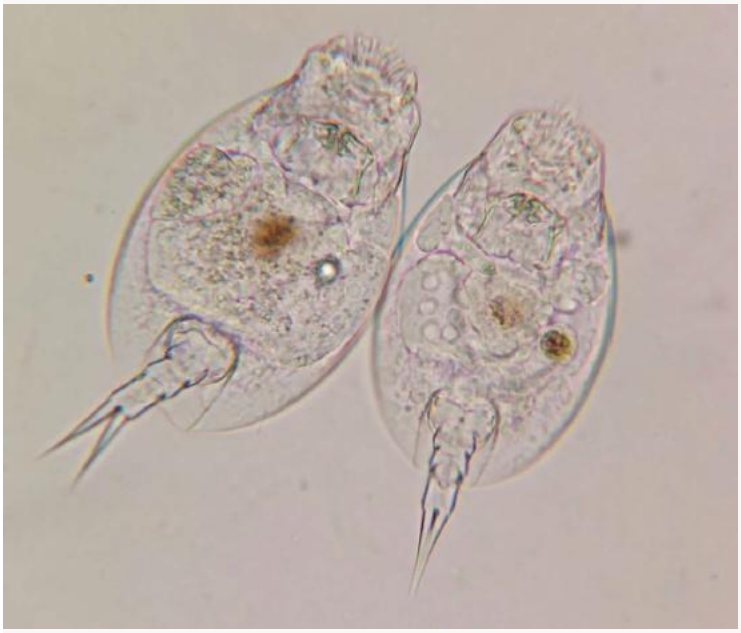
Rotational grazing

A system in which a grazing area is subdivided to give paddocks for alternating periods of grazing and resting, allowing time for application of fertilizers, recovery, etc. The duration and intensity of grazing can be varied. Grazing may be interspersed with conservation, especially early in the growing season, to maximize use of high-quality material. (TS)

See also: Grazing

Rotifer

A small marine crustacean. The rotifer *Brachionus plicatilis* is an essential part of the first feeding of many **marine fish** larvae. It may be 10–300 µm in size and can be cultivated in batches or semi-continuously at high densities and warm temperatures year-round. Recent improvements have led to intensive ultra-high-density mass culture techniques. Although rotifers can grow on simple media such as **yeast** enriched with **marine oils**, much work has been dedicated to improving their nutritional value with emulsions containing **highly unsaturated fatty acid**s, eicosapentaenoic (20:5 n-3) and **docosahexaenoic acid** (22:6 n-3). Bacterial pathogens associated with intensive rotifer culture may have a negative impact on larviculture. (KP)



Pair of rotifers from a pond sample in the north-east USA. Photo courtesy of Matthew A. Robinson. Licensed under CC BY-SA 4.0.

See also: Aquatic organisms; Fish larvae; Live fish food;

Phytoplankton

Roughage
Coarse **fodder**, plant material that is fibrous in nature and relatively indigestible. As **feed**, it is most valuable to ruminants, because of their ability to digest **cellulose**. Roughage is normally dry and includes **cereal** crop residues. Any **forage** allowed to reach maturity takes on the characteristics of roughage. (TS)
See also: Stover; Straw

Roughage restrictions
The need to get maximum productivity from livestock often leads to the feeding of a concentrated diet without adequate roughage. Under these circumstances livestock frequently resort to stereotyped oral behaviours, which stimulate salivation and may help to counteract acidity in the early stages of **digestion** in the **gastrointestinal tract**, produced when highly concentrated and processed feeds, based on **cereal**s, are rapidly digested. Dominant livestock may receive more than their share of roughage, when it is group fed, although the long eating time required by ruminant livestock when fed bulky forages mitigates against this. In extreme cases, roughage restrictions may result in **starvation**. Restrictions should be avoided by having sufficient feed reserves for an extended dry or cold period or in extreme cases by selling livestock or transferring them to another farm. Under Duty of Care legislation, which prevails in many jurisdictions, farmers are required to have sufficient forage stocks for their livestock. (CJCP)

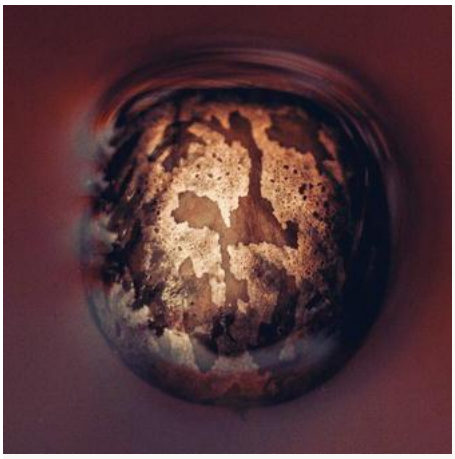
Rubber seed (*Hevea brasiliensis*)

This by-product of the rubber tree is a high-protein product, equivalent to 35% of the weight of the seed (see table). The protein has a **digestibility** of 53% in ruminants. The cake contains 90 mg **hydrogen cyanide** (HCN) kg^{-1} DM, a low concentration which is unlikely to have adverse effects. Rubber seed cake can be included in calf concentrate up to 30% and up to 25% for dairy cattle. Although some reports indicate that it can be included in pig and poultry rations up to a level of 20%, it is low in **methionine** and relatively unpalatable for non-ruminants. There are also reports of poor hatchability after rubber seed meal was fed to breeding hens.

Nutrient composition of rubber seed cake (% dry matter). (LR)

	DM (%)	**CP**	**CF**	**Ash**	**EE**	**NFE**	**Ca**	**P**
Rubber seed cake	20.6	35.1	7.1	10.5	12.5	34.8	1.00	0.80

CF, crude fibre; CP, cruide protein; DM, dry matter; EE, ether extract; NFE, nitrogen-free extract.



Floating rubber seed. Photo courtesy of Buwaneka Saranga. Licensed under CC BY 2.0.

Rubidium (Rb)

An alkali metal with an atomic mass of 85.4678. Its natural presence in the earth's crust is very limited. Analysis of human brain by neutron activation showed 18 mg Rb kg^{-1} cortex. There are no known physiological or biochemical functions for Rb in animals or plants but recent studies found that the concentrations of a variety of essential mineral elements (**calcium**, **phosphorus**, **magnesium** and several trace minerals) in tissues could be affected in rats fed diets containing variable amounts of Rb. Goats fed < 200 µg Rb kg^{-1} diet had decreased growth and increased spontaneous **abortion**s. Rb may support cell differentiation in bone marrow. Rb may have a pharmacological function similar to that of **lithium**, for example depression of **dopamine** synthesis and a neuroprotective function. (PGR; GMcLD)

Further reading

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Rumen

The first and largest compartment of the ruminant **stomach**. The oesophagus enters via the cardiac orifice and the rumen communicates with the **reticulum** through the wide ruminoreticular opening. It is partially subdivided by muscular folds of its wall into a number of smaller compartments or sacs. It is lined with a stratified squamous epithelium, raised into numerous small papillae that enlarge the absorptive surface area. (RNBK)



Rumen and omentum of an impala. Photo courtesy of Leodras. Licensed under CC BY-SA 4.0.

See also: Forestomach

Rumen development:

see Forestomach development

Rumen digestion

The **rumen** is a large organ. Together with the **reticulum**, to which it is closely connected, the rumen occupies most of the left

side of the abdomen. The volume of the rumen and reticulum may be as much as 200 l in an adult cow, and its contents are continually being mixed by strong cyclical muscular contractions, which occur about once a minute.

In ruminant livestock, most of the **digestion** of food occurs in the rumen, with additional digestion of protein, including **microbial protein**, in the **abomasum** and **small intestine**. Most of the absorption of nutrients occurs in the rumen (**volatile fatty acid**s and **ammonia** produced from microbial **fermentation**) and the small intestine (products of mammalian enzymic digestion). Further digestion of plant fibre and microbial protein, and absorption of volatile fatty acids and ammonia, occur in the **large intestine**, but this is relatively insignificant compared with the digestion in the rumen.

Microbial fermentation, in both the reticulorumen and the large intestine, yields **short-chain fatty acid**s (**acetate**, **propionate**, **butyrate**), **lactic acid**, **carbon dioxide**, **methane** and **hydrogen**. An estimated 400–600 different bacterial strains produce **enzymes** that degrade these **carbohydrates**. Typically, 60–80% of the **energy** and two-thirds of the **amino acid**s needed daily by adult ruminants are produced by the microbial fermentation. If **starch** is present in the diet of the ruminant, it is typically fermented in the rumen. Variable amounts of starch, particularly in **legumes** and heat-treated **grain**s, are not susceptible to endogenous enzymes in non-ruminants: this fraction of starch is termed **resistant starch**. It passes into the large intestine, where it is rapidly and completely fermented.

The two most important factors affecting digestion in the rumen are its speed (the rate of particle breakdown) and its extent (the proportion of the original food that is solubilized and absorbed into the **blood**). Both of these are affected by the rate at which undigested food passes from the reticulorumen.

Digestion in the rumen comprises the relatively slow microbial breakdown of plant cell wall components, mainly **cellulose** and **hemicellulose**, and the more rapid fermentation of **sugars** and soluble proteins, for example those in plant cell contents, which are broken down in a few minutes. The rates of carbohydrate digestion in the rumen vary between 200% and 350% h^{-1} for soluble sugars to 2–10% h^{-1} for more resistant cell wall **polysaccharide**s.

Food arrives in the rumen having been eaten, partly chewed, and mixed with **saliva** in the mouth for a relatively short period of time. **Particle size** is reduced during subsequent **rumination**, when additional saliva is mixed with the food.

Rumination effectively breaks plant structures and increases the surface area of the food to facilitate colonization by the **rumen microorganisms**. Bacteria, **protozoa** and **fungi** invade and attach themselves to the particles of food and secrete their digestive enzymes, further reducing the particle size until the **digesta** can pass through the reticulo-omasal orifice to the **omasum**, where considerable amounts of water are removed prior to digestion in the abomasum.

The speed with which food particles are reduced in size during rumination and digestion in the rumen determines how long they remain there. The reticulo-omasal orifice acts as a barrier to the

onward passage of large particles along the alimentary tract and is especially important when most of the diet is slowly digested cell wall material: the level of 'fill' or the bulk of food in the rumen then limits the amount the animal can eat. Physical processing, such as **chopping** or **milling**, by artificially increasing the surface area of food particles, increases intake by accelerating digestion in the rumen.

The second important aspect of digestion in the rumen is the extent of digestion, which is a reflection of the accessibility of the plant cell wall material to the rumen microorganisms. The major component of foods responsible for reducing the extent of digestion in the rumen is **lignin**. Foods generally contain low concentrations of lignin, < 10% of the **dry matter**, but small amounts of lignin have large effects on the extent of digestion in the rumen. The cell wall component of foods that contain relatively high concentrations of lignin (e.g. straw) is digested relatively poorly (about 50%), whilst the cell walls of foods that contain relatively little lignin (e.g. young pasture grass) are digested to a much greater extent (about 80%).

Digestion of food proteins in the rumen results in the production of ammonia in **rumen fluid**, which helps to **buffer** the acetic, propionic and butyric acids that are also produced. The fibrolytic bacteria in the rumen have a requirement for ammonia, and if the concentration of ammonia in the rumen is inadequate then both the rate and extent of digestion are likely to be reduced. It is important to avoid large losses of ammonia from the rumen to the liver, because of the toxic nature of ammonia. The rate at which

the liver can detoxify ammonia to **urea** is limited and excess ammonia in the blood can, in extreme situations, cause toxicity symptoms. The extent to which protein is digested in the rumen varies from 40% for heat- or **formaldehyde**-treated foods such as fish meal, to 90% for fresh pasture grass. Generally, the greater the extent of **protein digestion**, the more rapidly it occurs.

Sugars are normally digested almost completely in the rumen. Starch is digested to a variable extent, depending on its physical form. Normally 70–80% of the starch in ground **cereal** grain is digested in the rumen, a further 20–30% being digested further along the alimentary tract. Processes such as gelatinization and treatment with concentrated **sodium** hydroxide slow the rate of digestion of starch so that less is digested in the rumen and more in the small intestine. This has the advantage of providing more **glucose** than would occur if it were all digested in the rumen.

Lipids are often included in the diet of ruminants in an attempt to increase energy supply. **Unsaturated fatty acid**s such as **linoleic acid** and **linolenic acid** tend to be hydrogenated to **oleic acid** in the rumen, acting as a sink for hydrogen. **Fat** in the diet can reduce the digestion of fibre, because the **fatty acid**s coat the fibre surfaces and prevent bacterial colonization. To reduce this effect, fat can be saponified. (JMW; JAM; GMcLD)
See also: Dietary fibre; Fermentation products

Rumen fluid

Fluid accounts for 80–90% of total ruminoreticular content. It is important that the solids are held in fluid suspension to allow free

mixing of the content, microbial activity, **rumination** and onward passage. The fluid arises mainly from **saliva** and also from drinking water and food water. Its composition is affected by dietary and salivary composition, the products of microbial **fermentation**, **absorption** of solutes and passage of water across the rumen epithelium. Typical values are shown in the table, though they will vary considerably with food intake, time since feeding and other circumstances. (RNBK)

Typical contents of rumen fluid.

Diet	**VFA** mmol l^{-1}	**Ac** mol %	**Pr** mol %	**Bu** mol %	**Na** mmol l^{-1}	**K** mmol l^{-1}	**OP** mOsm l^{-1}	**pH**
Hay	80	70	20	10	100	30	250	6.6
Hay + concentrate	120	60	25	15	100	30	280	6.1
Green fodder	140	65	25	10	60	70	300	6.4
Mainly grain	100	55	25	20	90	40	250	5.8

Ac, acetate; Bu, butyrate; OP, osmotic pressure; Pr, propionate; VFA, volatile fatty acids

See also: Rumen; Rumen digestion

Rumen microorganisms

The archaea, bacteria, protozoa and fungi that colonize the rumen, either attached to food particles, free in the rumen liquor, or attached to the rumen wall. The ruminant host provides them with a favourable environment and regular food supply, which enables them to proliferate rapidly. In return the ruminant has access to the products of microbial **digestion**, including those from the **fermentation** of fibrous **polysaccharide**s which are not digestible by mammalian digestive **enzymes**. The majority of the rumen microflora are strict anaerobes. They digest by fermentation, yielding large quantities of **volatile fatty acid**s, which are mainly absorbed through the rumen wall, and microbial cell mass, which is rich in **protein** and **vitamins** for the ruminant to digest in its **abomasum** and **small intestine**. The symbiotic relationship between the ruminant and its microflora concludes with the digestion of the latter.

The rumen environment, notably the **temperature**, neutral pH, **turnover** rate and nutrient supply, is maintained as relatively constant by the ruminant. This favours the establishment in the rumen of a stable and very mixed microflora and the rapid digestion of ingested feeds. The composition of the microflora is thus controlled by the host to its own benefit. Any organism within the immediate environment that can live and reproduce in the

rumen is likely to be present. Regular constant feeds maintain the stability and variety of the microflora. Rapidly imposed feed changes can disturb this equilibrium. For example, the sudden introduction of acid feeds, or rapidly degradable ones, may reduce rumen pH to cause acidosis and indigestion. Reduction of pH below 6 reduces the activity of fibrolytic organisms, favours the domination of the rumen by acidophilic bacteria, and interferes with the digestion of **roughages**. Rumen microflora concentration tends to be lowest 2–4 h post-feeding and gradually increases until 16 h post-feeding. Increasing feeding frequency can reduce this effect.

Young ruminants acquire their microflora early in life through their contacts with adults and the environment generally. In calves, **cellulose** fermenters are detectable by 1–3 weeks old with most species being established by 6–9 weeks.

Rumen bacteria represent the largest population of microflora in the rumen. The concentrations of bacteria may be as high as 10^9–10^{10} ml^{-1} of rumen contents and may comprise up to 200 species. These bacteria are simple unicellular organisms that reproduce by fission. Many of the rumen bacteria are ciliate and motile. The majority of them are found attached to or contained inside food fragments. They can be classified by their principal digestive activities as in the examples given in Table 1. However, rumen digestive function is the total of the activity of many species. For example, many species in isolation will attach to cellulose particles and digest them slowly. The same organisms in cultures combined with non-cellulolytic organisms will deliver greatly

increased rates of digestion. An example of this is *Fibrobacter succinogenes*, which has a much brisker action in the presence of *Butyvibrio* species.

Table 2. Ciliate protozoa species.

Family	Genera
Isotrichidae (Holotrichs)	*Isotricha*
	Dasytricha
Ophryoscolecidae (Oligotrichs)	*Entodinium*
	Diplodinum
	Epidinium
	Ophryoscolex

Archaea are the second most abundant class, about 10^8 ml^{-1}. They are all methanogens and are responsible for the production of **methane** from H and CO_2 which are produced by other rumen organisms.

Ciliate protozoa are present in the **rumen fluid** in bulk equal to that of the bacteria, in concentrations of about 10^6 cells ml^{-1}. The many species come from two families, the Isotrichidae and Ophryoscolecidae (Table 2). Their interaction with rumen bacteria is complex, and their importance in rumen digestion is still debatable. *Ophryoscolecidae* protozoa engulf and digest bacteria, their main **nitrogen** source, in vast numbers and are the major cause of microbial turnover. This may account for the increased flow of nitrogen to the **duodenum**, and lower rumen **ammonia**

concentrations in rumen liquor, in defaunate animals. They also ingest **starch** granules, which reduces their exposure to amylolytic bacteria, protects the host against **lactic acidosis** and promotes bacterial cellulolysis. Methanogenic archaea adhere to protozoa around the hydrogenosomes and promote their digestive activity by removing accumulations of hydrogen.

Table 1. Average milk composition of different species

	Percentage composition				
Species	**Water**	**Fat**	**Protein**	**Lactose**	**Ash**
Buffalo	82–84	7.0–11.0	3.3–3.6	4.5–5.0	0.8
Cow	85–87	3.7–4.4	3.2–3.8	4.8–4.9	0.7
Goat	87–88	4.0–4.5	2.9–3.7	3.6–4.2	0.8
Sheep	79–82	6.9–8.6	5.6–6.7	4.3–4.8	0.9
Human	87–89	3.3–4.7	1.1–1.3	6.8–7.0	0.2

Source: Jilo (2016)

Rumen fungi are strict anaerobes that are chiefly found colonizing lignocellulose, indicating their ability to degrade plant components. They are capable of utilizing all plant polysaccharides other than pectin and polygalacturonic acid. They produce motile zoospores, about 10^3–10^4 ml^{-1}, which swim in the rumen liquid phase. These attach to and penetrate plant particles and form sporangia, which complete the life cycle by releasing zoospores. The vegetative phase is substantial, representing about 8–12% of the undegraded **dry matter** in the rumen. They are most

abundant in animals fed on **roughage** diets, and can be absent on low-fibre diets, indicating that they are not necessary for the survival of the rumen system.

There are three morphological types and at least 12 species are found in the rumen. Notable among these are *Neocallimastix frontalis*, *N. patriciarum*, *Orpinomyces bovis* and *Piromyces communis*.(JKM; GMcLD)

See also: Gastrointestinal microflora

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Rumen volume

The volume of the **rumen** plus **reticulum** can be measured most practically by emptying out and weighing the content, either at slaughter or via a rumen fistula. It varies somewhat with feeding habit, from about 13% of body weight in **grazing** ruminant species to 9% in browsers. It can vary more greatly between breeds, reaching 20–30% in cattle and sheep accustomed to eating **straw**. A large rumen volume permits a large intake of **roughage** together with prolonged retention and **fermentation** of fibre in the reticulorumen. (RNBK)

Further reading

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Ruminally available nitrogen (RAN)
Feed nitrogen or recycled **urea** nitrogen which is available to **rumen microorganism**s for synthesis into microbial **amino acid**s. RAN can be derived from the degradation of **feed protein** followed by amino acid **deamination** releasing **ammonia**. Alternatively urea can be hydrolysed to ammonia and CO_2 by microbial **urease**. (GMcLD)

Ruminant animals
(**sheep, cattle, goats, water buffalo, alpaca, llama and others)**Ruminants are members of the order Artiodactyla and include the Bovinae, Cervinae and other classes which include, for example, antelopes and giraffes. Their defining characteristic is that they have a highly developed four-compartment foregut **digestive system**. This involves a complex **stomach** (*see* Abomasum; Omasum; Reticulum; Rumen) with an enlarged reticulorumen to accommodate the bulk of their typically fibrous **diet**; a population of symbiotic **microorganisms** in the **reticulum** and **rumen** (*see* Rumen microorganisms) which are able to ferment plant structural **carbohydrates** (*see* Dietary fibre); and a rumen physiology which allows **rumination** and eructation. Ruminants are not the only animal class that has evolved a system of **foregut** fibre **digestion**, but they have developed this to a greater degree than any other **herbivore**.

Mammalian digestive systems (i.e. the **enzymes** and associated substances that aid digestion which are secreted into or are present in the **abomasum** and **small intestine**) are unable to digest structural carbohydrates (complex **polysaccharide**s) from plant materials. Nevertheless, ruminants generally consume diets with a large proportion (80–100%) of highly fibrous plant materials (**roughage** diets). In their rumen and reticulum, ruminants host a large population of **rumen microorganism**s – archaea, bacteria, **protozoa** and **fungi**. These microorganisms play a major role in the degradation of fibrous feed materials, producing **volatile fatty acid**s and **microbial protein** that provide a source of **energy** and **amino acid**s to the host animal. Ruminal microbes can also synthesize certain B **vitamins** and convert **non-protein nitrogen** sources into **microbial protein**. As the ruminant chews its prehended feed, its salivary glands add **saliva** to the feeds to form a bolus and to **buffer** the **pH** of the rumen and reticulum. Rumen microorganisms and the partially degraded (or digested) **digesta** pass through the last compartment of the stomach (abomasum) into the small intestine and **large intestine**, where further digestion and **absorption** of **nutrients** by the host animal occurs.

The anatomical and functional attributes of the small intestine (**duodenum**, **jejunum** and **ileum**) of ruminants are similar to those of non-ruminants, but they vary in length between approximately 12 and 30 times the body length of the animal. Microbial digestion also occurs in the large intestine (**caecum** and **colon**) of ruminants, but the extent and nutritional importance of

this is much less than is the case with hindgut fermenters – non-ruminant herbivores such as horses, **rabbits**, etc. – which have very large caeca and colons.

Ruminant animals can convert pasture, fodders, **silage**, **hay**, crop residues, brewery waste and some agricultural industry **by-product**s into valuable products. These include **meat**, **milk**, offal, **wool** and leather. Understanding the nutritional requirements and dietary regulations of ruminant animals is important to optimize animal performance and the quality of the final product. Numerous studies have investigated the effect of feeding systems and **feed** composition on the yield and composition of meat and milk from ruminants. The overall chemical, physical and sensorial quality, nutritional attributes and certain safety aspects of meat and milk are determined by the amount and type of **fats**, proteins, **minerals**, **vitamins** and bioactive compounds in the **diet**. The impact of these dietary elements is contingent on farm animal management practices, genetics and processing technologies and nutritional backgrounds. Of these, nutritional background is especially important, as it can alter the level and composition of fat and therefore the sensory properties of the products from ruminants.



Ruminants, such as this alpine cow, have a unique ability to digest the fibre in plant materials. They possess a large fermentation vessel, the rumen, which is filled with microorganisms – bacteria, protozoa and fungi mainly. Periodically they eructate boli of feed into the buccal cavity where it is chewed extensively and then returned to the rumen by swallowing. Photo courtesy of Julien Carnot. Licensed under CC BY-SA 2.0.

When the diets of **grazing** ruminants are low in **protein** or **energy** concentration, for example when animal production occurs in dry regions or seasons, it is common to add **supplement**s to the basal **diet**. These include silage, **legume** seeds and **cereal grain**s and non-protein **nitrogen** sources and **mineral** sources that are collectively used to increase the meat and milk production of the entire flock or herd. Such strategies can alter the physiochemical properties, nutritional attributes and sensory characteristics of meat and milk produced.

Nutritional interventions can change the eating quality, nutritional value and sensory attributes of ruminant animals' meat. It is expected that the practicality and effectiveness of these strategies will drive future investigation and the next generation of

insight into the pathways for nutritional-based enhancement of **meat quality**. In this pursuit, the fundamental action of any diet should not be forgotten, which is to support the growth and metabolic processes of these species with the provision of essential macro- and micro-nutrients so that the nutritional attributes and product quality are maintained from slaughter until the point of consumption of **meat** and their secondary or tertiary processed products. (ENP; HP; JKV; AK; BWBH; GMcLD)

Further reading

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Ruminant feeding

In most situations the major objective in feeding ruminants is to maximize voluntary intake. Only in a few specific situations is there a need to limit **feed intake** (for example, the pregnant beef breeding (suckler) cow in winter, when there is a modest loss of body weight, which is regained subsequently at pas ture). Failure to maximize **voluntary food intake** is the most common cause of suboptimal productivity in ruminant livestock. Thus the most important nutritional requirement of the ruminant animal is that for intake of **dry matter** (DM). Provided that the food is of sufficient quality, the animal's requirement for **energy** should be met, followed by those for **protein**, major **minerals**, **trace element**s and **vitamins**. The challenge to nutritionists is to be able to predict with accuracy the food intake of the animal in a range of dietary situations.

To maximize the potential voluntary food intake, all ingredients should be free of contaminants and offered *ad libitum* at least once daily with adequate access to food and fresh water at all times. Changes in diet composition should be made gradually, to avoid digestive upsets. To realize potential food intake, the **rumen** microbial population should be encouraged to grow as rapidly as possible by being provided with both available protein, from which the microorganisms can derive **ammonia** for **protein synthesis**, and available energy. The rumen environment should be conducive to the **digestion** of plant cell wall material, since in most situations the supply of nutrients to the microbial population is in the form of herbage and other plant material. When poor-quality plant material is offered, the animal should be given the opportunity to select the most acceptable parts and to reject unpalatable material.

Diets for productive ruminants usually comprise two different types of food: forages and concentrates. This distinction is historical and reflects the fact that traditionally most forages were relatively low in energy and protein and were digested slowly in the rumen. Most concentrates, on the other hand, were relatively high in energy and protein and were digested rapidly in the rumen. Today the division of foods into forages and concentrates can be confusing, since the nutritional specification of some forages, such as young pasture **grass**, clover and **maize** (corn) **silage**, may be similar to that of many concentrated foods. It is better to consider dietary ingredients in terms of their major nutrients, e.g. **starch**, **sugar**, **cellulose**, protein or **lipid**.

Diet formulation for ruminants involves meeting the

requirement of the animal within the specific nutritional constraints of optimizing rumen function and avoiding major nutrient imbalances. Thus diets are normally formulated to contain at least 400 g neutral detergent fibre (NDF) kg^{-1} DM to ensure adequate slowly digested plant cell wall material for **fermentation** in the rumen. If the animal's requirement for energy is particularly high and the concentration of NDF is less than 400 g kg^{-1} DM, then a source of long fibre, or effective NDF such as **hay**, must be included in the diet to stimulate **rumination** and **saliva** production. Total starch and sugar should not exceed 300 g kg^{-1} DM. Effective rumen degradable protein (ERDP) should match the supply of fermentable **metabolizable energy** (FME). The optimal balance for microbial digestion is 11 g ERDP MJ^{-1} FME.



Mechanical feed distribution is commonly used in intensive livestock units. Photo courtesy of USDA government. No copyright.

All dietary ingredients, especially those produced on the farm, should be analysed routinely to determine their composition and adjustments to the formulated diet should be made accordingly. Weekly analyses should be linked to reformulation twice a month, and monthly analyses to reformulation once every 2 months to allow systematic changes in composition to be distinguished from random variation.

Feeding systems comprise grazing, self-feeding of conserved forages and trough-feeding of mixtures of forages and other materials. Dairy cows are often fed at the time of milking in a stall or milking parlour. **Grazing** may be free-range or controlled in paddocks. Range pastures are normally grazed continually for many months and the herd or flock is allowed to roam over large areas to select food. The animals are gathered at specific times of the year for the **weaning** of young, shearing (in the case of sheep) and disease control.

In controlled grazing situations the supply of herbage is usually more abundant and access to new pasture may be adjusted on a daily basis, in an attempt to match supply with requirement. Thus at times of rapid pasture growth in spring or at the start of a **rainy season**, the area of land allocated to the herd or flock is reduced, and increased later in the grazing season when the amount of herbage dry matter per hectare, or its daily rate of growth, is reduced.

Herbage surplus to requirements is conserved either as hay or

as silage. Storage of conserved **forage** may be adjacent to, or above, the winter accommodation so that the handling of winter forage is simplified as far as possible. Silos may be built immediately next to the housing for the animals to self-feed the forage directly from the exposed silo face.

Trough-feeding is the most common feeding system on intensive livestock units. The trough should be easily accessible from the animals' lying area and also accessible to machinery for daily replenishment. Troughs should be cleaned out daily to remove rejected food which, if left, deteriorates and reduces the acceptability of new food that may be placed on top and mixed with it. Forage may be the sole food offered in the trough, with concentrates offered as a compounded pellet in the milking parlour, or via a separate food container elsewhere in the animal house. Alternatively, a mixture of foods may be offered in the trough as a **total mixed ration**. Voluntary food intake, but not the efficiency of food utilization, may be increased by offering the diet as a total mixed ration compared with offering the forage and concentrate part of the diet at separate times of the day or via separate routes of delivery.

Conserved forages and **by-product**s such as brewers' **grain**s and **straw** may be offered as a '**buffer** diet' to rectify deficiencies in the grazed pasture. The specific composition of the buffer diet should be formulated to match the nutrient deficiencies of the grazed pasture. Thus, if the pasture is **legume**-based or comprises very young leafy grass and is high in protein, a low-protein buffer diet should be offered. If on the other hand the deficiency is simply

a shortage of available pasture, then the buffer diet should be fully balanced for all major nutrients. (JMW)

See also: Beef cattle production systems; Dairy cattle production systems; Goat feeding; Sheep feeding

Ruminants, effects of nutrition on milk yield and composition

Composition is the primary concern in determining **milk** quality, which is an essential quality and economic parameter in dairy processing. Milk composition is affected by several factors, such as nutrition, genetics, environmental factors, **parity** and management practices. Among them, animal nutrition is vital in determining milk composition and yield. Thus, feed types and feeding strategies in dairy farming require special attention. Many studies have been conducted to elucidate the effect of feeding systems, feed types, and feed composition on milk yield and milk composition of dairy cattle, goats and water buffalo. Varying feed sources and efficient feeding management in dairy animals is also widely accepted as a strategy for enhancing profit margins and sustainability in dairy farming. Moreover, interest is growing in altering milk nutritional components for the well-being of consumers. The inclusion of non-conventional feedstuffs into ruminant diets is thus gaining popularity as a strategy to enable **climate**-smart livestock production, particularly under prolonged drought and hot conditions.

Nutrition effects on milk yield and composition

The impact of the nutrition can be both via short-term (daily)

nutrient intake and by carry-over effects influenced by changes to the **body condition** of dairy cows. The **nutrient requirement** of dairy cattle varies according to their milk production, stage of **lactation**, age, body size, health condition, stage of pregnancy, etc. Therefore, it is necessary to pay attention to the amount of feed given and its composition and nutrient value. Like all other animals, dairy cattle require **carbohydrates**, **proteins**, **fat**, **vitamins** and **minerals** from feeds for general **maintenance** and production (both pregnancy and lactation) purposes. The end-products resulting from microbial **fermentation**, **digestion** and **absorption** of these dietary nutrients are later utilized to synthesize milk components, i.e. milk proteins, milk fat, **lactose** and minerals in mammals (Table 1).

Table 2. Typical rumen bacteria, their energy sources and fermentation products *in vitro*

		Typical fermentation products					
Species	Typical energy source	**Acetic**	**Propionic**	**Butyric**	**Lactic**	**Succinic**	**Formic**

Species	Typical energy source	Typical fermentation products					
		Acetic	**Propionic**	**Butyric**	**Lactic**	**Succinic**	**Formic**
Fibrobacter succinogenes	Cellulose	+				+	+
Ruminococcus flavefaciens	Cellulose	+			+	+	+
Ruminococcus albus	Cellobiose	+					+

Species	Typical energy source	Typical fermentation products					
		Acetic	**Propionic**	**Butyric**	**Lactic**	**Succinic**	**Formic**
Streptococcus bovis	Starch				+		
Prevotella ruminicola	Glucose	+				+	+
Megasphaera elsdenii	Lactate	+	+	+			
Lachnospira multipara	Pectins	+			+		

Digestion of carbohydrate in ruminants to produce milk fat and lactose

The primary sources of carbohydrates (CHO) in the ruminant diet are **roughages**. Main CHO forms in a ruminant feed include structural CHO, which consist of around 50–85% of dry matter (DM) (e.g. **cellulose** and **hemicellulose**) and storage CHO (e.g. **starch** and soluble CHO, mostly **fructans**). Since there are no mammalian endogenous **enzymes** that can digest structural CHO, both ruminants (in the **rumen**) and hindgut fermenters (in the **caecum**) have developed a symbiotic relationship with microbes such as bacteria, ciliate protozoa and fungi, which have the required enzymes (microbial β-**glycosidase**s) to degrade structural CHO. The **volatile fatty acid**s (VFA) are formed by a two-step process that is due to the **metabolism** of **glucose** into **pyruvate** via **glycolysis** and conversion of pyruvate into VFAs, such as **acetate**, **propionate**, **butyrate**, **lactate** and other VFAs (Dryden, 2008). **Lignin** is a component associated with CHO, which is not digested by ruminal microbes. Generally, young pastures are rich in soluble CHO and contain less structural CHO. They have less lignin, resulting in about 80% **digestibility**, as CHO digestion depends on the degree of lignification. Carbohydrate digestion in ruminants consists of two phases: (1) breakdown of complex CHO into simple **sugars**; and (2) production of VFAs using simple sugars by ruminal microbes through fermentation (Table 2).

Fermentation of digestible fibre (cellulose and hemicellulose) results in VFAs such as acetic acid and butyric acid, which are later

utilized to synthesize milk fat. The fermentation of starch and sugars yields **propionic acid**, which converts to **glucose** in the liver via **gluconeogenesis** (see Fig. 1), and is later utilized to synthesize milk **lactose**. The gases (CO_2, CH_4, H_2) produced by the microbial fermentation and biohydrogenation process expel via eructation (30–50 l h^{-1}).

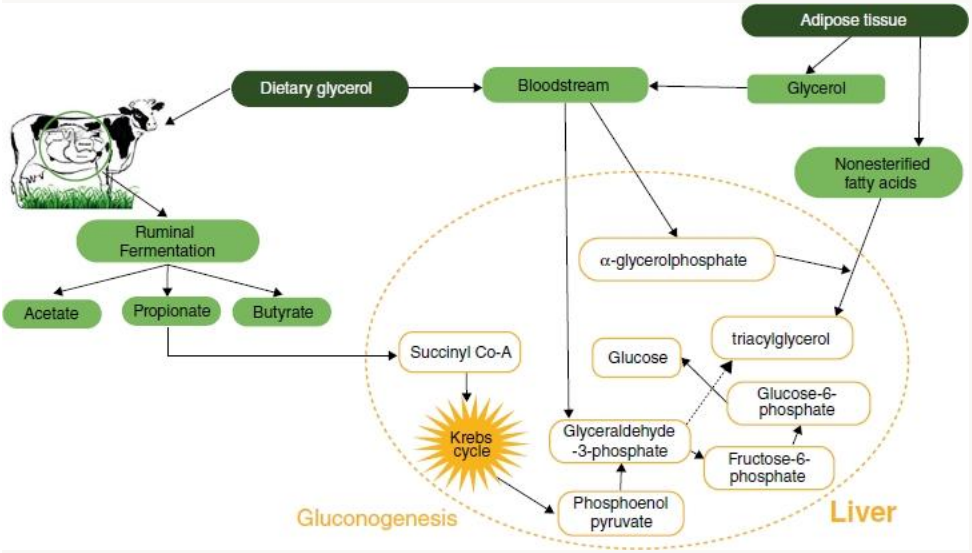


Fig. 1. Pathways of glycerol transfer/metabolism and liver gluconeogenesis in dairy cows.
Adapted and modified from Kupczynski *et al*. (2020).

Digestion of protein and non-protein nitrogenous (NPN) compounds in ruminants to produce milk proteins

Ruminants are largely independent of the dietary supply of **amino acid**s (AA), as rumen microbes can produce all the essential AA required, although high-yielding dairy cows may respond to rumen-protected **methionine** supplements. Most of the dietary proteins (rumen degradable intake proteins (RDIPs)) and NPN compounds are converted into **microbial protein**s in the rumen and then digested by proteolytic enzymes at the **abomasum** into

AA and small peptides (see Fig. 2). However, rumen undegradable intake proteins (RUIPs) (or bypass proteins or **protected proteins**) are directly passed into the abomasum and **small intestine** for endogenous proteolytic enzymatic digestion. These AAs are later utilized for the synthesis of milk proteins (Dryden, 2008).

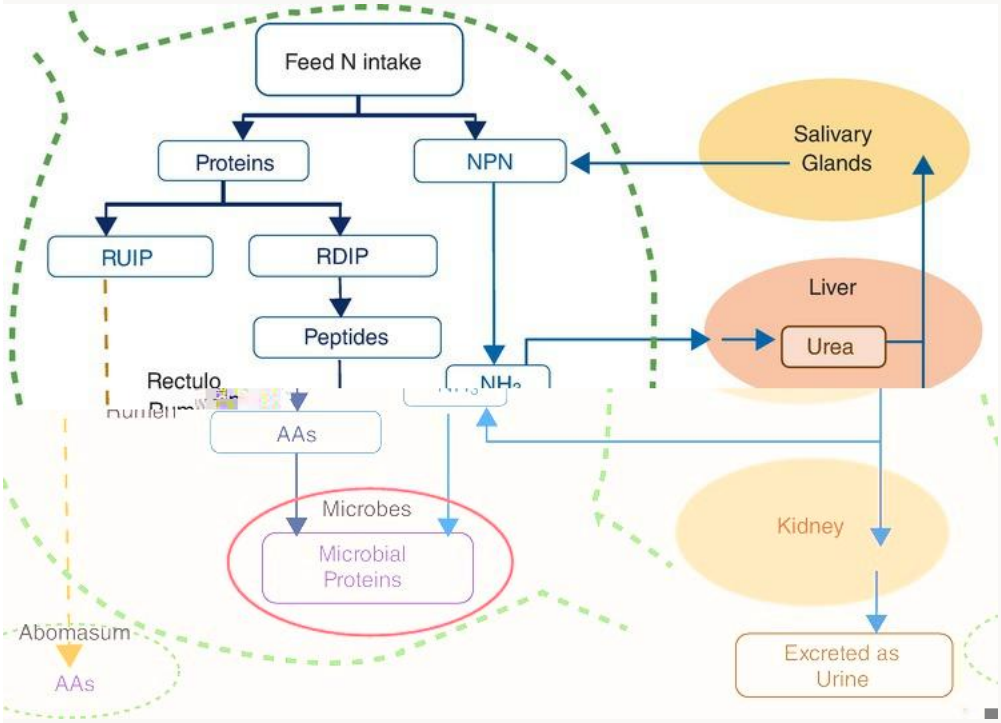


Fig. 2. Digestion of proteiin and NPN compounds in ruminants. Source: the authors.

Digestion of lipids in ruminants to produce milk fat

The dietary **lipids** can be **glycerol** (mainly **triacylglycerol**, **phospholipid**s and galactoglycerides) or non-glycerol-based (**free fatty acid**s). Most of these are fats (high melting point) or **oils** (low melting point) of animal or plant origin, respectively, or **glycolipid**s (galactoglycerides), which are predominantly found in forages. Up to around 10–30% of dietary lipids could be digested by pre-intestinal salivary or gastric **lipases** secreted from the cells

in the tongue, pharynx and **stomach**; the rest is mainly digested by pancreatic lipases. The most common end-product of lipase digestion of lipids is 2-monoacylglycerols (Dryden, 2008). The ruminal biohydrogenation (BH) process is also responsible for the alteration of dietary **fatty acid**s (FAs) in the rumen, with decreasing of the proportion of **unsaturated fatty acid**s (USFAs) and the formation of numerous unsaturated **isomer**s. Ruminal microorganisms hydrolyse triacylglycerols, ferment glycerol and hydrogenate double bonds within carbon chains of USFAs to minimize toxic effects of **polyunsaturated fatty acid**s. The branched-chain volatile fatty acids such as **butyrate**, iso-butyrate, valerate and iso-valerate are incorporated into ruminal bacteria, where they could act as the precursors of **long-chain fatty acid**. Most fats in ruminant diets contain C18 polyunsaturated fatty acids. In the rumen, C18 fats are hydrolysed by bacterial lipases releasing USFAs. These USFAs are biohydrogenated by bacteria into **stearic acid** (**saturated fatty acid**) and subsequently absorbed in the small intestine. Finally, these fatty acids are used to synthesize milk fats. However, the ability of ruminal microbes to digest fats and oils from feeds is limited. Thus, regular ruminant diets are low in fats (< 40 g kg^{-1} DM). Feeding diets high in fats (> 60 g kg^{-1} DM) may decrease ruminal microbial activity, fibre fermentation and **feed intake**, thus reducing milk quality and yield.

Biosynthesis of milk components

Lactose is the major milk sugar derived from glucose and **galactose** and the least variable component in milk. Lactose biosynthesis occurs in the Golgi apparatus in **mammary gland**s,

and the only precursor is **blood** glucose. Nearly 45–60% of this blood glucose comes from gluconeogenesis. Lactose synthetase, composed of two proteins (galactosyltransferase and α-lactalbumin), is responsible for lactose biosynthesis, and they appear just before parturition in the circulatory system and increase dramatically with lactation. Lactose is the major osmole in milk and cannot diffuse out of the Golgi membrane. Therefore, water is osmotically drawn into the Golgi to dilute the lactose and this determines the milk volume.

Milk proteins are one of the essential constituents in milk. Milk proteins consist of 80% **casein** proteins and 20% are **whey protein**s. Whey proteins are the most variable protein constituent among species. All milk proteins (αS1-casein, αS2-casein, β-casein and κ-casein) except serum **albumin**s, γ-caseins and immunoglobulins are synthesized in mammary epithelial cells from free AAs, peptides and plasma proteins extracted from the blood. Synthesized proteins are secreted into the lumen by secretory vesicles as clusters (micelles). Immunoglobulins and other pre-formed proteins are directly taken up from the basal lateral membrane and secreted to the lumen via the apical membrane.

Milk fat consists primarily of triacylglycerols (98%) and is the most variable component in milk. Triacylglycerols can be either saturated or unsaturated and vary in length based on carbon numbers. They can be further classified as short-chain, medium-chain or long-chain fatty acids. The rest of the milk fat includes monoacylglycerols, diacylglycerols, phospholipids, **cholesterol**s, **free fatty acid**s and cholesterol esters. Moreover, structural

carbohydrates such as cellulose are converted to **acetate** and **butyrate** (which is converted to β-**hydroxybutyrate** in the rumen wall) upon digestion and absorption, which enter the bloodstream and finally can be utilized to synthesize milk fats (Dryden, 2008). In many ruminants, most of the C4 to C14 and nearly half of the C16 fatty acids are synthesized *de novo* in the mammary glands from acetic acid and β-hydroxybutyrate, whereas long-chain fatty acids (mainly C18) are moved and absorbed into the intestine and subsequently translocated into milk triacylglycerols. The origins of the lipids for milk **fatty acid synthesis** are shown in Fig. 3.

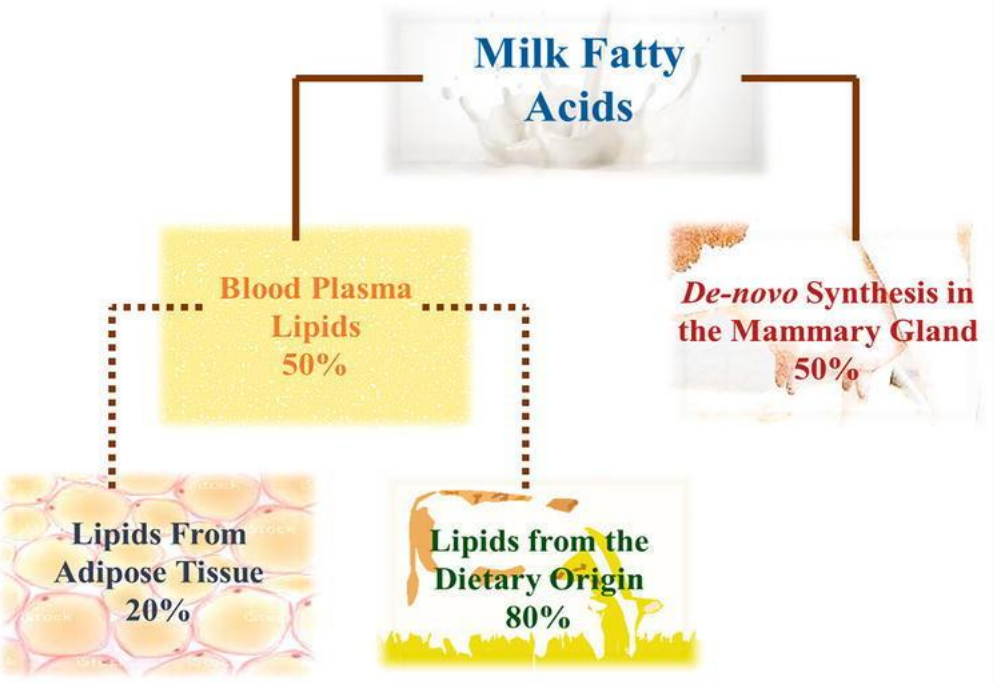


Fig. 3. Origins of the lipids for milk fatty acids synthesis. Source: the authors.

De novo synthesis of fatty acids occurs at the cytoplasm of mammary glands. The first step in *de novo* synthesis is the acetyl-CoA carboxylation derived from acetic acid and butyric acids. The resulting malonyl-CoA reacts with acetyl-CoA and forms C4

molecules in the next step. Then the chain elongation occurs, resulting in fatty acids, and the elongation generally stops at C16. Triacylglycerol synthesis occurs at the cytoplasmic surface of the smooth endoplasmic **reticulum** of mammary glands. Here the fatty acids are esterified to the hydroxyl groups of the glycerol molecules, and inside the mammary epithelial cells the triacylglycerols coalesce and form micro lipid droplets. The micro lipid droplets fuse to form larger droplets and are secreted into the lumen and incorporated into milk.

Mineral composition in the milk can vary from 0.2% to 2.0%. **Potassium** (K), Ca, Na and Mg are major cations found in milk; and citrate, phosphate, **chloride**, carbonate and **sulphate** are major anions. They can be found in the colloidal phase and serum phase. **Iron** (Fe), Zn, Cu, Mn, Se, I, Mo, Co, Cr, and Ni are microminerals found in milk in small quantities. **Aluminium** (Al), As, Pb and Hg are also in milk in minute concentrations and act in a buffering capacity. Milk vitamins are not synthesized in the mammary gland. They are absorbed directly from the blood originally sourced from the dietary means or synthesized in the body. Milk is a rich source of **vitamin A** and **B-complex vitamins** and contains a small amount of **vitamin C** and **vitamin D**. However, only a trace amount of **vitamin E** and **vitamin K** can be found in milk.
Since every nutrient directly affects milk component biosynthesis, and therefore the milk composition and yield, it is necessary to practise good feeding management and maintain optimum nutrition to obtain maximum production. (HP; JKV; HTMH;

ENP)

See also: Dairy cow feeding systems; Dairy cow milk production and milk composition; Dairy cows, feeding strategies to improve milk production and composition

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Rumination

The regurgitation of reticulorumen content to the mouth for further **chewing**. Periods of rumination last for 10–30 min, sometimes longer on coarse **roughage** diets. At intervals of about 1 min, a bolus of **digesta** is aspirated into the thoracic oesophagus during vigorous reticular and abdominal contractions combined with thoracic expansion. The bolus is transported to the mouth by reverse **peristalsis**, chewed and ensalivated, then swallowed to mix again with the contents of the reticulorumen. Also known as ‘chewing the cud’ or ‘cudding’. (RNBK)



Cows ruminate to break down feed into particles that can be swallowed and to add saliva prior to swallowing. Photo courtesy of Jim Champion. Licensed under CC BY-SA 2.0.

See also: Particle size; Rumen digestion

Ruminoreticular groove
A gutter-shaped structure that runs in the walls of the **rumen** and **reticulum** from the cardiac sphincter of the oesophagus to the reticulo-omasal orifice. Analogous structures are found in camels and other species that ferment food in a forestomach. Contraction of the muscular lips of the groove shortens and closes the groove, apposing the cardiac and reticulo-omasal orifices, so that swallowed fluid is conducted directly from oesophagus to **omasum**. Closure occurs reflexly during the **sucking** of **milk** by the young ruminant from its dam. Consequently the milk passes directly to the omasum and abomasum, bypassing the reticulorumen and so avoiding microbial **digestion**. The animal can be trained to drink milk or other fluids from a nipple-bottle or

trough so as to elicit reflex closure of the groove, which becomes conditioned to respond to the person and circumstances normally associated with feeding; this response can be maintained into adult life. The groove can also be caused to close by dosing with fluids containing **copper sulphate**, allowing drugs to be dosed directly to the **abomasum**. (RNBK)

Runt
A pig that is of small body size relative to others of its litter or age group. This results from growth retardation caused by poor nutrient supply or utilization at any stage of life. It can occur in the uterus during fetal development, during the **suckling** period if an adequately yielding teat is not accessible, or during later life if social competition limits feed access or ill-health stunts growth. (SAE)

Rye (*Secale cereale*)
A **cereal** grown predominantly in parts of Europe and North America, generally where **climate** and soil are unfavourable for other cereals or as a winter crop where temperatures are too low for winter **wheat**. The plant, which thrives at high altitudes, has the greatest winter hardiness of all small **grain**s and grows to a height of 1–2 m. Flower spikes comprise two or more spikelets that bear the florets, which develop into single-seeded fruits, or grains.



Rye, a hardy cereal at low temperatures that is used for both livestock feed and human food. Photo courtesy of Susanne Nilsson. Licensed under CC BY-SA 2.0.

Rye is the only cereal grain other than wheat to have the necessary properties for bread making. However, rye **flour** is inferior to that of wheat since it lacks the necessary elastic properties for baking. For this reason, rye and wheat flours are frequently blended for baking purposes. Rye grain is also used for making whisky, particularly in the USA. Rye has a similar **nutritive value** to wheat grain, being rich in **carbohydrates** and providing small quantities of **protein**, **potassium** and B **vitamins** (see table). The **amino acid** profile of rye is similar to that of wheat, slightly higher in the essential amino acid **lysine** but lower in **methionine**.

Chemical composition of rye grain and forages (as g kg^{-1} dry matter unless specified). (Sources: MAFF, 1990, *UK Tables of Nutritive Value and Chemical Composition of Feedingstuffs*; Piccioni, M., 1989, *Dizionario degli Alimentii per il Bestiame*, 5th edn, Edagricole, Bologna, Italy.)

Product	DM (g kg^{-1})	CP	EE	Starch	NDF	CF	Ash
Grain	869	119	12	–	357	20	18
Forage	223	26	8	–	–	76	17
Hay	913	67	21	–	–	325	50
Silage	303	35	10	–	–	108	25

CF, crude fibre; CP, crude protein; DM, dry matter; EE, ether extract; NDF, neutral detergent fibre

Like wheat, rye grains should generally be crushed or coarsely ground for feeding to livestock, though whole grains are often fed to sheep. The use of rye grains in animal production is similar to that of **barley** but it should be mixed with other cereals for most livestock, in order to avoid digestive disturbances. Sheep can be fed rye grain alone as the entire concentrate **supplement**. Coarsely ground rye can be included to about 40% of the total **compound feed** for dairy cows while maintaining the same level of performance as seen with barley and **maize**. Growing cattle can receive coarsely ground rye as part of a cereal mixture including maize, **oats** and barley, while pre-ruminant and ruminant calves can be fed rye meal mixed with **linseed** meal and wheat **bran**. Rye can be fed to horses as a replacement for oats and can be fed at levels of 3 kg per head per day without digestive disturbances. Growing pigs can be fed rye (**digestible energy value** 15.3 MJ

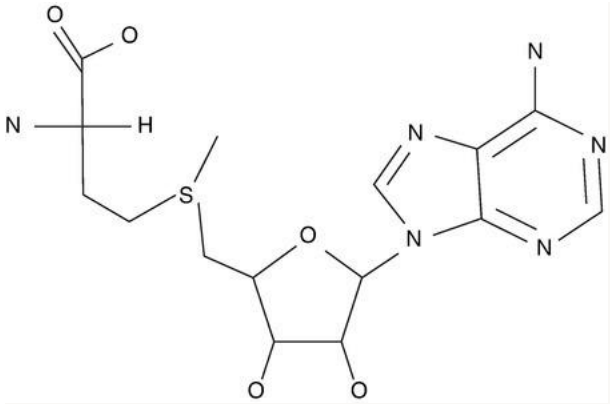
kg^{-1} dry matter) in a mixture with other cereals up to 0.1–0.2 of total daily intake. Rye is not given to poultry, because of **appetite**-depressing and growth-depressing factors in the bran and whole grain, respectively.

In addition to providing grain, rye is also grown as a **forage** and is particularly important in the spring. Forage rye is very palatable and has a higher **digestibility** than fresh **grass** pasture. Preserved as **silage**, it can be fed to dairy cows up to 40 kg per head per day, but mixing rye and maize silages is generally recommended to achieve the best levels of production. (ED)

S

S-Adenosylmethionine

Often abbreviated to SAM, this compound ($C_{15}H_{22}N_6O_5S$, molecular weight 398.4) is not a component of protein. It is synthesized when **methionine** is adenylated by ATP. *S*-Adenosylmethionine functions as the most important donator of methyl groups and is essential for the conversion of **putrescine** into spermidine and spermine in the body. (DHB; GW)



Safety factor

A safety factor (normally 5–10%) is usually incorporated in calculating nutrient allowances from **nutrient requirement**s to take account of animal variability and unforeseen environmental factors. A much larger safety factor is included if data is obtained from a different species, for example in toxicity estimations. (KJMcC; CJCP)

Safflower

Also known as bastard saffron, safflower (*Carthamus tinctorius*) belongs to the Asteraceae. It is an annual broad-leaved plant with a thistle-like appearance and orange to yellow flowers.



Safflower is rich in linoleic oil and oleic acid. Photo courtesy of CGWF.

Licensed under CC BY ND 2.0.

The crop flourishes in dry conditions. Historically the importance of safflower was the use of the dye (carthamin) within its flowers to colour food and clothing red or yellow. Currently the primary product of this crop is the edible **oil** derived from the seeds, which contain up to 45% oil and are comparatively rich in **vitamin E**. Varieties have been developed with high levels of **linoleic acid** (up to 75% – considerably higher than other vegetable oils). Uses for this linoleic-rich oil are primarily for salad oils and non-dairy spreads. Other safflower varieties are rich in **oleic acid**. The uses for this heat-stable oil are either as a cooking oil or as an industrial oil. After processing, the meal or cake that remains is used as a **protein supplement** for livestock. The crude meal contains approximately 24% protein, the decorticated meal 40%. After harvesting, the stubble can be grazed profitably by ruminant livestock. The seeds also contribute to birdseed products. (DA)

Sago

An edible starch extracted from the pith-like centre of several South-east Asian palms, chiefly *Metroxylon sagu*.



Sago palm (*Cycas revoluta*). Photo courtesy of Brewbooks. Licensed under CC BY SA 2.0.

Sago is obtained by grinding the inner stem content of fully mature (12-year-old) sago palm that is beginning to flower. The starch is extracted with water and dried. Sago is an important part of the human diet in some parts of East Asia. The sago pith, or rasps, is obtained by mechanical rasping of the barked sago trunks. The sun-dried rasps can be fed to cattle and older pigs and it has been included at < 50% in pig diets and < 25% in poultry diets. Feeding higher levels of sago rasps decreases production and reduces **feed conversion** efficiency. The dry matter (DM) content of rasps after **starch** extraction is 773 g kg^{-1} and the nutrient composition (g kg^{-1} DM) is **crude protein** 27, **crude fibre** 101, **ash** 210, **ether extract** 3 and NFE 659, with ME 10 MJ kg^{-1}. (JKM)

Sainfoin (*Onobrychis viciifolia*)
A leguminous perennial herb of the family Leguminosae (pulse family) indigenous in southern Europe and temperate western Asia.



Sainfoin (*Onobrychis viciifolia)* grows well in calcareous soils. Photo courtesy of Matt Levin. Licensed under CC BY-SA 2.0.

It is cultivated widely as a **forage crop** for its high **protein** content (*c.* 240 g kg^{-1} dry matter) and its ability to thrive on calcareous soils too dry or too barren for clover or **lucerne** (alfalfa) but is of less economic importance than lucerne. In the UK it is confined to a few areas in the south-east. The high feed value of the **hay** makes it a good feed for racehorses. The aftermath of hay production is very good for **fattening** lambs. As in other forages, the leaf contains higher levels of protein, **ether extract**, **calcium** and other minerals than the stem and so the composition of the plant is greatly affected by the increasing proportion of stem to leaf as the plant matures. The protein content declines rapidly at

flowering, with a subsequent increase in fibre content. (JKM)

Sal seed (*Shorea robusta* Gaertn.)

The seed of the sal tree, used for oil extraction. The oilcake, although high in **tannins** (8–14%) which render the **protein** indigestible, is a valuable **energy** component. It can be included up to 20% in ruminant rations and up to 10% for non-ruminants. Replacement of **maize** in pig rations by de-oiled sal seed meal has been reported in India for finishing pigs. Tannin levels can be reduced by treatment with 0.1 M NaOH, which allows higher levels of inclusion in rations. (LR)

Nutrient composition of sal seed (% dry matter).

	CP	CF	Ash	EE	NFE	Ca	P
Sal seed meal	8.6	1.3	3.1	2.5	84.4	0.20	0.20

CF, crude fibre; CP, crude protein; EE, ether extract; NFE, nitrogen-free extract.

Further reading

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Saliva

A highly viscous fluid containing **salts** and mucoproteins secreted from the salivary glands into the mouth. The salivary glands

represent a network of accessory structures, each of which drains into a main gland that opens into the mouth. The network includes three pairs of major glands: **parotid gland**s (located under the ears), lingual glands (located in the base of the tongue) and mandibular (or submaxillary) glands (between the other pairs). Minor glands in the tongue and buccal **mucosa**, with numerous secretory ducts emptying into the mouth, also contribute.

The composition and volume of secreted saliva is influenced by the diet and can be highly variable. Two basic types are produced: one is very thick, with a high content of mucus; the other is serous, i.e. watery and thin, and contains various **enzymes**. Saliva of non-ruminant animals is slightly acid and that of ruminants alkaline. On average, adult sheep secrete 5–10 l per day, pigs 15 l per day and cattle 130–180 l per day.

Saliva aids in **mastication**, bolus formation and swallowing. A large quantity of **bicarbonate** is secreted via saliva and serves to buffer the digesta. In ruminants, which produce large quantities of saliva, bicarbonate is essential for neutralizing the considerable microbial production of **short-chain fatty acid**s in the rumen. Other components of saliva (such as **urea**, **mucin**, phosphate, **sulphate**, **magnesium** and **chloride**) are essential for microbial **metabolism** in the rumen. Enzymes such as ptyalin, an α-**amylase** (in omnivores), and **lipase** (in **suckling** and young milk-fed animals) can initiate the **digestion** of macromolecules. Finally, saliva solubilizes a number of the compounds in the feed and thereby makes them detectable by the **taste** buds on the tongue. (SB)

Salmon culture

Culture of salmon freshwater stages began in Scotland in the 1850s but commercial culture of the marine phases essentially began in Norway in the 1960s. **Atlantic salmon** (*Salmo salar*) is the principal cultured species (2.6 million tonnes worldwide in 2019), with coho (*Oncorhynchus kisutch*) and chinook (*O. tshawytscha*) salmon cultured in smaller amounts. The major countries that farm Atlantic salmon include Norway, Chile, the UK, Canada and Australia.

All salmon species are anadromous. In the early stages they require culture in freshwater hatcheries and are transferred to sea cages at the smolt stage (seaward migrant phase). Adult salmon typically mature in autumn or early winter, but maturation may be manipulated by variation of **temperature** and **photoperiod** regimes and synchronized by injection of **luteinizing hormone**-releasing hormone (LHRH). Adults may be ripened in **sea water** but better-quality **eggs** are obtained from final maturation in **fresh water**. **Spawning** should utilize water of 4–7°C. The eggs and milt are stripped from adults manually by exerting pressure on the abdomen, mixed for a few minutes (1–10 million sperm per egg), then hardened in running fresh water, during which time the eggs swell through water uptake. Eggs (4–6 mm diameter) are reared in hatching trays supplied with running water at 0–8°C. Most commercial facilities use high temperature to shorten hatching times (about 2 months at 8°C). Use of water recirculation and biofiltration is becoming more common to make more efficient use of heated water.

The salmon hatchlings (alevins) have a large **yolk sac** that comprises *c.* 70% of their wet weight at hatch. Most of this must be absorbed prior to exogenous feeding. Alevins may be reared at 0–12°C, which may be increased to 16°C just before feeding. Many commercial hatcheries rear alevins at elevated temperatures to reduce the time to first feeding (*c.* 1 month at 12°C). Alevins should be reared in artificial **substrate** to reduce locomotor activity and promote better yolk utilization efficiency. Fry (*c.* 30 mm long at first feeding) may be started on commercial starter diets. The optimal rearing temperature from fry to smolt for most salmon species is near 15°C. The majority of Atlantic salmon smolts currently produced are '1+' smolts, at 14–16 months post-fertilization and an average weight of 80 g. The production of '0+' smolts at less than 12 months is becoming more prevalent. Many male smolts tend to become precociously mature at the end of the first summer, resulting in **growth** reduction and necessitating an extra year's growth to smolt size ('2+' smolts).

Most smolts are placed in sea cages in the spring at 5–7°C, with 0+ smolts placed in sea water in the autumn. Smolts are vaccinated against infectious bacterial pathogens, furunculosis and vibriosis, prior to seawater transfer. Smolt stocking densities are 4–12 m^{-3}, depending upon whether they will be divided among several cages later. Coho salmon have a freshwater phase of similar length to Atlantic salmon but chinook salmon, particularly the 'ocean type', can tolerate full sea water at 6–7 g. Culture cages may be made of wood, steel or plastic, with plastics becoming more prevalent. Industry development has resulted in increasingly larger cages and

more offshore locations. Sea cage volumes may vary from a few hundred cubic metres for older cage types to over 10,000 m^3 for more modern cages.



Sea cage for salmon, seen here at Brier Island, Nova Scotia, may be as large as 10,000 m^3. Photo courtesy of Miki James. Licensed under CC BY 2.0.

Salmon in sea cages are fed extruded dry feeds (7% moisture) containing 40–45% **protein** and 22–35% **lipid**, with **supplement**s of pigments and **micronutrient**s. Market sizes of 3–6 kg are attained in 16–24 months after smolt entry, at a final stocking density of 15–20 kg m^{-3} of cage volume. Potential hazards to salmon cage culture include various bacterial and viral pathogens, sea louse infestations, bird and seal predation, toxic algal blooms, low lethal temperatures and low dissolved **oxygen**. Some bacterial pathogens (e.g. bacterial **kidney disease**) are

controlled by antibiotics. Sea lice are controlled by insecticide baths and **feed additives** (e.g. Ivermectin). Predator nets and ultrasonic seal repellents reduce predation risks, while proper site selection and stocking densities can minimize the dangers of temperature, **algae** and low dissolved **oxygen**. (RHP)

Salmonellosis

Infection with bacteria of the *Salmonella* group can cause disease in animals and may be important as a cause of **food poisoning** in humans. There are many different serotypes of salmonella: some have distinct host-species preferences and there is a wide range in pathogenicity. Some salmonellae transmit vertically (parent to offspring), others laterally (animal to animal). Salmonellae can survive for long periods, weeks or months, in the environment. Food may be a source of infection, either at source or by subsequent **contamination**. (EM)



Salmonella bacteria (pink), a common cause of foodborne disease, invade a human epithelial cell (yellow). Photo courtesy of the National Institute of Allergies and Infectious Diseases. Licensed under CC BY 2.0.

Salmonids

The **Pacific salmon** and **rainbow trout** are members of the genus *Oncorhynchus*, of the family Salmonidae, which includes **Atlantic salmon**, **trout**, char, grayling, whitefish and several other groups. There are five species of Pacific salmon, but only two – the chinook (*Oncorhynchus tshawytscha*) and the coho (*Oncorhynchus kisutch*) – are farmed for food production. Rainbow trout (*Oncorhynchus mykiss*) are by far the most widely farmed trout, having been transplanted over the past century from their native environments in the northern temperate areas of the eastern and western Pacific to South America, Japan, China, Europe, parts of Africa, Australia and New Zealand. Atlantic salmon (*Salmo salar*) are native to the northern temperate areas of the eastern and western Atlantic and are the most widely farmed salmon species in the world, being farmed in Norway, Scotland, Iceland, Ireland, Chile, Canada, the USA, Tasmania and New Zealand. Other farmed species include the **Arctic char** (*Salvelinus alpinus*) and brown trout (*Salmo trutta*). Salmonids exhibit considerable plasticity with respect to freshwater and seawater existence as post-juveniles, but all spawn and live in **fresh water** as juveniles. Salmon prefer a seawater post-juvenile existence; they undergo a metamorphosis in spring that prepares them for migration to the sea. Salmon are farmed in floating sea cages, whereas trout are generally farmed in freshwater raceways and

tanks. However, rainbow trout can be adapted to **sea water** after they reach *c.* 100 g, and in Norway and Chile are commonly farmed in marine cages like salmon.

Salmonids are carnivorous **fish** that consume **zooplankton** and aquatic insects as fry and juveniles, and small fish, **shrimp** (**krill**) and squid as post-juveniles and adults. They grow best when fed high-protein, high-**lipid** feeds containing highly digestible **protein**. They have a limited ability to utilize **carbohydrates** and become hyperglycaemic when fed diets containing high levels of digestible carbohydrates. Salmonids require ten essential **amino acid**s and 15 **vitamins** (Tables 1 and 2). Like most other fish, they require **ascorbic acid**. Salmonids also require dietary sources of omega-3 **fatty acid**s, preferably docosahexaenoic (22:6) and eicosapentaenoic (20:5) acids. Salmonids can obtain many of the **minerals** they need directly from the water, but diets are generally supplemented with **copper**, **iodine**, **manganese**, **zinc** and sometimes **selenium**, plus sufficient available **phosphorus** to meet dietary requirements (*c.* 0.6% minimum). Salmonids are adept at utilizing dietary protein for **metabolizable energy**, in part because they readily excrete **ammonia** via the gills. While it is desirable to feed high-**lipid** diets to spare expensive dietary protein, digestible **protein:energy ratio**s are kept within a narrow range for grow-out fish. Various ways of expressing desirable protein:energy ratios are reported, such as 18–22 mg digestible protein MJ^{-1} **digestible energy**, about 42% digestible protein and 4.1 kcal g^{-1} diet, or 100 kcal g^{-1} protein. Salmonids vary in their tolerance of high-lipid diets according to their size and

species. Atlantic salmon exhibit higher growth and **protein retention** rates when fed high-lipid (*c.* 35%) diets, in contrast to Pacific salmon or rainbow trout, which tend to accumulate **fat** when fed diets containing more than 25% lipid, perhaps associated with their life cycle in nature (food scarcity in winter, voluntary **starvation** during long **spawning** migrations).

Table 1. Dietary amino acid requirements for salmon and trout (expressed as percentage of diet).

Amino acid	Salmon[a]	Trout
Arginine	2.04	1.5
Histidine	0.61	0.7
Isoleucine	0.75	0.9
Leucine	1.33	1.4
Lysine	1.7	1.8
Methionine + cystine	1.36	1.0
Phenylalanine + tyrosine	1.75	1.8
Threonine	0.75	0.8
Tryptophan	0.17	0.2
Valine	1.09	1.2

[a] Adapted from NRC (2011).

Table 2. Dietary micronutrient requirements and their deficiency signs for Atlantic salmon.

Micronutrient	Requirement[a]	Deficiency sign
Vitamin E	35 mg kg^{-1} diet	Muscle degeneration, anaemia, reduced carcass protein, increased carcass moisture and fat
Pyridoxine	15–20 mg kg^{-1} diet	Nervous disorders, anorexia, reduced alanine transferase activity
Vitamin C	50 mg kg^{-1} diet	Scoliosis, lordosis, anaemia, mortality
Vitamin K	2–10 mg kg^{-1} diet	Coagulation blocked, anaemia, mortality
Riboflavin	12–36 mg kg^{-1} diet	Fin rot, ophthalmic lens turbidity
Pantothenic acid	20–50 mg kg^{-1} diet	Gill tissue damage
Phosphorus	0.7% of diet	Low bone ash, calcium, phosphorus and magnesium, bone abnormalities, poor growth

Micronutrient	Requirement[a]	Deficiency sign
Manganese	20 mg kg^{-1} diet	Reduced haematocrit and vertebral manganese
Copper	6 mg kg^{-1} diet	Reduced serum copper and liver cytochrome C oxidase activity
Iron	73 mg kg^{-1} diet	Reduced haematocrit, red blood cell count and tissue iron level
Selenium	0.15–0.38 mg kg^{-1} diet	Muscular dystrophy-like signs
Iodine	0.6–1.1 mg kg^{-1} diet	
Astaxanthin	5 mg kg^{-1} diet	Poor growth, mortality in fry from females deprived of dietary astaxanthin

[a] Dietary requirements determined in one or two studies only, and generally with fry or fingerlings. Adapted from Hellend, Storebakken, and Grisdale-Helland (1991) in: *Handbook of Nutrient Requirements of Finfish* (ed. R.P. Wilson), CRC Press, Boca Raton, Florida, pp. 13–22.

A unique attribute of salmonids is their pigmented flesh and skin. In nature, they obtain the pigments, mainly **astaxanthin** and canthaxanthin, via the **food chain**; they cannot synthesize **carotenoid** pigments *de novo*. Astaxanthin has been shown to be an essential dietary nutrient for Atlantic salmon. Fry from female Atlantic salmon deprived of dietary astaxanthin exhibit slow growth and high mortality if not fed diets containing astaxanthin. Other salmonid species probably also require a dietary source of astaxanthin, canthaxanthin, or both, to produce viable offspring. In farming, salmon and trout diets are supplemented with astaxanthin, either from natural sources, such as krill, crustacean waste, *Phaffia* **yeast** and **algae**, or from astaxanthin produced by industrial synthesis, e.g. Carophyll pink®. Diets are typically supplemented to contain between 45 and 60 μg pigment g^{-1} and supplemented diets are fed during the grow-out period before harvest.

Feed formulations for salmonids are relatively simple: fish meal, fish **oil**, ground **wheat** or gelatinized **maize**, vitamin and trace **mineral supplement**s, plus carotenoid pigment for grow-out stages (Table 3). Depending upon the relative prices of fish meal and other **protein supplement**s, formulations often contain other **protein source**s, such as maize **gluten** meal or **soybean** meal, in place of a portion of fish meal. There are also concerns about long-term dependency upon fish meal as the main protein source in salmonid feeds. Rendered animal products have long been used in salmonid diets but in Europe, because of concerns

about BSE transmission and excessive **phosphorus** losses from farms, they are now limited to **poultry by-product** meal and **feather meal**. Another developing concern is the presence of organic contaminants in fish meals and oils originating from the North Atlantic.

Table 3. Generalized formulations (g kg^{-1}) used for grower and fingerling Atlantic salmon feeds and for grower rainbow trout.

Feed ingredient	Grower salmon	Fingerling salmon	Grower trout
Fish meal	480	600	360
Soybean meal	50	0	100
Poultry by-product meal	50	0	100
Feather meal	0	0	60
Wheat by-products	0	274	90
Ground whole wheat	104	0	104
Vitamin premix	10	10	10
Trace mineral premix	1	1	1
Choline chloride (60%)	4	4	4

Feed ingredient	Grower salmon	Fingerling salmon	Grower trout
Ascorbic acid	1	1	1
Fish oil	300	110	170
Proximate composition:			
Moisture	8%	8%	8%
Crude protein	41%	48%	44%
Crude fat	35%	17%	22%

Special diet **supplement**s are used to increase diet efficiency or enhance disease resistance. As more plant protein introduces higher levels of **phytate** in salmonid diets, supplementing diets with **phytase** is an effective means of increasing the availability of phosphorus. Immune stimulants and immune enhancers are also used, to enhance disease resistance.

Because salmonid diets contain high levels of unsaturated **lipids**, there is potential for auto-**oxidation**. This can be minimized by using only batches of fish oil with low oxidative status, and by addition of **antioxidant**s to fish oils. Dietary supplements of α-tocopheryl **acetate**, **ascorbic acid** and **selenium** provide additional metabolic protection against free-radical damage *in vivo*.

In trout farming, a kind of demand feeder is commonly used that delivers feed when fish move a rod suspended in the water. Wave and wind action limit the use of demand feeders in sea cages,

so feed is delivered mechanically, using pipes and blowers programmed to supply each cage with an appropriate amount of feed, divided into an appropriate number of meals per day. In some parts of the world, feed is delivered by hand, or by mechanical dispersing devices on each cage that are programmed to feed at intervals. In any case, feeding amount is based upon expected growth and feed efficiency ratios that vary with season (**photoperiod** and **water temperature**).

Salmonid feeds are expensive, and the potential for feed waste, especially in sea cages that can be 10 m deep, is relatively high. This has led to the development of sophisticated systems to detect pellets reaching the bottom of cages and recovering them for reintroduction at the surface, or stopping feeding when feed is detected at the bottom of pens. These systems are very effective and, as a result of their use, feed waste in salmon farming is low. Overall, the use of high-quality ingredients, cooking-**extrusion pelleting** and effective vaccines to prevent disease have made salmonid **aquaculture** one of the most efficient farming systems to convert ingredients not consumed directly by humans into high-quality food; **feed conversion ratio**s of 1.0 to 1.2 on a farm basis are routinely obtained. (RH; QS)

See also: Salmon culture

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Salt

The compound formed when the **hydrogen** atom of an acid is replaced by a **metal** (e.g. **sodium**, **potassium**). Common salt is **sodium chloride** (NaCl). Both sodium and chloride are required nutrients. **Ruminant animal**s are particularly likely to experience sodium deficiencies, especially far from the sea, where **forage** sodium contents are low. This may predispose to **calcium** and **magnesium** deficiencies. (NJB; CJCP)

Key reference

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Sample

A small portion representative of the whole. To sample is to select a small amount of a larger mass or to take a number of units to represent a large number of units, or a population, for statistical

analysis. For sampling certain populations or materials, there are three distinct ways in which a selection can be made: random; systematic; or authoritative. In random sampling, each individual of a population or each part of the mass of material has an equal chance of being selected as part of the sample. In systematic sampling, individuals are chosen at fixed intervals, for example every fifth animal in a population or every tenth bag of fish meal. Authoritative sampling requires individuals who are well acquainted with the material or the population to take a representative sample without regard to randomization. Other sampling procedures include stratified random sampling and sampling with replacement. For many materials, sampling error (the difference between the sample and the whole) is minimized by complete mixing, or homogenization, so that any one sample has the same composition as the whole. (SPL)

Saponification

The chemical process in which a fatty acid **ester** is hydrolysed by an aqueous alkali (e.g. **sodium** hydroxide, NaOH) to form the **salt** of the **fatty acid** and an alcohol. For example, when animal or plant **fats** (i.e. **triacylglycerol**s) are saponified, the sodium salt of the fatty acid (now a soap) is produced along with free **glycerol** (an alcohol). (NJB)

Saponins

Natural detergent-like **glycoside**s found in a variety of plants used for human and animal feeds. Their detergent activity derives from a steroid or triterpenoid nucleus with one or more side chains of

water-soluble **carbohydrates**. Saponins have multiple biological effects, some positive but many negative. Because of their foaming properties, they are extremely toxic to fish and have been used as fish poisons in native tropical rainforest cultures. Saponins are bitter and irritate mucous membranes of the mouth and **gastrointestinal tract** and may cause frothy **bloat** in ruminants. Many plants containing saponins cause clinical signs of toxicity: depression, **anorexia**, **diarrhoea**, weight loss, liver and kidney lesions and photosensitization. Low levels of dietary **lucerne** meal can reduce the growth rate of poultry and pigs. Saponins affect nutrient **metabolism** and mineral **absorption** (especially **iron**) by interacting with mucosal cell membranes, causing permeability changes or loss of activity of membrane-bound **enzymes**. (KEP)

Satiety

A state which, following the ingestion of a food, suppresses further ingestion. Satiety occurs after the termination of a meal and continues until the onset of **hunger** or initiation of a subsequent meal. It is defined as the period between meals that is characterized by a lack of hunger or desire to eat. Satiation is the inhibition of feeding that occurs during the consumption of a meal, and contributes to the termination of a meal. Because satiation occurs within a meal, it is dependent upon the positive and negative feedback signals that initiate and stop ingestion. Positive feedback signals are responsible for initiating and maintaining eating, and arise from the sensory properties of food. Negative feedback signals increase during a meal and eventually terminate ingestion. Negative feedbacks arising from **stomach** distension,

hormonal release, chemoreceptor stimulation and **metabolism** of ingested nutrients seem to be the primary factors that contribute to satiation. Peptides released from the **gastrointestinal tract** during a meal that may be candidates for controlling meal size include **cholecystokinin**, bombesin-like peptides, pancreatic **glucagon**, **insulin**, amylin, somatostatin, neurotensin, enterostatin, **apolipoprotein** AIV and glucagon-like **peptide**. Termination of a meal as a result of satiation should be differentiated from termination due to reasons such as competition from rival activities, malaise or depletion of the food source. (NJB)

Saturated fatty acids

Fatty acids with the general formula $CH_3(CH_2)_nCOOH$, where n may be 0 to 30 but is an even number in most natural **fats**. Odd-numbered and branched-chain saturated fatty acids are not uncommon in ruminant fats. The lower members are liquid at room temperature but those with more than ten carbons are solid, with melting points increasing with chain length. Saturated fatty acids do not absorb **iodine**. The physical characteristics associated with longer chain length and higher melting point decrease the ability of the fatty acids to interact with amphipathic molecules to form soluble micelles; thus, higher homologues of saturated fatty acids have lower intestinal **digestibility** than shorter chains. Saturated fatty acids are found in lower proportions in cholesteryl esters and **phospholipid**s of plasma and tissue membranes than are **unsaturated fatty acid**s. **Palmitic acid** (16:0) is the main product of **fatty acid synthesis** in animal **adipose tissue**,

whereas ruminant mammary tissue synthesizes 4:0 to 16:0. **Milk** fat typically contains 70% saturated fatty acids. **Stearic acid** is the primary product of ruminal biohydrogenation of dietary unsaturated fatty acids. Saturated fatty acids with 12–22 carbons can be desaturated by δ-9 desaturase, the product being the *cis* δ-9 monoene. Stearoyl-CoA (18:0) is the favoured **substrate**. (DLP)

Scales

The primary purpose of scales is to give fish external protection. Most bony fish have one of two types of scales: cycloid and ctenoid. Cycloids have a smooth edge whereas ctenoids have a toothed edge. The scales grow with the development of fish and leave rings like the rings of a tree, and so the age of most fish can be determined by examining their scale rings. Scale sizes vary greatly between species; freshwater **eels** have small embedded scales, the tunas have tiny scales and the scales of the Indian mahseer can reach over 10 cm in length. (SPL)

Scallops

Bivalve **mollusc**s of the family Pectinidae. The shells are usually rounded, with radiating ribs and wing-like projections (called 'ears') on either side. The outline and appearance have been much used in heraldry, murals, decorations, ornaments and jewellery. Many species are fished and cultivated worldwide, principally for the single large adductor muscle which the animal uses to swim by rapid 'clapping' movements of the shells, and which is good to eat. (DJS)



Scallops are both farmed and fished for human food. Photo courtesy of National Oceanic and Atmospheric Administration. Licensed under CC BY 2.0.

Scatter feeding

A system of providing a **pelleted feed** to restrained animals, in cages or houses, in which the feed is scattered over the floor of their enclosure. This increases **foraging behaviour**, provided that the entire diet is offered in this way. If feed is alternatively available in easily accessible feeders, animals will take it there, rather than from the **litter**. If foraging behaviour is increased, **maintenance** requirements are likely to be simultaneously increased due to the **energy requirement**s for foraging. Scatter feeding is common for zoo and **laboratory animal**s, for whom efficiency of feed utilization is less important than for livestock. It is also useful for dogs in the absence of their owners, as it satisfies their scavenging instincts, particularly if they have to sniff for the

food. Scatter feeding also provides mental stimulation and reduces the rate of intake of the food, which has benefits in reducing the risk of **bloat** and encouraging **chewing** of the feed and allowing time for adequate salivation to neutralize **stomach** acids. (CJCP)
See also: Anorexia

Scorch
The result of overheating of feed materials during processing, which results in discoloration and a reduction in nutritional value, especially as a result of **Maillard reaction**s. New technologies in processing, such as low-temperature and spray drying, can prevent scorching. (JKM)

Scour:
see Diarrhoea; Digestive disorders

Sea urchins
Sea urchins belong to the invertebrate phylum Echinodermata, meaning 'spiny skins'. The typical sea urchin is a rounded, globular organism, a few centimetres in diameter, with a rigid, hard internal shell made of many interlocking calcareous plates, and covered with a dense layer of moveable spines. The species may be of different colours with spines of different lengths. They occupy a range of habitats in all the oceans of the world, mostly **browsing** on rocky surfaces and among corals. 'Heart' urchins are heart shaped and live buried in sand. Sand dollars are quite flat and browse on the surface of the sand. All echinoderms have a unique natural hydraulic 'water vascular' system that powers the tube feet,

allowing the urchins to ‘walk’ and grasp their food.



Purple sea urchins (Strongylocentrotus purpuratus). Photo courtesy of Gregory Smith. Licensed under CC BY-SA 2.0.

Edible sea urchins are captured by trapping, dragging or diving. They have no conspicuous musculature and are fished exclusively for their roe, which is considered a delicacy. Most fisheries are seasonal, linked to the period when roe quality is at its best. Current landings are in the order of 100,000 t per year. Principal consumers are in Japan, which imports 97% of the global market, most produced in Chile. Some progress is being made with the culture of sea urchins but the amounts harvested to date are nominal. Some wild-caught urchins are being held in captivity and fed selected diets to improve roe quality and yield. (DJS)

Sea water

A complex solution of inorganic and organic solutes and dissolved gases with suspended particles such as mineral grains, aggregates

of organic particles and living plankton. The term 'salinity' is a measure of concentration of **salt** in sea water. The following dissolved ions (percentage of total salt) make the water saline: **sodium**, 55.04%; chlorine, 30.61%; **sulphate**, 7.68%; **magnesium**, 3.69%; **calcium**, 1.16%; **potassium**, 1.1%; **bicarbonate**, 0.41%; bromine, 0.19%; borate, 0.07%; strontium, 0.04%; and **fluorine**, 0.003%. Many of the elements in sea water are found in nearly constant proportions although the total salinity varies from place to place. The salinity of sea water ranges between 33 and 37 parts per 1000 ($g\ kg^{-1}$), of which approximately 85% is **sodium chloride**. Freshwater discharge from rivers as well as evaporation and **freezing** may affect the salinity and concentrations of various ions in the sea water.

Exchange of ions occurs across the gills, skin and oral epithelia in **fish**. Inorganic ions present in sea water such as calcium, magnesium, sodium, potassium, **iron**, **zinc** and **copper** can partially satisfy the mineral requirements of **aquatic organisms**. (DN)

Seasonal variation of pasture

The value of **grass**, either for **grazing** or for conservation, changes as the growing season progresses, largely due to increasing **maturity**, with **climate** and management causing changes between seasons. As the interval between defoliations increases, so does total dry matter (DM) yield, but increased fibre concentrations reduce the **digestibility** of DM. This is compounded by an increase in **lignin** content which, because it

complexes with cell wall **polysaccharide**s, further reduces the digestibility of the fibre fraction. **Metabolizable energy** content (ME, kg DM $^{-1}$) falls. Delaying the time of the first cut of the season increases yield at that cut but delays secondary growth. This can result in a reduced total yield (see table). **Crude protein** concentration falls (e.g. from 300 to 30 g kg^{-1} DM) but total stored **nitrogen** increases.

Effect of cutting frequency on grass yield and quality (from Leaver and Moisey, 1980). (a) Three-cut system

Cut	DM yield(t ha^{-1})	ME(MJ kg^{-1} DM)
Late May	4.6	10.6
Early July	3.2	9.8
Mid-August	1.8	9.6
Total	9.6	Mean 10.0

DM, dry matter; ME, metabolizable energy.

(b) Two-cut system

Cut	DM yield(t ha^{-1})	ME(MJ kg^{-1} DM)
Early June	7.8	9.6
Mid-August	3.7	9.0
Total	11.5	Mean 9.2

DM, dry matter; ME, metabolizable energy.

In temperate regions, the growing season is largely controlled

by ambient **temperature** but the time of plant maturity varies between species and between varieties within species. Perennial ryegrass (*Lolium perenne*) is generally regarded as an early-flowering variety and timothy (*Phleum pratense*) as late-flowering. Management of grassland through the growing season must ensure adequate grazing with sufficient material for conservation for winter feeding. In long-term leys and permanent pasture, it is also essential to allow the plant sufficient rest time to replenish root reserves.

In the tropics, growth is controlled by rainfall – both the amount of rain and its distribution through the year. Tropical grasses such as black speargrass (*Heteropogon contortus*) and Rhodes grass (*Chloris guyana*) exhibit a rapid fall in **protein** content and increased fibrousness at the end of the rains. The quality of standing **hay** is usually not greater than that of crop residues, depending on the amount of termite damage and the amount of senescence that occurs. Management of grazing for intensive production can mitigate this extreme seasonality of production by: (i) timely application of fertilizer; (ii) conservation of excess biomass; (iii) seasonal breeding programmes and the use of mixed-species swards, including **legumes**; and (iv) introduction of leguminous multipurpose trees to give the option of **browsing**. In smallholder livestock production systems, particularly in the drier areas, there is no tradition of conservation of forages to offset dry-season feed shortages. Fertilizer application to communal **rangeland**s is not a practical option. There is little or no evidence to suggest that cattle breed to coincide with the grass flush (peak

kidding times in goats are more predictable). (TS)

See also: Cutting herbage for livestock

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Seaweed

Seaweeds are multicellular **algae** of marine and **brackish water**s, more usually the readily visible larger forms. They come in three basic colours (red, brown and green) and display a large variety of forms and life histories. Seaweeds are typically rich in complex **polysaccharide**s, which make up their cell walls, and usually contain significant amounts of **protein**, **vitamins** (especially A and B) and **trace element**s. Of about 9000 known species, only about 50 are utilized, via either direct consumption or extraction of contents. Limited **digestibility** of the cell walls restricts human consumption of seaweed to relatively few (albeit very valuable) species, but ruminant livestock pastured along seacoasts traditionally have fed and thrived on kelps, rockweeds and other accessible seaweeds. Meal from the brown seaweeds *Ascophyllum* and *Laminaria* is used as a **supplement** to livestock feed, and the addition of *Chondrus* to diet has ameliorated cases of ovine ill-thrift.



Laminaria, *Alaria* and *Desmarestia* seaweeds, Newfoundland. *Laminaria* is one of several species that may be used as a livestock feed. Photo courtesy of Derek Keats. Licensed under CC BY 2.0.

Seaweeds also provide a natural food source for **aquaculture** marine **herbivore**s such as **abalone**, sea cucumber and **sea urchin**s, with certain species being more nutritious and more palatable to the animals. The other major commercial use of seaweeds is as sources of extractives, particularly gelling agents (**carrageenan** (*Chondrus*), agar (*Gelidium*, *Gracilaria*) and alginates (*Ascophyllum*, *Laminaria*)) derived from their cell walls and used as binders, **emulsifier**s and stabilizers in foods, pharmaceuticals and various industrial applications. Lesser uses are the production of foliar fertilizers (*Ascophyllum*), soil conditioners (especially calcified forms such as *Phymatolithon*) and sources of therapeutants (e.g. *Alsidium* and *Chondria* as vermifuges). Some species, in particular those with the trihalomethane bromoform such as red seaweed (*Asparagopsis taxiformis*), are under investigation to control **methane** emissions in ruminant livestock. Cultivation on a large scale for this purpose poses many problems, not least its impact on the **marine**

environment. Few seaweed species are toxic, though bromoform residues in **milk** and **meat** deserve consideration. Some are a nuisance as aggressive weeds. (CB; CJCP)

See also: Marine plants

Further reading

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Secretin

Secretin was the first **hormone** to be discovered (by William Bayliss and Ernest Starling in 1902). It is a 27-amino-acid polypeptide that is released into the circulation from endocrine cells of the **small intestine**. Sometimes referred to as nature's own antacid, secretin is released in response to the presence of the acidified meal entering the small intestine. It acts through a cyclic-adenosine monophosphate (cAMP)-mediated intracellular pathway to inhibit **gastric emptying** and stimulate the secretion of a **bicarbonate**-rich fluid from the **pancreas**. (GG)

Selection, feed:

see Feed selection

Selenium (Se)

A mineral element with an atomic mass of 78.96. It exists in three **oxidation** states of +6, +4 and −2, and shows both metallic and non-metallic properties. Selenium is present in all organs, with kidney, liver and bone having the greatest concentration; however, muscle and skeleton, as a whole, contain most of the Se found in the mammalian body. Selenium is an essential nutrient and is required for full activity of a number of **enzymes**, including the various **isozyme**s of **glutathione peroxidase**, thioredoxin reductase, and iodothyronine 5′-deiodinase types 1, 2, and 3, and is a component of selenoproteins P and W. Selenium can also be incorporated into most types of proteins in the form of selenomethionine as a substitute for **methionine**. Thus, Se is present in plant and animal products bound to certain proteins or incorporated into proteins as selenomethionine and **selenocysteine**. Methylselenocysteine is a soluble form of Se. Small amounts of Se can also exist in the body as inorganic selenite and selenate salts. The inorganic forms are reduced to selenide before incorporation into selenocysteine. Most of the Se in plant material is selenomethionine and that in animals is both selenocysteine and selenomethionine.



An adequate selenium intake by ewes during late pregnancy is essential for good lamb vigour at birth and the ability to generate heat from their brown adipose tissue, essential for survival in cold outdoor environments. Photo courtesy of Leiminide. Licensed under CC BY 2.0.

In non-ruminants, Se is absorbed primarily from the upper intestinal tract. More than 90% of intake is absorbed if Se is in the organic form, and 60% if in the inorganic forms of selenite or selenate. This suggests that Se **homeostasis** is not controlled to a large extent by **absorption**. Se absorption in **ruminant animal**s is somewhat less than in non-ruminants, which could be the result of chemical processes in the **rumen** that reduce Se to insoluble forms. The rate at which Se is eliminated from the body depends largely on the form of ingested Se. Selenium that is incorporated into proteins as a substitute for methionine, or as selenocysteine, has the slowest **turnover**, because it is eliminated only when the proteins are degraded. Before urinary excretion, all forms of Se are reduced in the liver to selenide and methylated. In animals, most of the Se is excreted in urine as the trimethylselenonium ion. It can

also be eliminated through the breath as dimethyl-selenide.

Variable signs of Se deficiency can occur in animals. Muscular dystrophy, or white muscle disease, is seen in lambs and calves that consume a selenium-deficient diet. **Exudative diathesis** is seen in poultry and liver necrosis in other species. Because Se is associated with enzymes with **antioxidant** properties, some of the signs of Se deficiency will respond to **vitamin E** supplementation; others will not.

The dietary requirement for Se is somewhat consistent among farm species. The US National Research Council recommends 0.1 mg Se kg^{-1} diet for growing beef cattle and 0.3 mg kg^{-1} for dairy cattle. The requirement for pigs depends on their age: young growing pigs require 0.5 mg Se kg^{-1} diet and older pigs require only 0.15 mg kg^{-1}. The requirement for horses and poultry is about 0.1 mg Se kg^{-1} diet, and for sheep the value is between 0.1 and 0.2 mg kg^{-1} diet. The maximal tolerable dose of Se for cattle and horses is 5 mg kg^{-1} diet and for sheep it is 2 mg kg^{-1} diet.

Selenium toxicity in grazing animals can be a problem, especially in areas where soil Se is relatively high. Numerous plants tend to accumulate Se in their leaves and, if consumed, can lead to Se toxicosis. The exact mechanisms involved in Se toxicity are not understood, but may include the inhibition of sulphydryl enzymes or the production of excess methylated selenium **metabolite**s that are toxic. Excess Se can also bind **glutathione** and remove it from critical biological reactions. (PGR)

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Selenocysteine

An amino acid, $HSeCH_2{\cdot}CHNH_3^+{\cdot}COO^-$, molecular weight 168, identical to **cysteine** but with **selenium** (Se) in place of the **sulphur** moiety. Selenocysteine is incorporated into proteins and, in some, forms part of the active site. Examples of **selenocysteine**-containing proteins are: thioredoxin reductase, which catalyses the reduction of thioredoxin; **glutathione peroxidase**, which is involved in the destruction of **peroxides**; and iodothyronine deiodinase, 5′ DI, which converts thyroxine (T_4) to 3,5,3′ **triiodothyronine** (T_3). (NJB; DHB; GW)

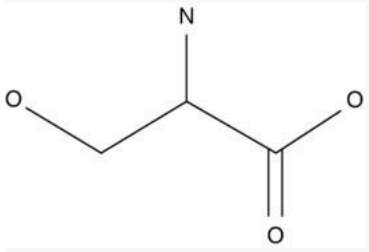
Semi-purified diets

Diets based largely on purified ingredients. Semi-purified diets are useful biological tools in establishing responses to specific dietary ingredients/nutrients in the absence of confounding factors. Thus, for example, a response to a **vitamin** should ideally be assessed under conditions where no other dietary ingredient contains that vitamin. Semi-purified diets should, wherever possible, be nutritionally adequate (except for that nutrient under investigation). Common ingredients are purified **starch**, **glucose**, soya **protein isolate**, **casein** and vitamin/mineral premixes. Vegetable **oil** is often added for textural reasons (to reduce dust

and maintain **palatability**). (JW)

Serine

An amino acid ($HO{\cdot}CH_2{\cdot}CH{\cdot}NH_2{\cdot}COOH$, molecular weight 105.1) found in protein. It is synthesized from **glucose** or **glycerol**, with **glutamate** serving as the amino donor. In addition to its role in **protein synthesis**, serine serves as a metabolic precursor of **glycine**, and in this process a hydroxymethyl group is contributed to the **folate** pool. Serine is thus considered an important precursor in the body for *de novo* methyl group synthesis. **Phospholipid** synthesis also involves serine; after diacylglycerol reacts with ethanolamine to form phosphatidyl ethanolamine, serine can be exchanged with ethanolamine to produce phosphatidyl serine. Both of these phospholipids can then serve as precursors for phosphatidyl **choline** (**lecithin**) biosynthesis. In this process, three methyl groups (from ***S*-adenosylmethionine**) are added to phosphatidyl ethanolamine to form phosphatidyl choline, which can be converted to choline.



A series of so-called serine proteases exist in which serine residue is the active site of the enzymes. This can trigger proton shifts from serine through **histidine** to aspartate. Proton shifts of this type can affect the catalysis potential of an enzyme, e.g. **chymotrypsin**.

Serine is catabolized via multiple metabolic pathways. Most is thought to be metabolized first to **glycine** and N^5, N^{10} methylene **tetrahydrofolate**. Glycine is then oxidized to CO_2 and NH_4^+, with N^5, N^{10} methylene tetrahydrofolate again being formed. Serine can also be deaminated by serine dehydratase to **pyruvate**, and this reaction yields NH_4^+ and H_2O. (DHB; GW)

Serotonin

5-Hydroxytryptamine (5HT, $C_{10}H_{12}N_2O$). Serotonin is formed from L-**tryptophan** by hydroxylation of position 5 in the benzene ring followed by a **decarboxylation** of the carboxyl carbon. It is found in high concentration in **blood** platelets and in the enterochromaffin cells in the intestine and in smaller amounts in brain and retina. Serotonin is a **neurotransmitter** produced by neurones in the **hypothalamus** and brainstem. It functions in pathways that relate to sleep and sensory perception. It is inactivated by the **enzyme** monoamine oxidase (MAO) which converts it to 5-hydroxyindol**e**acetic acid (5-HIAA), which is excreted in the **urine**. Serotonin can be converted to **melatonin** in a two-step process. High concentrations of melatonin are found in the pineal gland. (NJB)

Sesame (*Sesamum indicum*)

Sesame has a long history of cultivation, being an important **oil**-yielding crop 4000 years ago. A member of the family Pedaliaceae, it is an annual, erect plant 0.5–2.5 m high, depending on the variety. Flowers are bell-shaped, white to pale pink.



Harvesting sesame seed. Photo courtesy of USDA government. Licensed under Public Domain Mark 1.0.

The fruit is an elliptical pod containing up to 100 seeds. It is highly tolerant of dry conditions, though very intolerant of waterlogging. The seeds contain about 50% oil and 25% protein. The primary **fatty acid**s in sesame seed oil are **oleic acid** (47%) and **linoleic acid** (39%). The oil is used for cooking, salad oils and non-dairy spreads and has various industrial uses. The oil-cake or meal that remains after the oil has been removed is protein rich (34–50%) and is palatable to all livestock, including poultry. Sesame cake can have a laxative effect and it can taint **milk** if fed as a high proportion of the ration (< 3 kg per day in the case of the dairy cow). High concentrations of **phytate** can bind **calcium** and prevent its **absorption**, so care should be taken to increase the calcium provision in the ration when feeding sesame meal. Although sesame oil contains an **antioxidant**, sesamol, which delays deterioration, sesame meal will become rancid if stored for long. (DA)

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Sex differences

Sex differences affect appearance, psychology, **carcass** attributes and **meat quality**. Strictly speaking there are only two sexes, male and female, defined by the **genotype** and the presence or absence of a Y chromosome. In mammals the male is the heterogametic sex whilst in birds it is the female. In mammals, the genetic information on the Y chromosome facilitates the initiation and development of the testes whilst in birds it initiates the ovary. The sex-related aspects of **growth** are driven by the sex steroids: androgens secreted by the Leydig cells of the testis and **oestrogen**s secreted by the ovary. Although the activity of the testes is suppressed until early **puberty**, the Leydig cells from an early stage secrete androgens into the bloodstream at a rate that affects growth and the development of genitalia. In cattle, the female twin of a mixed-sex twin pregnancy is adversely affected by the androgens of its bull-calf sibling so that it is sexually undeveloped and becomes a ‘freemartin’.



Sexual dimorphism in *Bos gaurus gaurus* cattle in Malaysia. The male has strengthened shoulders to aid in fighting for access to females. Photo courtesy of Clive Phillips. Unlicensed.

At birth, male sheep and cattle tend to be larger than their female siblings and in normal circumstances this advantage continues through to puberty and thereafter in an exaggerated way to adulthood. Prior to puberty the main effect of sex differences is on growth rate and the **adipose tissue** depots associated with growth, males growing about 5–10% more rapidly and having up to 25% less fatty tissue than females. After puberty a considerable degree of sexual dimorphism occurs. Adult males are some 20% larger than females of comparable age. The choice of animals for domestication showed an understandable preference for those with herding or flocking tendencies. Related to this is the fact that the males compete for mastery of groups of females and tend to establish harems. The males of species that have evolved with these characteristics tend to be much larger and more muscular than the females. They also have differentiated features related to their

ability to fight and to impress rivals.

Bulls and rams are equipped for head-on confrontation, with massive heads, reinforced frontal bones on their skulls and substantial horns. The muscles of the neck are thickened and there is increased musculature in the shoulders. The characteristic male profile and weaponry signals not only maleness but also relative strength and may intimidate a rival without physical contact. An extreme example of this is the North American bison or buffalo, which has specially elongated dorsal spines on the cervical and upper thoracic vertebrae that increase the impressiveness of the profile. Boars grow larger than sows and have exaggerated weapons for attack in the tusks that protrude laterally from the mouth. They also have a remarkable defensive adaptation in the so-called shield **fat** that covers the shoulder region. This fat is specially reinforced with cross-linked **collagen** and is resistant to penetration by opponents' tusks (and butchers' knives). It is detectable in entire males of market weights above 100 kg **liveweight**.

The production of **meat** from entire male animals is a subject of ongoing debate. In agricultural terms, the castrated male forms a third sex category and less commonly the spayed or ovariectomized female a fourth. In most countries, bulls, rams and boars are castrated if destined for meat, though for different reasons. In the case of bulls, the safety of stock people amongst a herd of bulls is a major consideration. Extra fencing and handling facilities are required and there will be some damage and even losses from fighting. Bulls, however, grow faster and are leaner and require less

feed per kilogram of carcass gain than castrates or females. Though skilled tasting panels may detect a degree of extra graininess in the meat and a lack of intramuscular fat and succulence, many tests have shown the general public to be less perceptive and unaware of any difference. Sinclair *et al*. (1998) actually showed a reduced shear force for biceps femoris in meat from bulls relative to that from steers. A disadvantage of bulls in relation to castrates is that butchers note a lower killing-out percentage and a poorer carcass conformation. The relatively large muscle groups in the forequarters mean a higher proportion of the less valuable cuts.

In the case of sheep, a major concern of leaving males entire is that it would be impracticable in the context of hill sheep in that young rams would be capable of indiscriminately serving females in the flock, wrecking breeding protocols. Entire lowland male lambs have the same advantages as bulls in terms of efficiency and similar problems in terms of carcass conformation and meat texture.

The use of entire boars for meat production is controversial for a rather different reason. The problem is the presence of so-called 'boar **taint**' in the meat or, more exactly, in the fat. The offensive odour is now known to comprise two main components: androstenone or 5α-androst-16-en-3-one (an unpleasant musk-like steroidal **ketone** elaborated in the testicles) and **skatole** (1-methyl **indole**), a definitive contributor to faecal odours. Androstenone is converted by the submaxillary glands to androstenol, which is the male pheromone of the pig and is distributed by an aroused boar in the frothy **saliva** that it generates

in the presence of females. Skatole is a product of bacterial breakdown of tryptophan in the gut but, under the influence of testosterone, the gut preferentially absorbs it into the bloodstream, from which it is recruited as part of the sex odour of the boar when exhaling and is also liable to dissolve in the **body fat**. It is only a serious consumer problem in boars slaughtered in excess of 120 kg liveweight. **Castration** of boars is not routinely practised in the UK, Ireland, Australia or Denmark, though the latter country has on-line taint testing to eliminate tainted carcasses. Boars grow more rapidly to slaughter weight than do castrates or females, and because they are leaner they are more efficient at converting feed to liveweight gain. The leanness makes the appearance of the meat more acceptable and several studies have shown that meat from boars is more tender than that from gilts, a factor that is attributed to the beneficial effect of growth rate on tenderness (Blanchard *et al*., 1999).

In cattle slaughtered between 400 and 500 kg liveweight, the carcasses of females contain on average about 4% and castrates 3% more fatty tissue than those of bulls. In sheep slaughtered between 35 and 40 kg liveweight, similar differences in percentages of fatty tissue in the carcass are found for the respective sex categories. In pigs, the differences are greater, castrates being about 6% and females 5% fatter than boars (Lawrence and Fowler, 2002).

The anabolic properties of sex steroids as manifested in intact males and females have developed an impetus to deliver exogenous sex steroids to animals kept for meat. This practice is banned in many countries but not in others. In the past, birds have been

caponized using hexoestrol and cattle implanted with either natural steroids or analogues of sex steroids such as zearalenone and trenbolone. It is difficult to envisage the continued use of exogenous sex steroids or analogues in a world where consumers have become sensitized to the possible health risks of such practices. On the other hand, it is possible to foresee a diminution of castration as a routine agricultural practice and the development of appropriate husbandry systems for entire males.

Sex differences are also evident in human selection of, and attitudes towards, the food that they eat. Women tend to eat more fish and chicken, or to be **vegetarian**; men tend to eat more red meat. This difference arises in Western society because of greater concern by women than men for their health. (VRF)

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Sex ratio in chickens

The ability of commercial producers to separate the feeding of layers and broiler chickens, with benefits to feeding efficiency, is dependent on being able to segregate the sexes soon after hatching. Unlike many animals, in farmed species of poultry it is the female, not the male, that determines the sex of the offspring. This is a result of the female chicken carrying the Z and W sex chromosomes, while the male carries only Z chromosomes. Genes carried on one or both of these sex chromosomes control sexual differentiation during embryonic life, producing testes in males (ZZ) and ovaries in females (ZW), usually in a 50:50 ratio. Recent evidence indicates that sex-determining genes may operate not only in the gonads, to produce testes or ovaries, but also throughout cells of the body (Chue and Smith 2011).

In commercial production the correct conditions for **incubation** are replicated in artificial incubators. An unfortunate aspect of layer production is that about half of the chicks hatched are unwanted males which have to be disposed of humanely. Originally these chicks formed the basis of a chicken **meat production** system, which later developed into the broiler industry, i.e. chickens raised exclusively for meat. An active area of research in the 21st century is to sex **eggs** from egg-type chickens prior to incubation so that only female eggs hatch. Initial studies showed that access to the embryonic DNA allowed the sex to be determined accurately, but required the eggs to be punctured and led to decreased hatching rates. More recent studies (e.g. Galli *et al*., 2018) have shown that a minimally invasive method based on fluorescence and Raman spectroscopy of perfused extra-embryonic

vessels while leaving the inner egg shell membrane intact allows a sexing rate above 90%. This type of procedure is expected to be introduced commercially. (RB; NS)

See also: Chickens

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Sexual maturity

The stage in the life of an animal when the sex glands become fully functional so that the male is capable of producing fertile sperm and the female is capable of becoming pregnant. The age at sexual maturity varies between species and is generally somewhat lower in the male. (PJHB)

Sham chewing

This is chewing in the absence of any feed stimulus. This behavioural problem is common in pigs and is presumed to derive from inadequate **roughage** in the diet. In humans, the motivation to chew food items is also often thwarted by consumption of a highly processed diet lacking fibre. Chewing **gum** can assist such individuals to engage in the behaviour and satisfy the motivation to chew. (CJCP)

Sheep (*Ovis aries*)

Sheep belong to the order Artiodactyla (even-toed ungulates), suborder Ruminantia, family Bovidae, subfamily Caprinae, genus *Ovis*. There are about 200 breeds of sheep (Oklahoma State University, 1995–2022). Breeds can be divided into 'wool-type' and 'hair-type'. The former are largely European and British breeds, such as the Merino and its derivatives, and British Lincoln, Romney and Cheviot breeds, while 'hair-type' sheep include the West African Dwarf sheep and fat-tailed breeds. Franklin (1997) discussed differences in visual features such as shape and length of tail, length and diameter of wool fibres, and ear type (lop or erect). Different breeds also have markedly different types of horn (some have more than one pair), and British or European **wool** and **meat** breeds have different carcass conformations and fleece types from the 'hair-type' sheep.

In Europe, the Americas and Australasia most sheep are European and British breeds kept for wool production, but there are also dairy, meat and dual purpose (wool/meat and dairy/meat) breeds. With demand for wool as a textile fibre declining, meat breeds are becoming more economically important in western countries. Fat-tailed and dwarf breeds are found throughout Africa and Asia, and are mostly used for meat, coarse fibre (hair) and milk.

Sheep bred as primarily wool-producing animals can be classed into fine-woolled, medium-woolled and carpet-wool breeds. Fine wools have fibre diameters of 12–25 microns and are used for high-quality textiles. They are produced by fine-woolled breeds such as

the Merino (originating in Turkey and Spain), those derived from the Merino such as the Delaine and Peppin Merinos and the Rambouillet, and other breeds such as the fine-woolled Baikal. Medium-strength wool (25–39 microns) is produced by sheep such as the British long-wool breeds, for example Leicester, Romney and Cheviot, and stabilized crosses such as the Corriedale, Perendale and Polwarth. Carpet wool (diameter 35–40 microns) is obtained from the 'hairy/fat-tailed' breeds of Asia, Africa and the former USSR such as the Karakul (Deniskova *et al*., 2018) and from breeds including the Drysdale and Elliottdale which have been developed mainly from N-type Romney sheep in New Zealand and Australia.

Sheep meat

(mutton and **lamb**) and milk are obtained in western countries from special-purpose breeds. Meat breeds, such as the Dorset, Île-de-France, Southdown, Suffolk, Texel and Wiltshire Horn, have a short wool coat which is unsuitable for textile manufacture, and in some cases they shed their fleece (e.g. Wiltshire Horn and Dorper). Sheep meat is also produced from some long-wool sheep principally bred for wool production, but which can be used as dual-purpose wool/meat breeds, e.g. Cheviot, Coopworth, Perendale and Romney. In general, meat breeds are more fecund than wool-producing breeds and produce more milk. Dairy breeds include the Lacaunne, Awassi and East Friesian.

Fat-tailed sheep comprise about 25% of the world's sheep population. They are haired sheep of semi-arid and desert regions and are predominant in Africa, Arabia and Asia. Fat-tailed sheep are kept mainly for their meat and/or milk (e.g. Awassi, Darmara,

Dorper, Lori-Bakhtiari, Persian Blackhead). Their skins are used for leather, and some of these breeds also produce a fleece that is used in carpet and other textile manufacture. Fat-tailed sheep are either 'long tailed' or 'fat rumped'. They accumulate fat as an energy reserve in their rump and/or tail

The West African Dwarf sheep is a meat type and is the predominant type in central and south-west Africa (Oklahoma State University, 1995–2022). It is a small, slow-growing animal with an average litter size of 1–1.5 lambs. This sheep is reputed to be tolerant of trypanosomiasis ('sleeping sickness') transmitted by the tsetse fly. (JJR; GMcLD)

See also: Ewe lactation; Wool

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Sheep feeding

There is a wide variation in both the productivity of sheep systems and the quality of the feed resources that they utilize. Thus, the

practical application of feeding strategies involves matching flock requirements with the availability of feeds. As a result of the ability of sheep to digest and utilize feed of widely different qualities, there is considerable latitude in the choice of feeds. Factors that govern this are **nutrient requirement**s in relation to **appetite**, the cost of feedstuffs relative to their nutrient content, the ease of transport and handling of feeds and how well **forage** conservation during times of surplus or production and use of supplementary feed can be accommodated within the production system in order to provide for times of feed deficit.

For grassland flocks in temperate regions, nutritional management during the **grazing** season is based on sward height. In the case of spring-lambing ewes and their lambs grazing high-quality pasture (**organic matter** (OM) **digestibility** 75–80%) there is no benefit, in terms of lamb production, from feeding **cereal**-based **supplement**s when sward height exceeds 3 cm (Treacher, 1990). Above this level of availability of a highly digestible pasture, substitution rates (i.e. the reduction of herbage intake per unit of supplement) are large (> 0.9 g OM g^{-1} herbage OM), thereby cancelling out the ability of additional **starch**-based concentrate feeds to boost the ewe's **energy intake**. Oddly, despite the high **crude protein** content of pasture (about 17% of dry matter), substitution rates are much lower and ewe **milk** yields and lamb **growth** rates significantly higher when protein-based, rather than starch-based, concentrates are given, particularly when the **protein source** is high in **rumen** undegradable protein (Penning *et al*., 1988). The same is true for 6-week-old lambs

weaned on to either ryegrass or clover pastures even though, in the case of clover, its crude protein content appears to exceed requirements (Robinson, 1990a).

As the grazing season progresses and both the ewe's milk yield and the digestibility of her grazings decline, a gradual increase in pasture height from 3 cm to 6 cm is required, to minimize the seasonal decline in lamb growth rates. Following their **weaning** at 12–16 weeks, the growth of those lambs that have not been marketed for meat is particularly sensitive to herbage availability. If the aim is to ensure that these animals gain weight, sward heights should be increased to above 5 cm. At this point further increases in lamb growth rate can be achieved by again providing a small amount of a protein-rich concentrate. Alternatively, if the aim is to arrest the growth of the lambs for later marketing, the adoption of lower pasture heights and higher stocking densities is indicated. Subsequent re-alimentation of these animals in preparation for feeding for slaughter is best achieved by giving them, for a 2-week period, a diet rich in a high-quality rumen undegraded protein such as that supplied by fish meal (Ørskov, 1987). This ensures repletion of body proteins lost during the period of growth arrest, thus allowing the lambs subsequently to achieve normal growth on the lower-protein diets recommended for the pre-slaughter period.



The nutritional management of grazing sheep is based on sward height. Photo courtesy of Gerben Jacobs. Licensed under CC BY 2.0.

When lambs become overfat through delays in marketing, making them unacceptable to the meat industry, dietary manipulations can be used to bring their **body composition** into line with **carcass** specifications. The procedure involves reducing their energy intake to just under **maintenance** needs by, for example, the feeding of **barley straw** to appetite while at the same time providing them with a high-quality rumen undegraded protein at about 2 g per day kg^{-1} body weight. This feeding regimen is highly effective in reducing the fat content of the carcass, while at the same time promoting the growth of lean tissue (Vipond *et al.*, 1989).

After their lambs are weaned and prior to remating, ewes usually have to replace **body fat** reserves lost during **lactation**. Achieving target **body condition** scores at mating involves

adjusting stocking densities and pasture availability or, where pastures are inadequate, the provision of conserved **forage** with or without energy and protein **supplementation**. Where sward heights and green leaf masses are above 3 cm and 100 kg ha^{-1}, respectively, voluntary intake of herbage energy equates to 2–2.5 × maintenance in ewes of body condition score 2 (Treacher, 1990). This means that approximately 2 months are required to bring their body condition up to the optimum of 3–3.5 for maximum ovulation rate. If supplements are required, it is best to provide them in the form of high-quality conserved forage or as small amounts of fibrous concentrates (e.g. **sugarbeet** pulp or whole **oats**) that are slowly fermented in the rumen. This avoids the risk of acidosis and its accompanying adverse effects on the oocyte and early embryo (McEvoy *et al*., 2001). Whole **lupin** grains are also a useful supplement for enhancing ovulation rate, particularly as their beneficial effect is expressed following a relatively short pre-mating period (about 1 week) of supplementation (Nottle *et al*., 1990).

Although conserved forages can be used to improve ewe nutrition and body condition pre-mating, they are mostly reserved for the peak nutrient demands of late pregnancy and early lactation. Where ensiling is used as the conservation method, care must be exercised to avoid soil contamination of the herbage during the harvesting process as this can lead to listeria-induced **abortion**s and ewe deaths. For this reason, many sheep producers prefer to conserve forages by drying. This has the added advantage that voluntary intakes of hays are higher than of **silages** that have

a similar **nutritive value** but, when supplemented with cereal-based concentrates, **hay** intakes decline more rapidly than those of silage (Robinson, 1990b).

Home-grown cereal grains for on-farm mixing with high-quality protein balancers are widely used for supplementing conserved forages during late pregnancy and early lactation. In the case of pregnancy, they can be given at a constant level along with free access to forage or in gradually increasing amounts in proportion to fetal growth. Unless conserved forage is in the form of silage, there is no need to process the cereal grains, as the losses of whole grains in faeces are usually < 5%, which is the approximate cost of processing the grains. Even for silages, the extent of the comminution of the grains should be minimal in order to reduce the detrimental effects of their rapid **fermentation** in the rumen on the growth of the cellulolytic bacteria and thus on fibre **digestion** and forage intake. For lambs abruptly weaned on to all-concentrate diets at 5–6 weeks of age, there is the additional advantage that feeding cereal grains whole reduces the incidence of unacceptable soft **fat** in their carcasses (Ørskov, 1987). The preferred cereal grains for these early-weaned lambs are barley, **maize** and **wheat**. Because of their high content of husk, **oats** are unsuitable for feeding whole. Their undigested husk component remains in the rumen for an extended period, restricting the intake of **digestible energy**, and consequently their growth rate, to about 60% of that obtained using the other cereal grains. (JJR)

See also: Sheep nutrition

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Sheep meat

The edible component of sheep carcasses. It is usually classified by age of animal into: lamb (up to approximately 8 months); **hogget** (approximately 8 months to 2 years); or mutton (> 2 years).

Reference

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Sheep meat, effects of nutrition

Small ruminants (including sheep) consume a wide range of feeds such as grasses, fodders, shrubs, vegetative parts of small and large trees and their foliage – the latter is a point of difference to larger ruminants. The meats from sheep, such as lamb and mutton, are often niche components of a consumer's diet when compared with the meat from other farm animals (e.g. **beef** or **pork**), depending on societies, restaurants and markets. This is partially because of the religious aspects of sheep meat consumption, as well as due to its particular flavour and texture characteristics associated with the **fat** level and fat composition.

Vegetative parts of tree **legumes**, seeds and pods, shrubs, agroindustry co-products or novel pasture species are inexpensive and widely available in many parts of the world. These alternative feed resources can be used for **meat production** from small ruminants (sheep or goats) and many of them contain secondary **metabolite**s, such as **tannins**, flavonoids, **carotenoid**s and other phytochemicals. These secondary metabolites have different

mechanisms or aspects in bypassing the nutrients through the **rumen**. Such feeding practice can increase animal health and wellbeing by the alleviation of worm infestation as well as enhanced chemical, nutritional and sensory attributes of their meat products.

Carcass characteristics of meat from sheep (or lambs)

In production systems around the world, if fresh pasture availability is low, it is common for farmers to provide concentrate diets (in a **feedlot**), or **supplementation** with **grain**s or **protein** meals, that are high in **energy** and protein, to attain faster **growth** rates and desired carcass weights at slaughter. Such a strategy results in animals delivering larger carcasses at a younger age when compared with pasture feeding solely, which are consequently often fatter. The major fat depots of mammalian animals are subcutaneous, intermuscular, abdominal and intramuscular (marbling) fat. The quantity and quality characteristics of fat in the carcass or primal cuts are significantly influenced by animal nutrition. For example, feeding concentrate-based diets increases carcass fatness and mainly oleic and linoleic **fatty acid** concentrations in the fat depots. Conversely, pasture and **forage** feeding increase the level of **polyunsaturated fatty acid**s in the animal's fat depots, such as omega-3s and rumenic acids.

Supplementation of sheep diets with **lipids** and fats may be used as a strategy to increase the **nutrient availability** of diets for **fattening** sheep when the nutrient composition of pasture or forage is low. Due to the nature of feeds consumed and the

complexity of their four-chambered **stomach**, ruminants are accustomed to harvesting forage/**roughage** materials that consist of 1–2% lipids on a dry matter basis. However, when **oilseed**, oilseed meals or **oil** supplement a basal roughage diet, the fat concentration can be increased up to 4%. Feed with more than 6% lipids, on a dry matter basis in the diet, can negatively interfere with dry matter intake and **digestion** of feeds, with reduced microbial activity. This can therefore affect carcass weight and **muscle** (meat) composition at slaughter. Lipids in the diet can be effective at lower concentrations, because they contribute approximately 2.5 times more energy than carbohydrates and produce less heat than carbohydrates and proteins during digestion and **absorption**. This is because fat has a much lower heat increment in the rumen when compared with **starch** and fibre. Consequently, the supplementation of fat in the diet is associated with reduced metabolic **heat production** per unit of energy consumed from the diet.

When sheep of similar genetics and age are grown under the same feeding conditions and compared, the carcasses from faster-growing sheep have more fat than those of the slower-growing sheep (Ponnampalam *et al*., 2007). As such, within a **genotype**, at a particular age, there is variation in fat and muscle accretion, with faster-growing animals diverting more energy into fat deposition than lean, compared with slower-growing sheep. This may be due to the difference in the mature size and growth characteristics, which show a reduction in protein accretion as body weight increases. When carcass compositions of sheep of different

genotypes were compared at different ages of 4, 8, 14 and 22 months, it was found that carcass muscle content decreased from Merino to Poll Dorset to Border Leicester sires at each age when joined to Merino ewes, while carcass fat content increased in the opposite direction (Ponnampalam *et al*., 2008). This suggests that, between genotypes, the muscle and fat deposition vary as the animals grow older, due to differences in metabolic rate and dietary energy partitioning into body tissues and other organ growth. For example, Merinos tend to use more dietary nutrients towards **wool growth** while crossbred sheep tend to use more dietary nutrients towards fat or muscle deposition in the carcass. In young growing lambs, dietary nutrients are partitioned towards muscle and bone development and the rate of fat accretion in the body is relatively low (Searle *et al*., 1972). As the muscle growth begins to slow with age, the rate of fat accretion increases in the body and it has been reported (Vernon, 1980) that sheep enter into a fattening stage at around 7–8 months age (from 200 to 250 days), where accumulation of fat occurs, and this may be earlier in rapidly maturing breeds.

The plant species offered to the sheep also affect growth characteristics and energy partition in the body, which is often associated with plant botanical composition, nutrient characteristics (e.g. protein type) and **metabolizable energy** concentration. For example, it has been reported that lambs fed **chicory** plus arrowleaf clover, **lucerne** or **brassica** have fatter carcasses than lambs fed lucerne plus phalaris, or bladder clover, and this was attributed to the higher content of metabolizable

energy and **crude protein** for chicory plus arrowleaf clover and lucerne pastures (De Brito *et al*., 2017). Brassica forage had a lower metabolizable energy and crude protein content compared with several of the other forage types evaluated in this study. Excess fat in the carcass or primal cuts may decrease the economic value of the product, since excessive subcutaneous fat must be removed during the boning and retail process.



Sheep meat quality is affected by the type of diet the sheep are fed. Photo courtesy of David Hopkins

Chemical composition

Balancing the dietary protein and energy concentration of feeds in animal production is essential for maximizing muscle composition and meat nutritional value. Diets providing protein and energy above or below the **nutrient requirement**, at any physiological

stage, can be inefficient for optimum muscle production and **chemical composition**. For example, when dietary protein is offered in surplus by feeding high-protein diets, this will result in excess **ammonia** production within the **gastrointestinal tract** of sheep. This ammonia will be absorbed by the rumen, **reticulum** and **omasum**, carried in the portal vein to the **liver** and subsequently be converted to **urea** and ultimately excreted in the **urine**. Alternatively, suboptimal dietary protein provision can cause an imbalance in the **protein:energy ratio** of the diet and the amount of protein (**amino acid**s) absorbed in the intestine. This may then affect the rate and efficiency of **protein synthesis** and muscle composition in sheep (Ponnampalam *et al*., 2003). Generally, there is no response to increasing the **crude protein** content of concentrate diets beyond 15% on growth and muscle deposition in sheep.

If the energy concentration of the feed or ration is above the requirement for **maintenance** and growth of animals at a particular age or stage of **maturity**, the excess energy will be deposited as fat depots within the muscle (intramuscular) or between the muscles (intermuscular) or as **adipose tissue** on the external carcass (subcutaneous). This can negatively affect the chemical composition and fatty acid profile of the meat. A lower fat (lipid) content in meat may positively influence the acceptance of a **meat product**, as consumers sometimes will have reservations about the consumption of ruminant fat, especially from sheep, due to its high content of **saturated fatty acid**s.

Fatty acid profile

The fat content and fatty acid concentration in meat and meat-based products is vital because of the dietary nutritional guidelines that have been introduced by government authorities around the world. These are designed to maintain the daily intake of energy, protein and other nutrients by individuals so as to avoid **metabolic disorder**s associated with an imbalance of dietary intake or over-consumption. The nutrient concentration (e.g. **essential fatty acid**s) of animal-based foods (e.g. meat) is usually expressed in mg per 100 g of food (or a portion of meal), which may be related to nutrient intakes, human nutrition and health.

In general, ruminant fats are more saturated (i.e. higher **stearic acid**) than non-ruminant fats. Ruminant fats have a very diverse fatty acid composition, due to microbial activity and biohydrogenation of lipids in the rumen. As a percentage of total fatty acids, tallow typically contains 2–5% myristic, 20–26% palmitic, 7–17% stearic, 30–45% oleic, 0.5–2% linoleic and 2–4% ***trans*-fatty acid**s, respectively. Mutton tallow contains 5–10% more stearic acid than beef tallow, due to the greater biohydrogenation in the rumen of sheep. When sheep are fed pasture and forages (**grass silage** and **haylage**), their meat tends to have a greater concentration of omega-3 fatty acids, conjugated **linoleic acid** (LA) and a lower ratio of omega-6 to omega-3 fatty acids that is nutritionally favourable. Alternatively, when ruminants (sheep, goats or cattle) are fed with grain supplements or concentrate mixed rations high in grains, their meat has increased fatness, with increased levels of C16 and C18 monounsaturated fatty acids and C18 and C20 omega-6 fatty acids

(Nuernberg *et al*., 2005).

Diets rich in forages promote the growth of fibrolytic microorganisms that are responsible for the hydrogenating process in the rumen and, consequently, the increased production of C18:1 *trans*-11 (precursor of conjugated linoleic acid in tissue) and conjugated linoleic acid. The proportion of C18:1, C18:2 and C18:3 is highest in the meat of lambs grazed on red clover (a legume), compared with meat from lambs grazed on lucerne or perennial ryegrass, and this is related to the differences in the fatty acid composition between the forage types. There is a higher polyunsaturated:saturated fatty acid ratio for the legume compared with perennial ryegrass and a higher dry matter intake observed for lambs grazing on the legume. For finishing lambs fed diets based only on forage during dry conditions, it is often necessary to have a supplementation strategy. The type, level and duration of supplementation can alter the meat fatty acid concentration and, consequently, **meat quality** and sensory characteristics.

The 18-carbon omega-3 (C18:3 n-3) and omega-6 (C18:3 n-6) fatty acids are classified as essential fatty acids because they cannot be biologically synthesized by animals, including humans. They are called precursor fatty acids and are mainly deposited in the **phospholipid** fraction of muscle tissues. These 18-carbon precursor fatty acids must be provided via feed sources to sheep and other ruminants. The deposition of dietary LA in the muscle tissues further enhances the production of the longer-chain omega-6 fatty acids, C20:3 n-6, C20:4 n-6 (**arachidonic acid**) and C22:4 n-6 (adrenic acid), through desaturation and elongation processes.

Feeding pasture-based diets such as grass or silage results in meat with elevated levels of α-**linolenic acid** in comparison with sheep fed with concentrate-based diets containing **cereal** grains (**oat**, **barley**, **wheat**, **corn**) or protein meals (**lupin**s, **cottonseed**). This fatty acid further enhances the production of longer-chain omega-3 fatty acids, including C18:4 n-3 (stearidonic acid), C20:5 n-3 (**eicosapentaenoic acid** (EPA)), C22:5 n-3 (**docosapentaenoic acid** (DPA)) and C22:6 n-3 (**docosahexaenoic acid** (DHA)) in muscle tissues, through the desaturation and elongation process. **Triacylglycerol**s are the main lipid fraction found in intramuscular fat (IMF), mainly composed of saturated fatty acids and monounsaturated fatty acids, and are negatively related to the composition of polyunsaturated fatty acids. Polyunsaturated fatty acids in meat not only affect the flavour and storage stability; they are also positively associated with the lean content and nutritional value of meat. Meanwhile, specialized feeds and mixed rations that contain oilseeds and oilseed meals, such as flax, canola and camelina, as supplements, have been shown to increase alpha-linolenic acid and the longer-chain omega-3 fatty acids EPA or DHA in meat. Likewise, feeding marine-based products such as **seaweeds**, **algae**, fish meal and fish oil as supplements to sheep diets have been shown to elevate the levels of longer-chain omega-3 fatty acids EPA, DPA and DHA in meat. The deposition of omega-3 series polyunsaturated fatty acids can be increased in muscles due to the diversity and freshness of forage species, as well as the prolongation of forage intake when compared with finishing animals on a grain-based diet (Shingfield

et al., 2013).

Odd- and **branched-chain fatty acid**s are quantitatively minor fatty acids that can be found in the meat- and milk-fat from animals. These fats mainly come from intestinal digestion of bacteria washed out from the rumen in solid and liquid phases. The lipids of rumen bacteria differ between species. Cellulolytic bacteria usually contain more iso-fatty acids, whereas amylolytic bacteria are mainly rich in linear **odd-chain fatty acid**, with a few strains displaying high contents of anteiso-fatty acids. In one study, sheep fed perennial ryegrass, lucerne and **brassica** forages were reported to have concentrations of 220–393 μg 4-methyloctanoic acid g^{-1}, 89–170 μg 4-ethyloctanoic acid g^{-1}, and 35.1–63.6 μg 4-mythylnonanoic g^{-1} in subcutaneous adipose tissue (Frank *et al.*, 2016). This indicates that nutrition impacts on the accumulation of these fatty acids, mainly in subcutaneous adipose tissues. In muscle tissues the levels are very small and hard to quantify. Lambs fed a concentrate diet generally have more branched-chain fatty acids in subcutaneous adipose tissue than pasture-fed lambs, due to increased formation of propionic acid in the rumen of concentrate fed lambs.

Physicochemical properties

The nutritional background (feeding systems) of sheep can affect the colour, pH, tenderness and nutritional value of meat. These outcomes result from variation in the dietary composition, energy and protein concentration of a diet, **feed intake**, **grazing** behaviour and digestion processes of feeds consumed. Forage feeding generally improves the nutritional value of meat when

compared with finishing sheep or goats with cereal grain supplementation or a feedlot-type concentrate diet. The modification of dietary ingredients in sheep rations, such as the inclusion of oils from seeds and oilseed meal from industrial **by-product**s, is an alternative strategy to modify the nutritional value of meat when compared with feeding of low-quality pulses (lupins, faba beans, **lentils**) to animals consuming cereal **straw** or chaff. Some examples include the addition of **safflower**, licuri, cotton, **sunflower** and buriti to the diet. Feeding studies collectively show that, depending on the quantity, composition and source of the oil supplied in the diet, the ruminal metabolism and **intestinal absorption** of polyunsaturated fatty acids may be increased, allowing an increased deposition of polyunsaturated fatty acids in the meat (Salami *et al*., 2019; Ponnampalam *et al*., 2021a).

For lambs at the finishing stage (8–9 months), fat deposition within and between muscles (respectively, intra- and inter-muscular fat) is a critical factor affecting meat quality. A typical example of Australian finishing systems in summer to autumn is to use lupins, a legume grain, to increase dietary energy and protein concentration for sheep. For example, when 9-month-old first-cross sheep were fed either a basal diet of alfalfa hay:oat **hay** (20:80) *ad libitum* alone, basal diet supplemented with lupins (360 g per day) or the basal diet supplemented with lupins (180 g per day) and barley (180 g per day), this resulted in intramuscular fat contents from 3.3% to 4.2%. In this study, the daily metabolizable energy and crude protein intakes of lambs fed basal, basal plus lupins and basal plus lupins/barley diets were 8.2, 10.6, 10.8 MJ

and 124, 209 and 177 g, respectively (Ponnampalam *et al*., 2002). This shows that sheep provided with high-energy diets, such as fed in a feedlot or supplemented with legume grains, tend to deposit more fat in the carcass and muscle tissues than those finished with pasture- or forage-based diets that are often low in energy. Intramuscular fat is an important component determining the physicochemical properties, as it impacts on the tenderness, juiciness, flavour, colour and **water-holding capacity** of meat. The higher levels of fat in the carcass and primal cuts can contribute to lower water losses during cooking, resulting in more succulent meats. This is the result of the fat in the meat acting as a barrier to moisture loss. In addition, the fats (lipids) within the muscle and between the muscle cuts can provide juiciness and flavour to cooked meat based on the level and fatty acid type, which in turn can be enhanced by cooking in covered pots or covering with aluminium foil.

Lambs offered intensive feeding (usually in stalls) have a lower **acetate/propionate** ratio in the rumen. This is due to the provision of concentrate diets rather than allowing lambs to graze, which explains their higher growth rate and greater IMF deposition. Noting that pasture quality is likely to differ between Australia and New Zealand, and regions within a country, the IMF of meat from lambs grown in New Zealand is less than that from the animals grown in Australia and North America. This is due to the nutritional background of finishing animals, since sheep in New Zealand are mainly raised just on pasture whereas in Australia and the USA sheep often receive grain supplements to forages/pasture

or concentrated mixed rations (Phelps *et al*., 2018; Ponnampalam *et al*., 2002). Fat content preferences may vary over time and between locations. Early studies conducted in the USA in the 1980s showed that an IMF content of 3–3.5% was adequate for consumer satisfaction. However, studies conducted in Australia indicate that meat with IMF content of 4–5% is better for consumer preferences and **palatability** (e.g. Hopkins *et al*., 2006). In addition, properties such as the colour and tenderness (Warner-Bratzler shear force) of meat can affect the appearance, consumer appeal and softness of the meat. These parameters, together with fatty acid composition, predict the acceptability of meat by the consumers (Holman and Hopkins, 2021).

Meat tenderness is influenced by many factors, such as **collagen** content, collagen cross-linkage type, **connective tissue**, muscle fibre types, muscle **enzyme activity** and to some extent IMF content. These are affected by the nutritional background and age of animals. In general, meat from lambs fed a forage-based diet is less tender than meat from lambs fed concentrates. This effect could simply reflect a difference in carcass fatness and, thus, cooling rates during rigor development. For example, carcasses with a lower fat thickness are prone to fast chilling and an increased rate of carcass cooling, which can influence enzyme activity, impacting on tenderization of muscle proteins as well as shortening of muscle fibres, leading to tough meat. To meet consumer acceptability for Australian lamb, meat tenderness below approximately 30 Newtons is required (Hopkins *et al*., 2006), but this level will vary between countries, markets

and consumer groups. A recent study showed that the average tenderness of composite lambs (lamb) and yearling sheep (mutton) meat were 33.3 and 35.9 Newtons, respectively (Ponnampalam *et al.*, 2021b). Both composite lambs (crossbred) and Merino yearlings were finished on typical forage-based diets with cereal grains or camelina meal, and tenderness values were consistent and within the range for tender meat from previous studies conducted in lambs fed diets with oaten hay and cereal grain or oaten hay and **protein supplement**s.

Dietary protein and energy concentration can influence the tenderness of meat by altering either the components of connective tissues or the calpain enzymatic processes responsible for proteolysis. There is evidence that faster growth rates prior to slaughter can affect tenderness and cooking losses in meat. This could be due to a faster growth rate enhancing the deposition of younger muscle fibres with less structured connective tissues. The faster growth rate in younger animals may lead to more lean content and younger muscle fibres with less connective tissues and more soluble collagen – with these the **skeletal muscle** bundles are able to retain more water in the tissues.

The energy concentration of a diet plays a major role in determining the muscle energy status, which in turn is a crucial factor in maintaining the muscle pH at low levels post-slaughter. It is common for sheep grazing diets that contain low energy and low protein concentrations to produce meat with a higher pH after 24 h (pH_{24}) post-slaughter than those fed high energy concentrate diets. This is partially due to there being less muscle **glycogen** stored

within the muscles at the point of slaughter for grazing or forage-fed animals. The pH of meat between slaughter and pH_{24} has a marked influence on contraction, proteolysis and protein denaturation of skeletal muscle tissues, leading to changes in the structural (texture, tenderness) and functional (colour) attributes of muscle fibres during the conversion of muscle to meat. A higher muscle pH produces a dark meat colour, firm muscle texture and dry meat surface. Sheep meat that does not have the capacity to retain water will have major loss of liquid during post-mortem storage at retail display or during the cooking process, which can negatively affect its saleability.

The colour of lamb and sheep meat is a main influencer of customer purchasing behaviour, because it can impact on the decision making of individuals whether to buy the particular steak/primal cut or not to buy (reject). The feeding strategy can influence meat colour – often measured using the CIE spectrometry colour coordinates; lightness (L^*), redness (a^*) and yellowness (b^*). Lambs fed concentrates exhibit a lighter meat colour compared with those fed grass. This effect could be partly due to the ultimate pH of the muscle being lower in concentrate-fed animals than those fed grass, because of greater muscle glycogen concentration. A higher ultimate pH leads to a darker-coloured meat. Related to this, adding condensed tannins to the diet of lambs increases the lightness of meat. Saltbush feeding increases lamb meat colour stability, which is believed to be due to altered muscle ultimate pH or increased **vitamin E** concentration in meat leading to increased redness of meat at retail display

(Pearce *et al*., 2008).

The darker meat of pasture-fed lambs has been mainly attributed to (i) the lower energy concentration of forage diet that the animal has been consuming, in part; and (ii) the lower energy intake due to a loss, in part, of dietary energy as **methane** gas that is associated with the digestion of highly fibrous roughage materials. Pasture-fed sheep expend more energy during grazing as they walk comparatively longer distances to harvest their food, and this higher level of exercise leads to muscle with lower glycogen stores. By contrast, a recent study showed that the colour stability, i.e. the maintenance of redness of meat at display, under simulated retail conditions was greater in crossbred lambs and pure Merino sheep fed diets containing 55% roughage-based diet than feeding a ration containing 55% grain-based diet; clearly an effect unrelated to differences in pH (Ponnampalam *et al*., 2020). The latter effect is likely due to the influence of dietary vitamin E, established in previous research conducted in sheep and goats, as the forage-based diet containing lucerne had higher vitamin E (α-**tocopherol**) levels than the grain-based diet containing barley and oat grain.

Sensory characteristics

Lamb meat with a low fat content may have inferior sensory attributes and therefore less acceptance by the consumer. For example, the meat from lamb carcasses with 2.0 mm or less of subcutaneous fat thickness were classified in one sensory test as inferior in **taste** and satisfaction (Sañudo *et al*., 2000). The quantity and distribution of fat in the carcass or primal cuts has an

impact on sensory characteristics of meat, since IMF influences several sensory attributes, such as meat flavour, texture and overall liking. For lamb, Australian studies have suggested that the IMF needs to be 4–5% to ensure good eating quality (Hopkins *et al.*, 2006). Fat deposition represents an increased cost in terms of feed energy compared with lean meat deposition and, in some cases, carcasses can be penalized at the abattoir due to excessive fatness. Furthermore, the market preference is changing and the demand for healthier food is increasing, meaning that animals raised under extensive feeding systems may meet the consumer demand for lean meat and, in this context, the meat may contain less than 4% IMF.



Measuring meat colour on sheep carcasses. Photo courtesy of David Hopkins.

The taste of cooked meat is associated with flavour and aroma

development during **mastication** in the mouth and release of volatile compounds, from fatty acids, especially polyunsaturated and odd- or branched-chain fatty acids. Sensory studies conducted in lamb and sheep meat (mutton) reported complex flavour profiles, dominated by lamby, muttony, livery, metallic, grassy, bloody and greasy flavours; these are affected by the fat level, fat types and the mix of volatile compounds during cooking (Font-i-Furnols and Guerrero, 2014).

Vegetable oils can replace traditional ingredients, such as corn and **soybean**, in the diets of sheep. These will impact on the lipid content and composition of meat, as well as contribute to desirable modifications in the fatty acid content and sensory attributes, such as aroma, taste, tenderness and juiciness of meat. The inclusion of 30% sunflower seed cake in the diet of lambs can improve the sensorial appeal of lamb meat, in addition to improving health-enhancing compounds such as conjugated linoleic acids, the atherogenic index and the ratios of polyunsaturated to saturated fatty acids and polyunsaturated to monounsaturated fatty acids in the meat. In some cases, vegetable oils can improve lamb acceptability to consumers: lambs fed a diet supplemented with 24% licuri cake produced meat with improved sensory attributes that were linked to an increased concentration of omega-3 fatty acids (Costa *et al.*, 2018). In other cases, the inclusion of oils may cause a reduction in the nutritional and sensory attributes of meat. For example, supplementation with buriti oil did not improve the desirable composition of fatty acids in sheep meat; rather, it increased *trans* fatty acids, especially *trans*-10 C18:1.

In general, sheep meat flavour is positively correlated with monounsaturated fatty acids and negatively correlated with polyunsaturated fatty acids, including omega-3 and omega-6 fatty acids. The characteristics of taste have been altered with the increased concentration of omega-6 and omega-3 fatty acids and their proportions in meat. This outcome is likely to result from the organoleptic properties of lipids/fats or propagation of lipid **oxidation** from these fatty acids during storage and the cooking process. The formation of volatile-flavour substances in meat is closely related to its fatty acid composition. Saturated fatty acids in meat fat, especially the **long-chain fatty acid**s, solidify more during cooling, which directly affects the texture and taste of meat. The **unsaturated fatty acids**, especially polyunsaturated, while improving the nutritional value of meat, are also easier to oxidize, due to their unsaturated status causing to some extent **free radical** formation and lipid degradation during storage. On the other hand, during cooking they can oxidize and form volatile compounds, due to their lower melting point than saturated fatty acids. Most of the volatile flavour substances in muscle are the products of fat degradation due to oxidation, such as **aldehyde**s, alcohols, **ketone**s, acids, hydrocarbons and other compounds. These oxidation products can negatively or positively influence the flavour/aroma of cooked meat and some relevant research findings are discussed below.

The intensity of flavour or aroma characteristics of cooked meat can be influenced by the concentrations and types of omega-3 and omega-6 fatty acids in meat that are mostly dependent on the

nutritional background of diet as well as storage time and cooking methods. The flavour of meat from lambs fed concentrate diets supplemented with flax oil, fish oil, protected lipid supplements, fish oil with marine **algae** or protected lipid supplements with marine algae has been studied (Nute *et al*., 2007). Lambs fed with flax oil had the highest concentration of linolenic acid in their phospholipids and gave the highest ratings for meat flavour and overall liking and a lower rating for abnormal lamb flavour, similar to the findings from other studies (Choi *et al*., 2000; Vatansever *et al*., 2000). Diets supplemented with fish oil and protected lipid supplement with marine algae have produced meat with high concentrations of omega-3 fatty acids (EPA and DHA), but also more abnormal flavours, while reducing the rating of lamb flavour. Flavour intensity and flavour liking for lamb meat are strongly associated with linolenic acid concentration. The concentration of linolenic acid in lamb meat increases with grass feeding when compared with concentrate feeding, and the lamb flavour intensity increases and abnormal flavour is reduced. Grain-fed lambs by contrast deposit more linoleic acid (C18:2 n-6) in their muscles and have a less intense meat flavour, compared with grass-fed lambs which have intense flavour due to the deposition of higher linolenic acid (C18:3 n-3) levels in the muscles.

The sheep's diet influences the formation of branched-chain fatty acids, which are regarded as the main contributors to the mutton flavour in cooked sheep meat. The branched-chain fatty acids present in red meat, such as 4-methyloctanoic acid, 4-ethyloctanoic acid and 4-mythylnonanoic, are present in low

concentrations and are hard to determine quantitatively; and the critical concentrations that detrimentally affect the taste or flavour of meat from sheep, goats or cattle are not known. Recent studies (Schiller *et al*., 2015; Frank *et al*., 2016) have been able to identify the dietary effects on the concentration of 4-methyloctanoic, 4-ethyloctanoic and 4-methylnonanoic acids in subcutaneous **adipose tissue**, since these branched-chain fatty acids are present in greater concentration in subcutaneous adipose tissue and thus easier to quantify. However, the subcutaneous fat layers or depots are mostly trimmed during carcass processing at the abattoir level, then during primal cut preparation at the retailer level and finally during the cooking process, so the final impact of these on sensory traits is small. It is well established that, in ruminants, appropriate applications of **antioxidant**s (natural or synthetic) in feeds can be used to alleviate the off-flavour development from lipid oxidation of **animal fat** in meat and processed meat products. (ENP; BWBH)

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Sheep nutrition

Despite major differences between breeds in the quantitative expression of **production** traits, some of which can be single gene effects (for example, the *collipyge* gene for increased muscularity), it is extremely difficult, at the whole-animal level, to demonstrate differences between breeds in the amounts of energy or protein required for maintenance and gain. Nonetheless, selection within a breed for increased **muscle** growth is accompanied by alterations in the responses of muscle **protein synthesis** and degradation, and of **oxygen** consumption, to **feed intake** (Oddy, 1999).

Selection for production traits stimulates pre-absorptive as well as post-absorptive effects on efficiency. For example, selection for **wool** production increased the quantity of rumen **microbial protein** at a fixed level of food intake, resulting in a 30% increase in the uptake of α-amino **nitrogen** in portal blood (see review by Oddy, 1999). Pregnancy also enhances by approximately 15% the quantity of α-amino nitrogen reaching the **small intestine**. So too does cold stress (Kennedy *et al*., 1976). For these latter two examples there are accompanying decreases in rumen **retention time** and, in the case of cold exposure, a reduction in diet

digestibility equivalent to about 0.2 units per degree fall in the ambient **temperature** below 20°C.

For breeds kept in high latitudes the males (intact and castrated) exhibit seasonal fluctuations in metabolic rate equivalent to approximately ±15% of the annual mean (Blaxter and Boyne, 1982; Argo *et al*., 1999); highest and lowest values coincide with the longest and shortest days, respectively. These seasonal effects on **metabolism** precede similar fluctuations in appetite and correspond to seasonal fluctuations in the circulating concentrations of thyroid hormones. The seasonal effect on appetite is smaller for females than for males and very small in breeds such as the Dorset Horn, which are much less seasonal in their breeding activity than the Soay or Suffolk or indeed the Scottish Blackface and Shetland, with which their intakes have been compared (Iason *et al*., 1994).

Estimates of **energy requirement**s for **maintenance** are based on calorimetric determinations of fasting metabolism and take into consideration a 15% higher value for intact males than for castrates or females; they also embody a decline in **fasting metabolism** with age. AFRC (1993) gave the fasting energy requirement (F) of female sheep as F (MJ per day) = $0.25(W/1.08)^{0.75}$ up to 1 year of age and $0.23(W/1.08)^{0.75}$ beyond 1 year old. In these equations W = **liveweight** (kg) and 1.08 is the factor used to convert liveweight to fasted weight. Additional energy costs for activity are estimated to be 2.6 and 28 J W^{-1} m^{-1} moving horizontally and vertically, respectively, and 0.42 kJ W^{-1} h^{-1} for standing as opposed to lying. The energy cost of body

positional change is estimated to be 260 J W^{-1}. Dividing the sum of fasting metabolism and activity costs by k_m (the efficiency with which metabolizable energy, ME, is used for maintenance) provides estimates of ME requirements for maintenance. Because k_m varies with q_m (the proportion of **gross energy**, GE, that is metabolizable, i.e. q_m = ME/GE), it is calculated for diets of different **metabolizability** using the relationship $k_m = 0.35q_m + 0.503$.

Energy requirements for liveweight gain in growing lambs are calculated from estimates of their energy gains in **fat** and protein (39.3 and 23.6 MJ kg^{-1}, respectively). For practical application, energy gains (EVg, MJ kg^{-1} liveweight gain) are estimated to be $2.5 + 0.35W$ for males, $4.4 + 0.32W$ for castrates and $2.1 + 0.45W$ for females, where W = body weight (kg). Dividing these values by k_f (the efficiency of ME utilization for growth) provides estimates of ME requirements for **growth**; in this case $k_f = 0.78q_m + 0.006$. For **wool** production, the energy gain is estimated to be 23.6 kJ g^{-1}. Using the CSIRO (2007) estimate of efficiency (18%) of use of ME for its production gives an ME requirement of approximately 130 kJ g^{-1} or 650 kJ per day for a daily wool growth of 5 g.

The preceding principles are also used to estimate ME requirements for **pregnancy**. For this calculation AFRC (1993) estimated energy retention in the conceptus, E_c (MJ per day), to be $0.25W_0 (E_t \times 0.07372e^{-0.00643t})$, reflecting the exponential nature of fetal growth. In this equation, t is the number of days from conception, W_0 is the total weight (kg) of lambs at birth and E_t is

obtained from the relationship $\log_{10}(E_t) = 3.322 - 4.979e^{-0.00643t}$. Again, dividing these estimates for energy gain in the conceptus by k_c, the efficiency of ME utilization for conceptus energy gain, provides estimates of the ME requirements for pregnancy. AFRC (1993) took a standard value for k_c of 0.13. This value is calculated from the **net energy** needed for fetal growth expressed as a proportion of the total amount of ME used for the growth of the fetus plus growth of the uterus and the placental and uterine tissues. There is evidence that, as for k_m and k_f, k_c varies with the metabolizability of the diet (Robinson *et al.*, 1980), with the regression coefficient of k_c on q_m being 0.53, i.e. intermediate between the values for k_m and k_f. For energy requirements in lactation, *see* Ewe lactation.

AFRC (1993) based protein requirements on **metabolizable protein** (MP), in which MP = 0.6375(MCP + DUP), where MCP = microbial **crude protein** and DUP = digestible undegraded feed protein. Requirements of MP are estimated to be $2.1875W^{0.75}$ g per day for the maintenance of growing lambs and $2.1875W^{0.75} + 20.4$ g per day for adult ewes. For growth, MP is estimated to be used with an efficiency of 59%. In the AFRC (1993) system this gives a requirement for males and castrates, including the requirement for wool, of $(334 - 2.54W + 0.022W^2) \times \delta W + 11.5$ g per day, where δW = daily liveweight gain (kg) and W = liveweight (kg). For females the coefficients for W and W^2 are 4.03 and 0.036, respectively. Pregnancy requirements, according to AFRC (1993), are based on an efficiency of utilization of MP for conceptus

protein gain of 85% and are estimated to be $0.25W_0$ ($0.079\ TP_t \times e^{-0.00601t}$) where t = days from conception, W_0 = total lamb birthweight (kg) and TP_t is obtained from the relationship $\log_{10}(TP_t) = 4.928 - 4.873e^{-0.00601t}$. Other estimates of the **nutrient requirements** of sheep are given by INRA (1989), CSIRO (2007) and NRC (2007).

Sheep, in particular the long-woolled breeds, have a higher requirement for the **sulphur-amino acid**s (S-AA) **methionine** and **cyst(e)ine** than other animals as these are used in the production of keratin (*see* Wool growth and quality, effects of nutrition). Supplementary S-AA are incorporated into wool protein, with a gross efficiency of about 0.2 (CSIRO, 2007).

AFRC (1991) used the preceding principles for estimating the requirements for the major mineral elements, **calcium** and **phosphorus**, but linked them to energy intake, the major determinant of animal performance. For growing lambs the AFRC (1991) estimates for calcium requirements increase from 0.7 g per day for a 20 kg lamb maintained on a diet of q_m 0.5, to 4.0 for the same lamb gaining 200 g per day on a diet with a q_m of 0.7. The latter value rises to 5.4 g per day at the higher growth rate of 300 g per day. Corresponding values for phosphorus are 0.5, 2.5 and 3.7 g. During pregnancy, estimates of daily calcium and phosphorus requirements (g) for a diet with a q_m of 0.5 fed to a 40 kg ewe carrying a single fetus increase from 1 to 3.6 g for Ca and from 1.1 to 2.8 for P over the last 12 weeks of pregnancy. For a 75 kg ewe with twin lambs and receiving a higher-quality diet (q_m = 0.7), the corresponding values are 1.2 and 6.9 for Ca and 0.8 and 3.5 g for

P. (JJR; GMcLD)

See also: Ewe lactation; Sheep feeding

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Shell-less eggs:

see Egg formation; Eggshells

Shellfish

Shellfish are generally considered to include all edible marine and freshwater invertebrates that have some sort of external or internal shell. In addition to the **mollusc**s, they include crustacean groups such as **shrimp**s and prawns, crabs, **lobster**s and crayfish, as well as planktonic **krill**, which are normally considered to be the food of the great baleen whales. **Sea urchin**s are also considered to be shellfish by reason of their calcareous tests.

Crustaceans in particular have been the subject of important fisheries. Total landings of shellfish in 2020 were about 44.8 million tonnes, of which about 44.0 million tonnes came from Asian countries. The most popular are shrimp, especially whiteleg shrimp *Panaeus vannamei,* and red swamp crawfish, *Procambarus clarkii* (FAO, 2022). Many species are now being cultivated intensively. Some tropical marine shrimps are cultivated traditionally by allowing naturally spawned juveniles to enter

lagoons which are then sealed from the open sea. The shrimp are then fed until such time as they are large enough for harvest. Hatchery technology has developed to the point that some crustaceans can be cultivated independently of wild larval production. Freshwater species are also cultivated. Technology is now being developed for the culture of lobsters, crayfish and crabs. (DJS; QS; CJCP)

See also: Mollusc culture

Reference

FAO (2022) *The State of World Fisheries and Aquaculture 2022. Towards Blue Transformation*. Food and Agriculture Organization of the United Nations, Rome. doi:10.4060/cc0461en

Shellfish culture

Shellfish, principally **mollusc**s and crustaceans, have been cultivated for centuries. In some cases, such as the marine **shrimp** and prawn, people have taken advantage of natural seasonal migrations of the species by trapping naturally spawned larvae in shallow lagoons and estuaries. The young shrimp are allowed to feed naturally until they are of harvestable size.

People have also captured naturally spawned spat of molluscan shellfish species such as mussels and oysters and retained them on the seabed, or on artificial structures, where they grow naturally until they can be harvested. **Scallop** seed are now being captured and grown in nets or cages to a size where they are less vulnerable to predation and are then released back on to the seabed for further natural growth before being harvested by traditional fishing techniques.



Shellfish research on Vancouver Island, Canada, is developing ways of cultivating shellfish efficiently. Photo courtesy of VIU Deep Bay. Licensed under CC BY 2.0.

The development of hatchery and nursery technology now allows some species, both crustaceans and molluscs, to be cultivated from the egg stage through to market size. This has opened opportunities for selective breeding and the enhancement of desirable market qualities, and the culture of the species beyond its normal range.

While shellfish culture has made extremely rapid strides, it has also been accompanied in some places by serious problems of disease which plague some segments of the industry. The cultivated tropical shrimp industry has also caused environmental degradation, which is only now being rectified. (DJS)

See also: Mollusc culture; Shellfish

Shells:
see Eggshells; Oyster shell

Shiso (*Perilla frutescens*)
From the Lamiaceae/Labiatae family, an annual herb plant in the mint family that is a native of mountainous regions of China and India. It stands about 1 m tall, with small flowers and grey-brown seeds and shiny green/purple leaves. The popularity of shiso in the human diet is due to the fact that it is a rich source of omega-3 **fatty acid**s of plant origin and can replace fish oils, thereby helping to preserve the **marine environment**.



A field of red shiso. Photo courtesy of Suomi. Licensed under CC BY-SA 4.0.

According to the recommendation of the World Health Organization (WHO), the daily consumption of omega-3 fatty acids,

for example by consuming 2 g of α-**linolenic acid** (ALA), will help to achieve the desired ratio of omega-6 to omega-3 fatty acids of less than 6 (Cherian and Poureslami, 2012). This will have benefits for the immune system of the host (humans and domestic animals), to prevent **blood** clots in the veins and sudden strokes, treating autoimmune problems and preventing severe inflammatory activities. This highlights the importance of consumption of omega-3 fatty acids in daily food plans. The seeds of this plant contain 30–40% **oil**, including 54–65% of omega-3 fatty acids (mainly α-linolenic acid), 11–16% of omega-6 fatty acids (mainly **linoleic acid**), 14–23% of omega-9 fatty acids (mainly **oleic acid**), and the rest as **saturated fatty acid**s (Asif, 2011; Hou *et al*., 2022). More than 271 valuable bioactive compounds have been identified in its leaves and seeds, including phenolic acids, flavonoids, essential oils, triterpenes, **carotenoid**s, phytosterols, fatty acids, **tocopherol**s and policosanols. Recently, in addition to omega-3 fatty acids, a number of individual compounds with medicinal properties, such as rosmarinic, luteolin, chrysoeriol, quercetin, catechin, apegenin, shishonin, perylaldehyde, tourmantic acid and isogumactone, have been identified. Shiso is claimed to have significant **antioxidant**, antimicrobial, anti-allergic, anti-depressant, anti-inflammatory, anti-cancer, neuroprotective and anti-Alzheimer effects in humans and **laboratory animal** models, but it requires more studies (Ahmed, 2018; Hou *et al*., 2022). Research studies on domestic animals also show that the inclusion of **shiso** in the diet can lead to the production of products (meat, milk and eggs) enriched with omega-3 fatty acids, with potential

benefits for improving the health of the animal (Asif, 2011). (AS; BH-G; CJCP)

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Short-chain fatty acids **Saturated fatty acid**s with chain lengths from two to six carbons. They include **acetate** ($CH_3{\cdot}COO^-$), **propionate** ($CH_3{\cdot}CH_2{\cdot}COO^-$), **butyrate** ($CH_3{\cdot}CH_2{\cdot}CH_2{\cdot}COO^-$), valerate ($CH_3{\cdot}CH_2{\cdot}CH_2{\cdot}CH_2{\cdot}COO^-$) and caproate ($CH_3{\cdot}CH_2{\cdot}CH_2{\cdot}CH_2{\cdot}CH_2{\cdot}COO^-$). With the exception of caproate, all are end-products of **fermentation**. (NJB)

Shrimp

Shrimp are related to other animals with jointed appendages such as insects (Phylum Arthropoda) but are further characterized by a hard shell or exoskeleton (Subphylum Crustacea). Grouped with other large crustaceans (Class Malocostraca) such as **lobster**s and

crabs, they have five pairs of walking legs but lack the large pincers and their body tends to be laterally flattened. The abdomen or shrimp 'tail' makes up about half the body and is filled with **muscle**. This muscular tail can be contracted suddenly to escape from danger. The high demand for shrimp tail meat stimulated the development of culture techniques for marine shrimp in the early 1970s. Shrimp **aquaculture** has grown rapidly and now produces almost a billion tonnes of shrimp each year. (DEC)

See also: Crustacean feeding; Prawn

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Shrimp culture

Cultured shrimps include mainly whiteleg shrimp (*Penaeus vanname*), giant freshwater prawn (*Macrobrachium rosenbergii*) and tiger shrimps (*Penaeus monodon*, *Penaeus chinensis*, *Penaeus japonicas*). The most rapid growth is achieved at levels of **lipid** in the diet of 5–6%, whereas more than 10% lipids often reduces growth due to poor **digestion** rates and accumulation of lipids in tissues. Lipids may be added as n-3 LC-PUFA, including **cod liver oil**, menhaden fish **oil**, pollock liver oil, and short-neck clam oil, or

some plant oils as sources of n-6 PUFA. (QS; CJCP)



Shrimp pond with aerator in Indonesia. Shrimp aquaculture now produces almost a billion tonnes of shrimp each year. Photo courtesy of Herman Gunawan. Licensed under CC BY-SA 3.0.

See also: Shellfish culture

Silage

Ensilage originates from the Greek *en* (in) and *siros* (pit), with the product being called silage. Silage making is an anaerobic **fermentation** process and if silage is well made the predominant acid is **lactic acid**, with lesser amounts of acetic, propionic and butyric acids. Silage has become one of the main methods of storing green nutritious **fodder** in times of plenty for feeding ruminants and horses when feed is scarce. A wide range of crops and **by-product**s can be ensiled and a brief but by no means exhaustive list follows: **grasses**, including ryegrasses (*Lolium* spp.), cocksfoot (*Dactylis glomerata*), timothy (*Phleum pratense*), fescues (*Festuca*

spp.) and brome grass (*Bromus* spp.); **legumes**, including clovers (*Trifolium* spp.), **lucerne** (*Medicago sativa*), **sainfoin** (*Onobrychis viciifolia*), **peas** (*Pisum sativum*), **beans** and vetches (*Vicia* spp.) and **lupin** (*Lupinus* spp.); **brassica**s such as **kale**, **turnip**, mangolds, **rape** (*Brassica* spp.) and radish (*Raphanus sativus*); whole-crop **cereal**s such as **maize** (*Zea mais*), **barley** (*Hordeum* spp.), **sorghum** (*Sorghum vulgare*), **wheat** (*Triticum sativum*) and **oats** (*Avena sativa*); and by-products of **sunflower**s (*Helianthus annus*), **potato**es (*Solanum tuberosum*), **sugarbeet** (*Beta vulgaris*), **sugarcane** (*Saccharum officinarum*) and citrus fruit. The type of crop ensiled has a significant impact on silage composition. For instance, legume silages are high in **true protein** and low in **metabolizable energy**, and vice versa for **whole-crop silage**. With grasses, the more mature the crop is at harvesting, the lower will be the **digestibility** and **crude protein** concentration.

There are two key parameters that give an indication of crop ensilability: the concentration of water-soluble **carbohydrate** (WSC) and the buffering capacity (BC). The WSC is fermented by lactic acid bacteria to lactic acid, which preserves the **forage**. Thus the higher the WSC concentration, the easier a crop will be to ensile. The BC is the ability of the crop to neutralize the lactic acid. The higher the BC, the greater is the acid requirement to lower the pH. The BC is related to the amount of protein in the forage. Low-protein crops generally have high WSC levels and vice versa. **Legumes**, with high protein contents, have a high BC but low WSC concentrations and are more difficult to ensile than, say, a whole-

crop cereal with a low protein content and a high WSC level. However, successful ensilage of the legume can give large benefits in terms of the **nutritive value** of the protein conserved for animal feeding.

The process of ensiling starts when the crop is tightly packed into a container and sealed to prevent the access of **oxygen**. Provided that forage is packed tightly, sealed quickly and maintained in an oxygen-free environment, silage fermentation should proceed and a stable product result. The container can, in reality, be anything, as long as it is clean and can be sealed to prevent the ingress of air. The advent of polythene has widened the scope of shape, size and form of silo.



A silage pit dug into a hillside, covered with plastic sheet, weighted down with old tyres to exclude air. Photo courtesy of Phil Catterall. Licensed under CC BY-SA 2.0.

Four main silos are commonly used.

1. Clamp or pit. These types of silo are the most common permanent structures. They consist of two side walls and usually

a back wall and they can be made of earth, wooden sleepers or concrete. Herbage is packed into the silo in thin layers (ideally no more than 30 cm at a time) and consolidated. The layers are built up and finally sheeted with polythene and sealed. The polythene sheet is weighted down with tyres or sandbags to minimize air ingress.

2. Bales. These are placed into polythene bags or wrapped in polythene film.
3. Towers. These are tall cylinders built of concrete or steel, typically 5 m in diameter and can be 20 m high. They are an ideal way of making silage as there is minimal air exposure. However, if the herbage is not wilted sufficiently then the extreme weight can cause problems at the base of the structure.
4. 'Sausage'. This is a polythene sausage, typically 2.4 m in diameter and of variable length up to 30 m, that is sealed at one end, packed by a silo packer machine and subsequently sealed at the other end.

Once the material to be ensiled has been sealed in the silo, the in-silo processes begin. There are four main phases: aerobic; fermentation; stable; and aerobic feed-out.

Aerobic phase

Residual oxygen trapped in the silo during packing is removed by plant respiration or by aerobic microorganisms present on the plant material at ensilage. Oxygen is depleted from the silo within a matter of minutes, provided that further ingress of air is inhibited.

Fermentation phase

This can take from 2 days up to a month to complete, depending on

factors such as crop type, crop **dry matter** and whether an additive was applied. Initially two bacterial populations develop: the undesirable enterobacteria group of Gram-negative, facultatively anaerobic organisms producing mainly acetic and **formic acid**s, **ethanol**, **carbon dioxide** and **hydrogen**; and the desirable lactic acid bacteria (LAB), which are Gram-positive facultatively anaerobic organisms that are either homofermentative, producing solely lactic acid from hexoses, or heterofermentative, producing a mixture of predominantly lactic and acetic acids from hexoses. The LAB will dominate in the production of a good silage. At pH 6, both enterobacteria and LAB can grow and produce lactic and acetic acids. As the pH falls the enterobacteria die out, while within the lactic acid fermentation there is a succession from the *Lactococcus* and *Enterococcus* spp. at the more neutral pH range to the *Pediococcus* and *Lactobacillus* spp. at the more acid pH range. Provided that there is sufficient available energy, the fermentation will continue down to a low enough pH (*c.* pH 4 or below, depending on crop type and dry matter) to remain stable. However, if the pH does not fall below approximately pH 4.2, depending on dry matter (DM) content and crop type, the enterobacteria continue to grow and ultimately sacchorolytic clostridia can increase in number. These organisms convert lactic acid into butyric acid, which results in a rise in pH followed by growth of the proteolytic clostridia that deaminate protein and **amino acid**s. The end-product of such a fermentation is a noxious-smelling unpalatable silage. A rapid fermentation to a low pH brings about a better silage quality because it inhibits

detrimental biochemical changes more rapidly. The rate is affected by many factors but most significant is the makeup of the natural flora, which in turn is affected by the cleanliness of the silo and the herbage being ensiled. Clean crops result in lower numbers of undesirable bacteria. However, even a natural flora of predominantly LAB can contain many organisms that are not efficient at carrying out a rapid silage fermentation and so, by inoculating the silage, the silo is swamped with the best type of silage-fermenting bacteria.

Stable phase

This occurs between the end of fermentation and feed-out. Provided that anaerobic conditions are maintained, and a sufficiently low pH within the silage mass has been obtained, then few if any changes occur.

Aerobic feed-out phase

This applies predominantly to silage produced in clamps; it is less important for silages made by other procedures in which air ingress at feed-out is less problematic. Once the clamp has been opened the silage face becomes aerated and spoilage organisms, particularly **yeasts**, moulds and acetic acid bacteria, can proliferate. If yeasts (in grass and whole-crop silage) and acetic acid bacteria (in whole-crop silage) have survived the ensiling phases and the silage has been poorly compacted, then fermentation of lactic acid and residual **sugars** to acetic acid occurs, resulting in a rise in pH and silage heating. The rise in pH enables secondary colonizers such as moulds to grow and so composting begins and there is great loss of **nutritive value**.

Ironically, high-quality silages are more prone to aerobic deterioration and poor-quality silages with high concentrations of acetic and butyric acids are unlikely to deteriorate aerobically. (DD)

See also: Volatile fatty acids (VFAs)

Key reference

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Silage additives

Four categories of material are added to silage to improve crop preservation and feeding value, or to reduce silage losses.

1. **Fermentation** stimulants to promote rapid **lactic acid** fermentation. They can be inoculants containing lactic acid bacteria from the genera *Lactobacillus*, *Pediococcus*, *Lactococcus* and *Enterococcus*, which convert **forage** water-soluble **carbohydrate** into lactic acid, or **enzymes**, **cellulase**s, **xylanase**s, hemicellulases, pentosanases and **amylase**s, which release water-soluble carbohydrates from forage **polysaccharide**s. These enzymes are often applied alongside inoculants and are frequently called biological additives. Alternatively, carbohydrate-rich **by-product**s such as **sugarbeet** pulp, citrus pulp and **molasses** may be added as **energy source**s to promote the activity of epiphytic lactic acid bacteria.
2. Fermentation inhibitors to inhibit microbial growth. These may

be sulphuric, hydrochloric, formic or **benzoic acid**s, which work by direct acidification, or other chemicals with **antimicrobial activity** such as **formaldehyde**, **sodium** nitrite, **sodium chloride**, sodium hydroxide and **ammonia**. Clostridia phages are viruses that inhibit clostridial growth.

3. Absorbents to retain **silage effluent** in the clamp and avoid environmental pollution. These are often by-products such as **straw** and sugarbeet pulp, but can include rolled **barley**, polymers and bentonite.
4. Inhibitors of aerobic deterioration. These include long-chain **organic acid**s such as **propionic** and **caproic acid**s, or **salts** of sulphite or benzoate, or bacteria with anti-fungal end-products such as *Propionibacteria*, *Bacillus* or *Serratia*.

Additives were traditionally used as an insurance against poor ensiling conditions. More recently additives, and particularly inoculants, have been shown to improve animal performance under ideal ensiling conditions. (DD)

Silage effluent

The juice that flows from low-dry-matter silage. Silage effluent can range from 0 l to 250 l t^{-1} herbage ensiled, depending on the herbage **dry matter** content. Environmental pollution from silage effluent in watercourses is attributed to its high biochemical **oxygen** demand in the range 12,000–83,000 mg O_2 l^{-1}. In the initial stages of **fermentation** the composition of effluent reflects that of the cell sap of the ensiled crop. The predominant change is the disappearance of soluble **carbohydrates** and the production

of **organic acid**s, mainly **lactic acid**, in well-fermented silages. The ranges in composition reported for major constituents are (g l^{-1}), 6–110 dry matter; 0–26 lactic acid; 0.5–6.5 acetic acid; 1–31 water-soluble carbohydrate; 1–5 total **nitrogen**; 2–22 total **ash**. Much of the total N is in the form of **non-protein nitrogen** but significant quantities of nutritionally important **amino acid**s have been reported. **Mineral** elements are found in effluent in the same proportions as in herbage but their concentration in dry matter is higher. **Potassium** (1–8.5 g l^{-1}) and **calcium** (0.2–3.6 g l^{-1}) are the predominant elements but significant quantities of **manganese**, **copper** and **zinc** have also been reported. (RJ)

Silica

Silicon dioxide (SiO_2), the main component of sand or glass. (PGR)

Silicon (Si)

A non-metallic element with an atomic mass of 28.086, and one of the most abundant elements in the earth's crust. Earlier studies in **laboratory animal**s suggested that silicon might be an essential nutrient but those studies have not been validated. Some of the studies indicated that silicon is associated with **connective tissue** and bone **metabolism**, because animals fed diets low in Si had less bone **collagen** and hexosamine content than animals fed higher amounts; however, bone **mineral** content and animal **growth** were not affected. No dietary Si requirement has been set for any of the farm animal species. (PGR)

Further reading

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Silver carp (*Hypophthalmichthys molitrix*)
One of the four major Chinese carps and a typical filter-feeding **fish** of the Cyprinidae. It is ubiquitously distributed in major waters of China and other Asian countries (Xie and Chen, 2001). Silver carp has great value for biological control of bloom-forming cyanobacteria in ponds, reservoirs and lakes, and has been introduced to many countries around the world to control **phytoplankton** (Freeze and Henderson, 1982; Farrington *et al*., 2017). The silver carp has the second-highest production yield among all the farmed fish species around the world, with its production reaching 4.90 million tonnes in 2020 (FAO, 2022). The Yangtze River harbours the most abundant natural population of silver carp and the middle reaches of the Yangtze River are the main **spawning** grounds (Sha *et al*., 2021). (QS)



Silver carp are easily disturbed by a boat or rocks thrown into the water. Photo courtesy of the Asian Carp Regional Coordinating Committee. Licensed under CC BY 2.0

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Simulation modelling

When applied to animal nutrition, simulation modelling is the process of representing, through a series of mathematical equations, an animal, its (feeding) conditions and the resulting changes in the animal, and the eventual fate of the diet. Such simulation models are used to make predictions or answer questions, such as what will happen if a particular animal is fed in a particular way at a particular point or over a period of time. Because the models operate in a virtual environment, they make it possible to simulate a variety of (hypothetical) changes, something which in real life may be either difficult or very expensive to do. Such models can be static, i.e. they predict outcomes at a single point in time; or dynamic, i.e. they predict animal responses over a period of time. They can also be clas sified as deterministic, where the outputs of the model relate to a single animal; or stochastic, where the outputs apply to a population of animals and are characterized by a degree of inherent randomness, reflecting the random variation in the initial conditions.

The development and application of such models are now some 50 years old, with the efforts of Whittemore and Fawcett (1974) being perhaps the first formal attempt to predict the responses of

livestock, in their case a growing pig, to variations in **energy** and **protein** intake. Since then, simulation models have been used to predict livestock responses to changes in their management, such as changes in their nutrition (e.g. different feeding and dietary regimes) or physical environment (different ambient **temperatures** and humidity), or simultaneous changes in both. These attempts have usually been dynamic and deterministic. More recently, animal nutrition models have been extended to predict the consequences of changes in livestock **genotype** or phenotype alongside changes in their management, such as feeding regimes. In order to do so, animal nutrition models needed to become stochastic so as to account for the variation between individuals in, for example, their **nutrient requirement**s or their responses to nutrient intakes. Currently, an unresolved challenge is to model the responses of individuals to changes in their infectious environment, such as in the presence of a pathogen, under a variety of nutritional conditions. Given the very rapid advances taking place in the manner in which animals are managed (such as through precision feeding and smart nutrition) and the increasing rate of genetic selection through the use of genomic tools, it is likely that efforts to develop animal nutrition simulation models will intensify, leading to more accurate predictions and applications in relation to such matters. (IK)

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Sinapic acid
A hydroxycinnamic acid derivative that occurs in woody angiosperms worldwide. Part of the biosynthetic pathway of **lignin**, sinapic acid is dehydrogenated to the corresponding sinapyl alcohol, a primary **substrate** for peroxidate-catalysed **oxidation**. **Free radical**s are generated by peroxidase activity and condense to form lignin. Lignin greatly reduces the **digestibility** of cell wall **carbohydrates**. (JAP)
See also: Cinnamic acid

Single-cell protein
A generic name for protein derived from **algae**, **yeasts**, **fungi** and bacteria grown on a multitude of **substrates**, including **carbohydrates**, **ethanol**, methanol, **mineral oils** and their **by-product**s and other organic waste materials. These microorganisms can be cultured by using residues supplied by other industries such as agriculture, food, or urban areas. Hence, the application of single-cell protein (SCP) for developing innovative fish meal offers a double solution by reducing the management of residues and by providing a sustainable source of proteins to **aquaculture**. The microorganisms used (SCPs) have important advantages over traditional sources of proteins as they require shorter production time, less use of land and production unaffected by weather conditions (García-Garibay *et al*., 2003). The **crude protein** content is 400–880 g kg^{-1} but up to 25% of the **nitrogen** (considered as crude protein) is **nucleic acid** nitrogen. Despite this, **amino acid** contents are high and **digestibility**

coefficients in pigs are about 0.8. Crude protein digestibility in poultry is 0.5–0.6, due to the excretion of nucleic acid nitrogen as uric acid, and in **fish** about 0.6–0.9 (Yang *et al*., 2021). The apparent **metabolizable energy** values are 12–16 kJ/g, depending on the type of single cell protein and the animal consuming it. Inclusion levels in diets are normally less than 100 g kg^{-1}. (QS; TA)

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Skatole

3-Methyl-H-**indole**, C_9H_9N. Skatole is formed from the amino acid L-**tryptophan** by intestinal bacteria. Indole, 2,3 benzopyrrole (C_8H_7N), is also produced by **fermentation** of L-tryptophan. Both are responsible in part for the odour of faeces. (NJB)

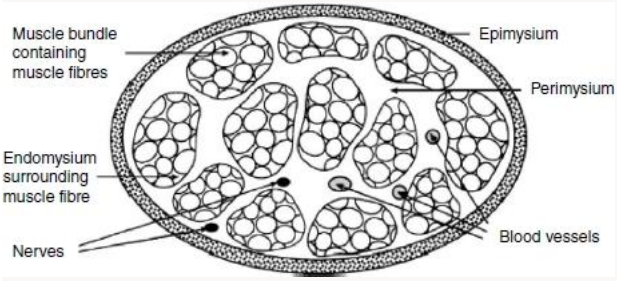
Skeletal muscle

Striated muscle having fibres connected at one or both extremities with the bony skeleton of the body, i.e. the axial and appendicular muscles. The major function of skeletal muscle is the generation of force or the performance of work in the form of movement or

support of the skeletal structures. The outstanding property of muscle is therefore contractility. Skeletal muscles, both avian and mammalian, contain the contractile proteins **actin** and **myosin**, whose filaments are arranged in an interdigitated pattern, giving rise to the 'striated' appearance. Muscle cells also contain the regulatory contractile proteins troponins I, C and T, tropomyosin and α-actinin. Skeletal muscle contraction is generally initiated by the arrival of an excitatory electrical signal at the neuromuscular junction which is transduced into the physical interactions between the contractile proteins. This process by which muscle membrane depolarization is linked to contraction is known as excitation–contraction (EC) coupling.

Skeletal muscle fibres can be broadly divided into three different categories of twitch muscle fibres: types 1, 2a and 2b. Many muscles are mixed in nature in that they have varying proportions of the different muscle fibre types but one particular type may predominate, depending upon the muscle's primary function. Type 1 fibres are termed slow oxidative and possess many mitochondria (oxidative), have high myoglobin contents (red), high capillary densities, small fibre diameters, low **glycogen** storage, slow contraction rates and a tonic contractile action. The speed of contraction is due to the presence of a myosin isoform that hydrolyses ATP very slowly, resulting in a slow cross-bridge formation cycle. Such muscles are very efficient for slow repetitive movements or for sustaining isometric force, e.g. in the maintenance of posture. Thus muscles such as trapezius (shoulder) and soleus (leg) which are active a great deal of the time tend to

have a very high proportion of type 1 fibres.



Diagrammatic representation of cross-section of a skeletal muscle.

Type 2a fibres are fast oxidative-glycolytic. These 'reddish' fibres are intermediate between the other fibre types in terms of their capillary density, fibre diameter, mitochondrial numbers and glycogen storage. They have high myoglobin contents and fast, phasic contractile properties. Type 2b fibres are fast glycolytic; these too are fast phasic fibres and, in common with type 2a, possess myosin isoforms and other contractile proteins capable of very rapid ATP **hydrolysis** and cross-bridge formation. They can thus develop force very quickly and predominate in muscles involved in high power output over a short period (for example longissimus in pig, semitendinosus in cattle and pectoralis major in poultry). Type 2b or 'white' fibres have relatively large diameters, are low in myoglobin, capillary density and mitochondria but exhibit high glycogen storage capacities. In meat animals, fibre type has some marked implications for **meat quality**. Glycolytic fibres, as might be expected, tend to exhibit high post-mortem glycolytic rates and thus produce more **lactate** and have a lower pH_u.

In poultry, genetic selection for desirable production traits has led to differences in fibre-type composition and fibre growth. Thus the modern **broiler chicken** possesses pectoralis major muscles

(breast) composed exclusively of large-diameter type 2b, an observation not made in any other animal. In addition, transformation of small-diameter type 2a fibres to large-diameter type 2b in some selected lines has contributed greatly to increased muscle production. For a description of the nature and pattern of growth and development of skeletal muscle, *see* Muscle. (MMit)

See also: Body composition; Growth; Meat composition

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Skimmed milk:

see Dairy products; Dried skimmed milk

Skin diseases

Nutritional factors in skin diseases include **minerals** (e.g. **zinc**) and **essential fatty acid**s. **Parakeratosis** is a zinc deficiency in pigs, characterized by excessive keratinization of the epidermis with skin lesions and scaling (dandruff). Excessive dietary **calcium**

and dietary **phytates** provoke zinc deficiency. Pruritus (itching) is a common problem in dogs. A deficiency of **linoleic acid** causes dry, itchy skin, dermatitis and an unkempt, lustreless hair coat. **Fatty acid supplement**s containing mixtures of omega-3 and omega-6 fatty acids are effective in treating atopic pruritus in dogs. Evening primrose **oil**, containing *cis*-gamma **linolenic acid** (GLA), is also an effective treatment; it promotes synthesis of **prostaglandin**s which have anti-inflammatory properties. Provision of these fatty acid supplements increases dietary **vitamin E** requirements. (PC)

Slaughterhouse waste

Most slaughterhouse waste is further processed for use in other industries to produce meat and bone meal, **bone meal**, **blood meal**, **feather meal** and tallow; however, some unprocessed waste may be fed directly to animals such as mink. Processed **by-product**s have traditionally been used as sources of high-quality **protein** in the feed of all farm species. However, since **bovine spongiform encephalopathy** these practices have now ceased in Europe, with specific exceptions. (MG)

Slurry feeding

Digested slurry can be incorporated into the diet of farm livestock. However, the promising results from experimental studies have not been converted into farm practice. The major benefit is a reduction in the cost of feed. Concerns about the spread of disease, reduction of feed quality and public resistance to the practice make it unwise to follow this particular route, unless such concerns can be

satisfactorily addressed. (CJCP)

Small intestine
The section of the digestive tract between the **stomach** and the **large intestine**. It is divided into **duodenum**, **jejunum** and **ileum** and is the principal site of **digestion** and **absorption** of nutrients. (SB)

Smoltification
A process in some salmonids of transformation from the juvenile freshwater phase to the seaward migrant phase (smolt). It includes morphological changes (silvering of the scales, lowered condition factor, darkening of paired fins), physiological changes (increased hypo-osmoregulatory capacity; increased levels of cortisol, **thyroid** hormone and **growth** hormone) and behavioural changes (development of schooling behaviour, loss of territorial behaviour). Smoltification is under control of **temperature** and **photoperiod**. (RHP)

Smooth muscle
Smooth muscle lacks the visible cross-striations (the Z lines associated with **actin** and **myosin** filaments) of skeletal and cardiac muscle. In smooth muscle, actin fibres are attached to dense bodies in the cytoplasm and to the cell membrane and so no repeat striations are apparent. Rather than discrete structures, smooth muscle can be found in sheets, as in the walls of the hollow viscera, uterus and ureters, or in multi-units, such as those found in the iris of the eye. Smooth muscle is characterized by irregular

contractions that are not dependent on a nerve supply. (NJB)

Snakehead (*Channa* spp.)

Indigenous species in Asia, belonging to the Channidae family. The genus consists of more than 20 species, such as *Channa argus*, *Channa maculata*, *Channa asiatica*, *Channa gachua*, *Channa micropeltes* and *Channa striata* (Zhao *et al*., 2018). In China, the snakeheads are important freshwater aquatic products, with the total output almost reaching 0.5 million tonnes every year since 2012 (China's Ministry of Agriculture, 2012–2020).



Snakehead (*Channa argus*). Photo courtesy of Brian Gratwicke. Licensed under CC BY 2.0.

The northern snakehead (*C. argus*), the blotched snakehead (*C. maculata*) and their hybrids (both cross and reciprocal cross) are the main cultured stocks. The northern snakehead is mainly cultured in the northern regions of China, because of its excellent cold resistance. The hybrid (*C. maculata* ♀ × *C. argus* ♂) were cultured mainly in southern China, because they were easy to domesticate, feeding on compound diets, and had faster growth, but poor cold resistance. The reciprocal cross of the hybrid (*C.*

argus ♀ × *C. maculata* ♂) has obvious heterosis and additionally acquired good cold resistance from its maternal parent, and is expected to replace the northern snakehead culture (Ou *et al.*, 2018). The blotched snakehead is now kept mainly as breeders to produce hybrid stocks. (QS)

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Sodium (Na)

An alkali **metal** with an atomic mass of 22.9897. Sodium is usually associated with the **chloride** ion in mammalian systems. They, along with **potassium** (K), maintain the **electrolyte** balance of the body. Sodium is essential in the diet of animals, including humans. It constitutes one of the main extracellular ions and helps to maintain water balance. However, the intracellular concentration of Na is quite low. Electroneutral Na^+ transport accounts for most intestinal Na^+ **absorption** in the period between meals and for ileal Na^+ absorption post-prandially. Na entry into the cell occurs with the co-transport of **glucose** and **amino acid**s, and the transport of **hydrogen** ion. The body

balance of Na is controlled through excretion by the kidneys and involves many factors, including the hormones **aldosterone**, angiotensin, **rennin** and antidiuretic **hormone**, as well as plasma Na concentration and renal **blood flow**.

One of the key roles of Na is the maintenance of an electrical potential across the membranes of all cells. This is accomplished to a great degree by the sodium–potassium pump, or Na^+/K^+ pump, in the membrane that exchanges three Na ions inside the cell for two K ions outside the cell. The Na^+/K^+ pump is an ATPase and is especially important in the propagation of impulses in muscle and nerve cells. Other **ion transport**ers located in cell membranes involving Na exchange are the Na–H exchanger, the Na–K–Cl co-transporter and the Na–Ca exchanger.

Almost all farm animal feedstuffs have very low Na concentrations and so most animal diets require **supplementation** with common **salt**, NaCl. **Grazing** animals will supplement their own diet either from natural salt licks or from salt blocks provided for them, or sodium fertilizers can be used. Sodium may be applied to grazing fields in the form of sodium **nitrate** or chloride, but the latter causes corrosion in the applicators. The fertilizer will encourage longer grazing times and improve milk output and quality, if the pasture is grazed by dairy cows. The enhanced sodium content in herbage and reduced potassium content improves the magnesium and calcium divalent cation uptake (Phillips and Chiy, 1995).

The US National Research Council recommends from 600 mg Na kg^{-1} diet for growth to 1000 mg kg^{-1} for early **lactation** in beef

cattle, and 1800 mg kg^{-1} diet for lactating dairy cows, but only 1000 mg kg^{-1} diet for growing heifers and bulls. The Na requirement for pigs ranges from 1000 to 2500 mg kg^{-1} diet, depending on the stage of growth: young growing pigs require more than mature adults. The requirement for poultry is 1500 mg Na kg^{-1} diet, regardless of the age of the birds. For growth and maintenance of horses the requirement is 1000 mg kg^{-1} diet but increases to 3000 mg kg^{-1} diet for working horses. For sheep, the requirement is between 900 and 1800 mg kg^{-1} diet.

Animals that are Na deficient can have depressed plasma Na concentrations; they become lethargic and appear weak and confused. Signs of high Na intake include increased water intake; however, very high intakes can even result in reduced water consumption, probably because of the accompanying **anorexia**. Cattle have been shown to tolerate as much as 9% NaCl in the diet without ill effect, but sheep have been observed to reduce their food consumption at 10% dietary NaCl. Pigs seem to be more sensitive and cannot tolerate 5% NaCl in their diets without developing tremors and **convulsion**s. There was increased mortality in chickens fed 4% dietary NaCl. (PGR; CJCP)

See also: Chloride; Potassium

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Sodium chloride

Common **salt**, NaCl, molecular weight 58.5, a crystalline white solid, abundant in nature. Widely used as a source of sodium and chloride in animal feeding. Also used to prepare physiological saline (0.9% sodium chloride) with osmolality comparable to that in living organisms. (JAM)

Sodium hydroxide treatment:

see Alkali treatment

Soft-shell turtle

The Chinese soft-shell turtle, *Pelodiscus sinensis*, is the main cultured species of turtle and is mainly farmed in China. The world production yield was about 321,000 t in 2018. *Pelodiscus sinensis* is widely distributed in China, Japan and Korea, and it is nutritious, flavoursome and with some medicinal value (Wu and Huang, 2008).



Soft-shell turtle prepared for human consumption. Photo courtesy of BilHoller. Licensed under CC BY-SA 2.0.

The Chinese soft-shell turtle has been a valuable aquatic product since ancient times; it has now become an important **aquaculture** animal in China. Because the Chinese soft-shell turtle is a carnivorous aquatic animal, the fish meal (FM) content is approximately 60% in the commercial diet; therefore, aquaculture development of the turtle is restricted by the high price of FM. Recently, many studies have analysed the substitution of FM in the diet for the Chinese soft-shelled turtle with other **protein source**s and obtained positive results, such as the use of fermented **soybean** meal (Zou *et al*., 2012), **cottonseed** meal protein hydrolysate (Wang *et al*., 2018), **poultry by-product** meal and addition of **bile** acid (Ji *et al*., 2017), soy **protein concentrate**s (Zhou *et al*., 2016) and black soldier fly (*Hermetia illucens*) larvae meal (Li *et al*., 2021). (QS)

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Soil ingestion

Soil may be ingested either voluntarily or involuntarily by farm animals. Involuntary soil ingestion occurs mainly in **herbivore**s consuming pasture that is short. The soil may be consumed directly or attached to plant roots, or leaf material when rain has splashed it on to lower leaves or livestock convey it from poached areas of the field onto leaves. Soil may also contaminate harvested root crops for ruminants, such as **fodder beet**, or it may be incorporated into **grass silage** when the soil surface is not flat or the mower is set too low. Soil ingested in this way can increase **teeth** wear in sheep, especially, and the high content of **silicon** (90% of some sandy soils) may complex essential minerals, such as **magnesium**, **iron** and **manganese**. Most silicon ingested directly is excreted without being absorbed, but that in leafy plants is more readily absorbed and high concentrations of **silica** in the

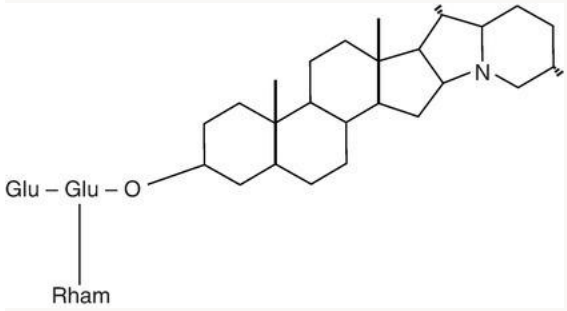
urine can cause the formation of siliceous calculi and **urolithiasis**. This condition is most likely if water intake is low and less urine is passed.

Voluntary soil consumption is typically observed in mineral-deficient herbivores, especially in cattle deficient in **sodium**. Apart from minerals, herbivores also consume many microorganisms in the soil, some of which may be beneficial, others harmful. For example, *cara inchada*, a progressive periodontitis in young Brazilian cattle whose teeth are erupting, is believed to be due to enhanced actinomycete concentrations in newly cultivated land. The actinomycetes produce an antibiotic, which facilitates the attachment of a pathogenic bacterium, *Bacteroides melaninogenicus*, to the gums. Conversely, the consumption of benign soil mycobacteria may protect grazing cattle from developing tuberculosis when they are challenged by *Mycobacterium bovis*. (CJCP)

See also: Geophagia

Solanin (solanine)

A glycoalkaloid commonly found in fresh **potato** sprouts and other *Solanum* species. $C_{45}H_{73}NO_{15}$, molecular weight 868. The **glycoside** of solanidine may also be classified as a solanum **alkaloid**.



Solanin is a cholinesterase inhibitor primarily causing neurotoxicity. Solanum alkaloids are also known for teratogenic effects and **gastrointestinal tract** irritation through inflammation of the **intestinal mucosa** and ulceration. Symptoms include apathy, drowsiness, salivation, laboured breathing, trembling, weakness and paralysis. (DRG)

Sole

A name commonly applied to a large number of **flatfish** (Pleuronectidae), frequently as trade names. The more important include: Dover sole, applied to *Solea vulgaris*, an important European species, and to *Microstomus pacificus*, a commercial species on the west coast of North America; lemon sole (*Microstomus kitt*) of Europe; petrale sole (*Eopsetta jordani*), an important North American west-coast species; and grey sole (or witch flounder) (*Pseudopleuronectes americana*), important in the western North Atlantic. Scientifically the name applies to the flatfish family Soleidae of Europe and North Africa, which includes the Dover sole. (RHP)

Solid-state fermentation

A microbial fermentation that occurs in a solid medium, in contrast to liquid fermentations such as brewing. Some **fungi** have evolved to take advantage of multiple food sources. Solid-state fermentation using white rot fungus *Pleurotus florida* is an effective delignifier of **brassica** haulms that can increase the **protein** content by 7.8% to produce highly digestible mycoprotein-rich fermented ruminant feed. Oyster **mushroom**s

degrade **cellulose** in **sugarcane bagasse** or spent **rice straw**, trapping and consuming nematodes, which provide additional **nitrogen**. The addition of **oilseed cake** to the rice straw can increase fat and protein content of the mushrooms. (JKM)

Solids-not-fat

The major portion of **milk** consists of water (87–88%), followed by solids (12–13%), of which approximately 3.7% is **fat** and 9% is solids-not-fat (SNF). The SNF of milk is primarily proteins (**casein**:**whey** protein; 80:20), **lactose**, minerals (**ash** content), acids, enzymes and vitamins. Estimation of SNF content is of interest to dairy producers and can be calculated by the difference between percentages of total solids and **butterfat**. In practice, the determination of the milk SNF can be performed by using a simplified equation (0.25 × LR) + (0.22 × fat%) + 0.72, where LR is the lactometer reading at a given temperature. This method has been widely used due to its simplicity and rapidness. However, there are also milk analysers available to make quick analyses of milk for fat, SNF, proteins, lactose and water content, **freezing** point, **salts** and total solids.

Knowledge about SNF is an important consideration in dairy processing, since SNF provides critical functional properties to milk and dairy products. For example, caseins are important for coagulation, lactose for **fermentation** and ice cream formation properties. SNF also contains **enzymes** (e.g. proteolytic and lipolytic enzymes) that are important for cheese maturation and shelf-life of ultra-high-temperature milk products. Minerals (mainly **calcium** and **phosphorus**) are important for casein

micelle integrity, coagulation and unique product characteristics, in addition to their nutritional benefits to the consumer. Ghee is a product obtained by clarifying the butter with high heat, which leaves part of the SNF in the product, thereby acquiring a specific flavour. However, there are constraints and challenges associated with SNF in dairy products, such as high lactose levels in ice cream producing a sandy texture, which is a product quality defect. Whey powder, skimmed milk powder, concentrated skimmed milk and buttermilk are some examples of common sources of SNF. Factors affecting milk SNF composition include the stage of **lactation**, **environmental temperature**, season, nutritional status, breed and genetic differences. In some cases, milk is standardized based on fat or SNF content for marketing of fluid milk or manufacturing of cheese, milk powder or butter. This is mainly achieved by blending cream with skimmed milk (powder) in appropriate proportions.

Lactose is the predominant **carbohydrate** present in milk, with smaller fractions of **glucose**, **galactose**, **oligosaccharide**s and numerous glycoconjugates (**glycolipid**s, glycoproteins, glycosaminoglycans, mucins, etc.). Methods for the determination of specific milk carbohydrates include iodometric estimation of lactose, enzymatic **hydrolysis** of lactose and determination of glucose, fractional crystallization, and modern chromatographic procedures, including preparative thin-layer **chromatography**, molecular sizing, affinity chromatography and high-performance liquid chromatography (HPLC). The protein fraction of milk consists mainly of casein (αS1-casein, αS2-casein, β-casein and k-

casein) and whey proteins (α-lactalbumin, β-**lactoglobulin**, **lactoferrin**, lactoperoxidase and bovine serum **albumin**) with numerous minor proteins and enzymes occurring in milk that are derived either from the epithelial cell or from the **blood**. Proteolytic activity is mediated through proteases and these proteases can be indigenous or exogenous. Plasmin is a principal indigenous proteolytic enzyme in milk. Plasmin, an indigenous serum protease, is found in milk together with its inactive **zymogen**, plasminogen. Various plasminogen activators are found in milk and these activators convert plasminogen to plasmin. Plasmin could hydrolyse predominantly the β-casein and up to some extent α-casein into γ1, γ2, γ3 casein and proteose-peptones. Regulation of plasmin activity and identifying the variation of plasmin level is crucial to control the quality of processed dairy products. Further, plasmin activity may be beneficial or detrimental, depending on the type of dairy product and the extent of hydrolysis by plasmin. For example, in cheese making the breakdown of protein by plasmin forms desirable flavour and texture, which is beneficial. In the case of ultra-high-temperature milk products, plasmin can be involved in the development of bitter flavour and age-related gel formation by hydrolysing casein–casein and casein–calcium **phosphate** interaction sites of the casein micelles. Milk proteins are heterogeneous, because they are subjected to genetic polymorphism and post-translational modifications. SNF also contains **non-protein nitrogen**ous substances, which may represent 4–5% of the total nitrogen. Milk protein concentration is most commonly determined by the

Kjeldahl method. The total nitrogen value can be obtained by multiplying the protein content obtained by the Kjeldahl method by a conversion factor of 6.38 (based on the average nitrogen content of 15.7% in bovine casein and whey proteins). Detection of genetic polymorphism of milk proteins can be achieved through various electrophoretic and chromatographic techniques. Recent studies have shown that there is a relationship between disease risk and consumption of a specific bovine β-casein fraction, either A1 or A2 genetic variants. Although there are many inconclusive results, several studies have shown that populations which consume milk containing high levels of β-casein A2 variant have a lower incidence of cardiovascular disease and type 1 **diabetes**. Moreover, consumption of milk with the A2 variant may be associated with less severe symptoms of autism and schizophrenia. (HP; JKV; ENP)

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Solubility
The tendency of one substance to be taken up homogeneously into another. Examples include solids taken up in a liquid (such as **sugar** in water, when the sugar loses its crystalline form and becomes molecularly dispersed in the water). Other examples are miscible liquids such as **ethanol** in water, when the ethanol is distributed uniformly in water, in contrast to immiscible solvents (**oil** vs. water) where identifiable layers are apparent. Other mixtures can be a gas in a gas (e.g. **hydrogen** in **nitrogen**). Solubilities vary from 0 to 100%. (NJB)

Somatotrophin
A protein hormone also known as **growth** hormone (GH). It is produced in an episodic manner by the anterior pituitary gland. It may act directly on the metabolic activity of some tissues through the presence of GH receptors on the cell membrane and indirectly via its stimulation of the production of **insulin-like growth factor**s 1 and 2 (IGF-I and IGF-II) in the **liver** and peripheral tissues. Originally extracted and purified from pituitary glands, it is now available in much larger quantities due to the use of genetic engineering to enable bacterial production of human (HST), porcine (PST) and bovine (BST) somatotrophin. In pigs, it has been used to increase growth rate and lean **carcass** mass. In dairy cows, it is used to increase **milk** yield by as much as 40%. The use of PST and BST is permitted in North America but not in the EU. (JRS)

Sorbic acid

2,4-Hexadienoic acid, CH_3·CH=CH·CH=CH·COOH. Sorbic acid is found in the berries of mountain ash trees and can be produced commercially. It is used as a fungicide, in drying oils and as a plasticizer and lubricant. (NJB)

Sorghum (*Sorghum bicolor*)
A cereal **grain** plant of the **Gramineae** (**grass**) family that originated in Africa. Those sorghums that are cultivated mainly for their grain belong to the species *Sorghum vulgare*, which includes varieties of grain sorghums and grass sorghums, grown for **hay** and **fodder**, and broomcorn, used in making brooms and brushes. Grain sorghums include durra, milo, shallu, kafir corn, Egyptian corn, great millet and Indian millet. Sorghum is especially valued in hot and arid regions for its resistance to **drought** and heat. It is the main food grain in Africa, Asia and China. It is also grown in the southern parts of the USA, where it is the second most important feed grain.



Sorghum, an important crop in hot, arid climates. Photo courtesy of

Cindy Sims Parr. Licensed under CC BY 2.0.

The plant grows to a height of 0.5–2.5 m and may reach a high of 4.5 m. Stalks and leaves are coated with a white waxy bloom and the central portion or pith of the stalks of certain varieties is juicy and sweet. The grains vary widely in colour, shape and size among different types but they are smaller than those of **wheat** (about 66% the weight of wheat grains). Kafir sorghums, originally from South Africa, have medium-sized seeds which may be white, pink or red. Milo sorghums, originally from East Africa, tend to be more tolerant of heat and drought than the kafir types and have large seeds, which are pale pink to cream in colour. Feterita sorghums, from Sudan, have very large seeds, which are chalky white. Durra sorghums, from the Mediterranean area and from the Near and Middle East, have large, flat seeds. Shallu sorghums, from India, have pearly white seeds; the plant is late maturing, thus requiring a relatively long growing season. Koaliang sorghums, typically grown in China and Japan, have brown seeds with a bitter **taste**. Hegari sorghums, also from Sudan, are similar to kafir sorghums and have chalky white seeds.

Nearly all the sorghum grain cultivated in the USA is used for livestock feed. Where used for human food, the grain may be roughly ground and made into bread-like preparations, used after grinding and stewing as a porridge or made into **flour** for mixing with wheat flour for breads. Varieties with waxy **endosperm**s are a source of **starch**, having properties similar to tapioca. The grain is used in native beers, particularly in Africa.

The grain or kernel comprises about 84% **endosperm** (largely

starch), 10% germ and 6% **bran** (**pericarp** or surface layers). Sorghum contains a similar protein content, at a mean 113 g **crude protein** kg^{-1} dry matter (DM) to that of wheat and higher than that in **maize**. Starch concentration ranges from 690 to 761 g kg^{-1} DM and is concentrated in the endosperm, as in other cereal grains. The grain is generally low in fibre (mean 107 g neutral detergent fibre kg^{-1} DM) and contains about 30 g **oil** (as **ether extract**) kg^{-1} DM (see table).

In common with maize, sorghum grain is wet-milled to produce starch. The starch is also used in the manufacture of **glucose** for human use. Starch from 'waxy' sorghums is used in adhesives and for sizing paper and fabrics, also in the 'mud' used in oil drilling. The grain is also used in grain distilleries and butyl alcohol production. As a livestock feed, sorghum can be grown for grain production, giving sorghum **stovers** and leaves as **by-product**s, or grown to provide a **forage crop** that can be fed to livestock as a fresh forage or following conservation as hay or **silage**. Conservation as hay or silage helps to eliminate the risk of toxicity due to the presence of a cyanogenetic **glycoside** which, as a result of the enzymatic activity in the gut, releases cyanidric acid. Sorghum grains can be fed fresh to livestock after removal of fibre or ensiled. Stover and leaves may also be ensiled. The **nutritive value** of the grains is similar to **barley** grains, while the stover and leaves have a higher nutritional value than maize.

Tannins, which confer resistance to insect and bird damage, are present in sorghum grains. They bind to protein and starch and

thereby reduce the availability of these nutrients to the animals consuming them. The depression in **digestibility** is more marked in non-ruminants than in ruminants, because of the positive effect of **rumen** degradation. Treatments to reduce the tannin content (seed skinning, **flaking**, etc.) are not always economically viable. The grains are generally processed by coarse grinding and this is particularly effective for cattle and horses.

Sorghum grains can be used as a substitute for maize grains in dairy cow diets without any detrimental effect on milk but their nutritive value for beef cattle is about 90% of yellow dent maize, mainly due to their lower oil content. **Feed conversion ratio** for milk and **meat production** is improved by 0.2 and 0.3, respectively, following the grinding or **pelleting** of sorghum grains. The grain can be fed to dairy cows or beef cattle at about 500 g per head per day as part of a feed mixture containing other cereal grains, cereal brans, **linseed** meal and **soybean** meal. Sorghum is also a useful feed for **fattening** lambs, with no differences in terms of nutritive value between the grain and meal. Sorghum can be substituted for maize in pig diets with a relative feeding value of over 0.9; however, it presents some difficulties in ration formulations for poultry owing to its low overall content of pigments, which are particularly important for egg yolk colour.

Chemical composition of sorghum grain and forages (as g kg^{-1} DM unless stated otherwise).

	DM (g kg^{-1})	CP	EE	Starch	CF	Ash	GE (MJ kg^{-1} DM)
Grain	897	113	30	730	20.1	17	18.7
Grain silage	686	68	–	–	25	12	–
Stover hay	828	57.9	12.7	–	342	140	–
Stover silage	346	55.7	18.2	–	296	112	–

CF, crude fibre; CP, crude protein; DM, dry matter; EE, ether extract; GE, gross energy.

The **energy value** of sorghum for ruminants is 13.2 MJ **metabolizable energy** (ME) kg^{-1} DM, which is comparable to that of barley and slightly lower than that of maize. The energy value for pigs is similar to that of maize and higher than that of barley grain. The energy value for poultry is intermediate between the values for maize and barley. Sorghum harvested as a forage crop can be fed to cattle following the same recommendations as used for maize, and sorghum silage can be substituted for maize silage for beef cattle, but with a nutritive value 15–33% lower. Sorghum stovers are best utilized when tender and juicy and they can be used by livestock of moderate performance levels. (ED)

South American camelids, effects of nutrition on meat quality

South American camelids, including llamas (*Lama glama*) and alpacas (*Vicunga pacos*), are not primarily used for **meat production**, but instead for fibre production or as sumpter animals (pack animals). These functions notwithstanding, llama and alpaca meat are important food resources, consumed by many around the globe, especially the rural communities of the Andean highlands. Much effort has therefore been applied to determine and improve the quality of South American camelid meat and help producers to diversify and grow its market share. Fundamental to these outcomes is the replacement of the traditional native pasture feed base with improved pasture mixes and concentrate **supplementation**.



Alpacas thrive in dry exposed conditions. Photo courtesy of Brian Ireland. Licensed under CC BY SA 2.0.

South American camelid meat is characteristically lean, with

low levels of intramuscular fat (IMF) (0.5–3.0%) and high levels of protein, vitamins and minerals (e.g. vitamin B, **zinc**, **iron**). These properties, as well as the eating quality of South American camelid meat, are manageable via nutritional strategies – the latter especially important because of the comparative toughness of South American camelid meat when compared with meat from other ruminants. For example, the nutritional effect of the supplementation of llamas with **sorghum–wheat bran** concentrate was an increase in the dietary protein and **energy intake**s, when compared with **lucerne hay** supplementation, and more fat deposition in the muscles (higher IMF levels) (Mamani-Linares and Gallo, 2014). The fat levels of alpaca meat have likewise been increased with better diets – evident in the comparisons made of animals raised on improved pastures with those raised on unimproved traditional pastures of lower nutritional value (Smith *et al.,* 2017). Evaluation of alpaca **meat quality** traits has found no seasonal effect on IMF content, ultimate pH, cooking losses and tenderness values, although energy, **crude protein** and neutral detergent fibre levels of pasture varied significantly between the seasons (Biffin *et al*., 2020).



Alpaca carcasses, which are characteristically lean with little subcutaneous fat. Photo courtesy of David Hopkins, unlicensed.

The tenderness of llama and alpaca meat is comparable, having a Warner-Bratzler shear force range of 40–95 newtons, depending on animal age, muscle and post-mortem intervention (Popova *et al*., 2021). Based on the available research for South American camelids, the selection of feeding systems has only marginal effects on tenderness, but it will impact on the **fatty acid** composition and nutritional value of the meat. The levels of omega-3 fatty acids in the meat are highest in llamas and alpacas fed pasture-only diets, and these levels decline when the animal is supplemented with a grain-based concentrate. Increases in the omega-3 fatty acids (EPA and DHA), as well as total **polyunsaturated fatty acid**s, have

been attributed to extensive rearing on high-quality pastures (Smith *et al.,* 2019). Indeed, the low levels of IMF and high levels of **vitamin E** in South American camelids grazing in this system could act to preserve this fraction in the meat until consumption – as demonstrated by its low susceptibility to peroxidation. These same nutritional outcomes also contribute to the colour stability of llama and alpaca meat, a concept to note when selecting production systems to enhance the quality and retail potential of South American camelid meat. (BWBH; ENP)

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Sow

A female pig kept for **piglet** production. A young sow during her first **parity** may also be referred to as a **gilt**. Each sow will produce 2 to 2.4 litters of pigs per year, depending on length of **lactation**, for many years. Under commercial conditions, sows are often culled after six litters as maternal performance deteriorates. (SAE)

Soybean

The soybean has been cultivated in China for at least 3000 years but is now of global importance, with a world production of over 100 million tonnes annually. Soybean products are estimated to be present in about two-thirds of all manufactured food products today. It is equally important as an animal feed. The reason for its success is its high **protein** content (40% of dry matter, 50% when decorticated), which is the highest protein concentration of all seeds grown for animal feed. The **oil** content (20% dry matter) is comparatively low but the oil is commercially important. It contains a high proportion of **polyunsaturated fatty acid**s (< 60%), including linolenic and **linoleic acid**s. Soybean products are good sources of **iron**, **calcium**, **zinc** and most of the B **vitamins**, though they should be supplemented with **vitamin A** when fed to cattle. The oil is used in salad and cooking oils and in non-dairy spreads. As an **emulsifier** it is used in a variety of food products and it also has a variety of industrial uses. Soya **flour** contains no **gluten**: it is used in baking, as a meat substitute, and as a substitute for cows' **milk** and other traditional dairy products.



Soybeans ready for harvesting in Maryland, USA. Photo courtesy of Scott Robinson. Licensed under CC BY 2.0.

Soybeans, usually cracked or ground, can be fed to ruminants without processing but, before being fed to non-ruminants, must be heated to inactivate the **trypsin inhibitor**s present. **Urea** should not be fed with soybean seeds as they contain **urease**, which converts the urea into **ammonia**. Further antinutrients include phyto-**oestrogen**s, which may reduce the reproductive efficiency of some animals, **goitrogen**s (**iodine antagonist**s) and **haemagglutinin**s. If fed in large quantities (20–25%) the carcass **fat** may be too soft.

Soybean meal or soybean cake, the residue after the oil has been extracted, is an excellent source of protein (up to 57%), with an **amino acid** profile similar to that of milk. For non-ruminants, the efficiency of **digestion** of these proteins is impeded as they are bound within the cell wall **carbohydrates**. Nevertheless, soybean meal is an animal feed for both ruminant and non-ruminant

livestock, including pigs, poultry, horses and fish, and also companion animals. The hulls that remain after the seeds have been decorticated (also called soybean mill feed) are also of use as a fibre-rich addition to the diets of ruminants. (DA)
See also: Antinutritional factors; Digestive enzyme inhibitors

Spawning
The release of **eggs** and sperm from mature parent **fish**. Spawning may be allowed to proceed naturally by placing sexually mature males and females together in a spawning container, or fish may be spawned artificially by stripping eggs and sperm by manual pressure or injection of air or isotonic fluid into the body cavity. Manual stripping is most easily performed on species (e.g. salmonids) where the ova are shed into the body cavity prior to spawning. In species where the ovarian lumen is continuous with an oviduct, natural spawning may be required. (RHP)



Spawning Yellowstone cutthroat trout (*Oncorhynchus clarkii bouveri*). Photo courtesy of Yellowstone National Park Services. Licensed under

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Specific gravity
A physical measure, the weight of a given volume relative to the same volume of water at the same temperature and pressure. Because **fat** (**adipose tissue**) is much less dense than lean **meat**, specific gravity is sometimes used to estimate the ratio of fat to lean meat in a **carcass** by weighing it first in air and then in water. The estimate is somewhat affected by the proportions of skin, bone and muscle in the carcass, and by the mineralization of the bone. (MFF)

Spermidine:
see Polyamines

Spermine:
see Polyamines

Sphingolipids
Complex **lipids** containing the basic unit sphingosine (a complex amino alcohol derived from **palmitic acid** and **serine**), a **long-chain fatty acid**, phosphate and **choline**: it contains no **glycerol**. Sphingolipids are found in cell membranes and particularly in brain and spinal cord lipids. (DLP)

Spinach (*Spinacta olerecea*)
A hardy annual vegetable with edible leaves, grown in Europe, the Americas and the Far East. It is suitable for inclusion in ruminant diets and can be fed to dairy and beef cattle at 30% and ewes at

20% of total diet. The dry matter (DM) content of spinach is 90 g kg^{-1} and the nutrient composition (g kg^{-1} DM) is **crude protein** 190, **crude fibre** 100, **ether extract** 15, **ash** 105 and **neutral detergent fibre** 215, with MER 9.5 MJ kg^{-1}. (JKM)

Spray-dried animal plasma

According to the American Association of Feed Control Officials (AAFCO), animal plasma is defined as 'the product obtained by spray drying plasma which has been separated away from the cellular matter (red and white blood cells) of fresh whole blood by chemical and mechanical processing. The protein portion of this product is primarily **albumin**, **globulin**, and **fibrinogen** type proteins'. Spray-dried animal plasma (SDAP) is rich in highly digestible functional proteins contained in **blood** collected from healthy animals during the processing of beef, mutton, pork, or poultry destined for human consumption and is commonly used in livestock and companion animal nutrition. Animal plasma contains a complex mixture of functional proteins such as albumen, globulins, **transferrin**, **growth factor**s, bioactive peptides and other nutritional components that retain their biological activity after spray drying (Campbell *et al*., 2019). Functional plasma proteins support biological activities such as those related to animal growth, immune responses, behaviour and **welfare**, tissue repair, defence mechanisms and **reproduction** when orally consumed (Araújo *et al*., 2010; Pérez-Bosque *et al*., 2016a; Liu *et al*., 2018).

How is spray-dried animal plasma produced?

Spray-dried animal plasma is produced from blood collected at abattoirs that process meat from healthy livestock that have been determined as fit for human consumption by government-appointed food safety inspectors. Anticoagulants are added during blood collection to prevent coagulation, then the blood is transferred in an enclosed system to a designated blood-processing area in the abattoir, where it may be separated by centrifugation into plasma and red cell fractions or kept intact as whole blood. In either case, the plasma and red cell fractions or the whole blood is immediately chilled before storage in an insulated tank at the abattoir. Depending upon the manufacturer, liquid plasma (or whole blood) is transported to a centralized spray-drying facility where it is transferred to a holding tank and scheduled for further processing. At the spray-drying facility, the animal plasma is concentrated and then spray-dried at high temperatures that rapidly desiccate the liquid into a dry powder within seconds, much like spray-dried milk products. The dried plasma is packaged in new bags or totes and subjected to quality control and assurance standards before release for sale. Most commercial SDAP products contain 70–80% **crude protein**, < 16% **ash** and < 10% moisture. The guaranteed crude protein and ash content can vary depending upon the species origin (i.e. bovine, porcine, ovine, avian) and the variable processing methods used by different manufacturers to remove ash before spray-drying.

Applications and functionality of SDAP in livestock and companion animal nutrition

The pig industry has used SDAP in pig feed for over 30 years

because of the well-documented benefits it has on pig growth performance and health (Torrallardona, 2010; Balan *et al*., 2021). Spray-dried animal plasma was recognized as the sixth most important discovery in pig nutrition in the past century by the American Society of Animal Science (Cromwell, 2009). As a feed ingredient, SDAP is highly digestible by pigs and poultry, but when included in diets it also improves **nutrient digestibility** of the complete diet in **monogastric** animals. SDAP has a similar functional protein profile as that of colostrum and **milk**, therefore its use in commercial milk replacers has grown considerably over the past few years (Thornsberry *et al*., 2016; Morrison *et al*., 2017; Henrichs *et al*., 2021). In addition, SDAP is commonly used in canned dog and cat food products for its high protein content and **palatability** and its physical properties, including gelling, **water-holding capacity** and emulsification (Polo *et al*., 2009).

What are the modes of action of SDAP?

Supplementing SDAP in animal feed has been associated with an increased efficiency in the immune response to either stress or pathogen challenge, resulting in improved health, growth, welfare and feed efficiency (Campbell *et al*., 2003; Araújo *et al*., 2010; Pérez-Bosque *et al*., 2016a,b; Belote *et al*., 2021). Inflammation induced by either stress or pathogen challenge in various tissues of the gastrointestinal, respiratory, or reproductive systems was significantly mitigated in animals provided SDAP **supplementation** in their feed (Bosi *et al*., 2004; Nofrarías *et al*., 2006; Campbell *et al*., 2006, 2019; Peace *et al*., 2011; Maijó *et al*., 2012). Collectively, the results from these studies suggest that oral

consumption of SDAP supports a more efficient immune system response to stress or pathogen challenge, thereby reducing nutrient demand by the immune system and providing more nutrient supply to support growth and productivity.

The SDAP supplementation in feed for chickens can reduce gut permeability, improve nutrient uptake and improve structural integrity (Campbell *et al*., 2019). These beneficial responses were likely mediated by a reduction in the expression of intestinal tissue pro-inflammatory **cytokines**, and by an elevation in the expression of anti-inflammatory cytokines, along with an increased expression of defensins (Pérez-Bosque *et al*., 2010). Results of studies with a mouse model showed: (i) reductions in lymphocyte activation and infiltration; (ii) the lessening of oedema; and (iii) changes in the gut microbiota of animals fed diets supplemented with SDP (Pérez-Bosque *et al*., 2016b). Collectively, these changes suggest that the immune system modulation effects of dietary SDP provide for a more rapid restoration of mucosal **homeostasis** of the gut. Similar effects have been reported in other mucosal systems of the respiratory and reproductive tracts, indicating that the effects of feeding SDP are not limited to the **gastrointestinal tract** (Campbell *et al*., 2019).

SDAP is a unique **animal protein** ingredient that is utilized extensively in livestock and companion animal diets because it is highly digestible, supports a more efficient immune system response to environmental and pathogen stress, and provides high-quality protein with physical properties to recipes for the manufacturing of canned pet food products. Recognition of these

biological functions and physical properties allows the livestock or companion animal nutritionist to design a nutritionally balanced feed or food that supports optimal health and welfare of the animal (Campbell *et al*., 2019). Furthermore, animal blood co-products like SDAP support sustainable animal agriculture by adding value to our resources and reducing environmental waste and carbon emissions. (WHT; LER; JP; JMC; JDC; YS)

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Sprouted grain:

see Germination

Squid meal

A by-product (heads, feet and viscera) of squid-processing. When

mixed with **soybean** meal, it is a very good phagostimulant to improve feed **palatability** and **feed intake** in aquatic animals. Thus it is a useful aquafeed ingredient for **shrimp**, crab and **fish**. However, squid viscera contain a high level of **cadmium**, a harmful **heavy metal** with a very long biological half-life that causes both hepatic and renal damage in mammals and fish (Goering *et al*., 1994). Cadmium has an effect on membrane **protein** and this affects **enzyme** activities, causes damages in membrane structure and tissues in animals (Chan and Cherian, 1992) and induces variations in enzymatic **antioxidant** activities, and so it is very necessary to control its content in diets strictly. Of course, it also will cause cadmium deposition in aquatic products, which could be harmful to human consumption if a high level of squid meal is included in aqua-feed. (QS)

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St John's wort (*Hypericum perforatum*)

A herbaceous plant of height 50–80 cm, a native of Eurasia, that grows on the sides of rural roads, abandoned fields and forested areas. It has numerous branched stems and small, oval leaves that secrete essential **oils**.



A field of St John's wort. Photo courtesy of John Tann. Licensed under CC BY 2.0.

Its yellow petals are small and contain secretory glands. In the northern hemisphere it flowers from May to October. The flowers produce essential oils and **tannins**, similar to **green tea** (Zargari, 1997). A heteroside called hyperine, of bright yellow colour, is extracted from the petals, pistil and fruit, and a quercetin compound (Zargari, 1997; Kholghi *et al*., 2022). Flavon, phytosterone, stearic, palmitic and **myristic acid** and cerylic alcohol compounds are present in the leaf and stem of the plant. The therapeutic properties of this plant are diverse, but it is particularly used in pharmaceutical formulations to improve digestion, relieve nerve pain, control epilepsy, disinfect the urinary tract, strengthen the respiratory and uterine system, remove arteriovenous inflammation, act as an anthelmintic and heal wounds (Zargari, 1997; Kholghi *et al*., 2022). The compounds of

this plant impact on the **neurotransmitters, glutamate** and acetylcholine, reducing depression by enhancing cholinergic signalling (Kholghi *et al*., 2022). However, taking St John's wort without medical advice is not recommended, as the drug interferes with many conventional medications. With its abundance of hypericin, this plant stimulates the nervous system. When included in the ration of farm animals, **feed intake** in ruminants has been observed to decline; in poultry it enhances the immune system, reduces stress and improves the effectiveness of vaccines (Zargari, 1997; Behboodi *et al*., 2021). (AS; BH-G; CJCP)

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Stability maintenance

Of the form and activity of a chemical substance, in animal feed, certain components such as **vitamins**, **enzymes** and **unsaturated fats** are liable to become changed in form or function during processing or subsequent storage. The stability of enzymes and vitamins can be improved by encapsulation within a

protective layer. The stability of unsaturated fats can be improved by inclusion of **antioxidant**s. (KJMcC)

Stachyose

A tetrasaccharide of **galactose**-galactose-**glucose**-**fructose**, $C_{24}H_{42}O_{21}$, molecular weight 667. Also called lupeose, it is a constituent of the seeds of many Leguminosae. It is resistant to the digestive **enzymes** of animals but is readily fermented by the intestinal microflora. (JAM)

See also: Carbohydrates; Oligosaccharides

Stages of growth

Stages of growth are subsets of the overall growth process, usually separated by physiologically significant events such as birth, **weaning**, **puberty** and **maturity**. Almost every description of a stage is an oversimplification. For example, prenatal growth is not a continuum of one type of event; the blastocyst (in polytocous species) goes through a repertoire of changes as it stakes its claim on uterine space by rapid elongation. The fetus then becomes a template for subsequent growth and there is a phase in which most tissues and organs are initiated. Post-natal growth is a reflection of the animal's need to achieve functional independence at weaning and reproductive competence after puberty. The initial part of the post-natal growth curve indicates a steadily increasing increment of gain in mass per unit of time, described as the 'self-accelerating phase'. The second feature is that part of the curve in which the change from acceleration to deceleration takes place. This is usually at puberty. The final part of the curve shows a steady

decline in the increment of mass gained each day, called 'self-decelerating', until the 'mature' or asymptotic weight is attained. The final stages of growth are degeneration, senescence and death. (VRF)

Stallion

An adult uncastrated male horse or pony, normally over 4 years old. In Britain, entire males over 2 years old must be licensed.

The stallion is subject to the same seasonal influences as the **mare**. His **fertility** is greatest in summer and least in winter. Seasonal changes in **blood** concentrations of **luteinizing hormone**, follicle-stimulating hormone and testosterone, and consequential changes in testicular size, sperm production and libido, are functions of changes in **photoperiod**. Increased fertility earlier in the season may be obtained by increasing the photoperiod artificially and increasing the energy and protein content of the daily feed.



Feeding stallions needs careful attention during the breeding season.

Photo courtesy of AJ Mexico. Licensed under CC BY 2.0.

Physical activity of the stallion increases in the breeding season, increasing his **energy expenditure**. However, at no time should the stallion be allowed to fatten. In consequence, high-fibre balanced feeds are satisfactory when given out of the breeding season in accordance with the equations under '**Horse feeding**'. Proposed minimum **nutrient requirement**s for the stallion are also given under the latter entry but there is little published research work to establish these. During the off-season, the stallion may be fed either typical grass **hay** at 1.75–2.0% of body weight per day or top-quality **lucerne** (alfalfa) at 1.5–1.75% of body weight per day. These diets should be supplemented with adequate amounts of minerals and vitamins. During the breeding season, the nutrient requirements of stallions are generally 25% above those for the **maintenance** of mature stallions during the off-season. The increased requirements of breeding stallions for nutrients can be met through a combination of **roughage** (e.g. containing 10% **crude protein**) and concentrate (e.g. containing 10–14% crude protein) at a total **feed intake** of 1.5–2.5% of body weight per day. The ratio of roughage to concentrate may be 50:50 or up to 70:30 (g g^{-1}), depending on the quality of feed ingredients. The diet of the stallion should provide sufficient protein (for example, 40 g crude protein per **megacalorie** of **digestible energy**), minerals (for example, 1.2 g **calcium** and 0.87 g **phosphorus** per megacalorie of digestible energy) and vitamins (for example, 1073 IU **vitamin A** per megacalorie of digestible energy, and 80 IU **vitamin E** kg^{-1} diet). (DLF; GW)

Further reading

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NRC (National Research Council) (1989) *Nutrient Requirements of Horses*. National Academy of Sciences, Washington, DC.

Standardized digestibility:

see Digestibility

Starch

A **polysaccharide** consisting of two main macromolecules: **amylose**, a linear polymer of α-D-glucopyranose units linked by 1→4 bonds (molecular weight 100,000–600,000); and **amylopectin**, linear chains of D-glucopyranose linked by (1→4)-α-D linkages with about 5% of (1→6)-α-D bonds at branch points (molecular weight 100,000–1,000,000). After **cellulose**, starch is the most abundant **carbohydrate** in plants and the principal reserve substance of most higher plants. Found in high concentrations in cereal **grain**s, pulses and tubers, it is the major dietary **energy source** for many animals. (JAM)

See also: Maltodextrin; Maltose; Maltotriose; Storage polysaccharides

Starch equivalent (SE)

The starch equivalent system (developed by Kellner in Germany) can be considered the first widely adopted **net energy** system. It

expresses the efficiency with which 1 kg of feed is used for **lipid** deposition relative to 1 kg of pure **starch**. (JvanM)
See also: Energy systems

Starvation
A severe or total lack of food for a prolonged period, as distinct from **anorexia** or **malnutrition**. This is the most extreme form of **undernutrition** and is associated with a reduced metabolic state. It necessitates mobilization of body reserves, resulting in loss of weight, slimming, emaciation and eventual death. After an initial weight loss, the total **energy expenditure** is similar to that in normal individuals, with a decrease in resting energy expenditure and an increased energy-related physical activity. The time taken to die in the absence of food depends on the size of the animal's body energy reserves in relation to its **maintenance** requirement. Typically, the smaller the animal, the shorter is its period of survival – from a few hours for a shrew to many weeks for an elephant. Starvation induces a reduction in activity and **metabolic rate**, which falls to as little as one-half of normal. **Blood glucose** is maintained at normal levels in non-ruminants so that neural function is initially not seriously affected. However, low blood pH due to increased production of **ketone** bodies may eventually cause damage to kidneys and other organs. **Triiodothyronine**, the steroid **hormone**s and **leptin**, a **protein** expressed in the **adipocyte**s, are among the most sensitive indicators of starvation. Animals have metabolic strategies (such as the mobilization of **body fat** and protein to provide energy and **glucose**) to adapt to starvation so that they can survive for various periods of time,

depending on species. During starvation, all tissues are affected but the adipose tissues of the body are metabolized to the greatest extent, then muscle, bone and finally nervous tissue, thereby protecting the vital organs and tissues during undernutrition. In mammals, birds and fish, starvation is characterized by three phases: (1) the mobilization of both fat and protein reserves as the major sources of energy and glucose; (2) the mobilization of fat as the primary source of energy and the conservation of body protein and glucose, with fat reserves reaching a critical threshold; and (3) a shift to the mobilization of the protein reserve as the main sources of energy and glucose.

In humans, the initial phase (the first 7 days) of starvation is associated with gradual increases in: (i) the **hydrolysis** of **triacylglycerol**s in white **adipose tissue** to release **fatty acid**s and **glycerol**; (ii) the **oxidation** of fatty acids in the **liver** to produce ketone bodies (**acetoacetate** and β-**hydroxybutyrate**); (iii) **protein degradation** in the whole body (primarily **skeletal muscle**) to generate **amino acid**s; (iv) the use of ketone bodies as major metabolic fuels in extrahepatic tissues (primarily the brain and kidneys); and (v) the conversion of glucogenic amino acids, **glycerol**, **lactate**, and odd-carbon-number fatty acids into glucose in the liver and kidneys. Between Days 0 and 7 of human starvation, the plasma concentrations of glucose decrease gradually from ~5 mM to the nadir value (~4 mM), whereas those of acetoacetate and β-hydroxybutyrate gradually increase from ~0.05 to ~1 mM and from ~0.1 mM to ~4.2 mM, respectively. During the mid- and late phases of human starvation, protein degradation in

tissues is reduced gradually, due to its inhibition by elevated ketone bodies to conserve protein in the whole body. The loss of 50% protein from the body is not compatible with survival. Non-obese humans who have an adequate intake of water do not survive a 30-day period of starvation, but obese individuals can survive at least 37 days of starvation.



Young children in the Yemen are particularly vulnerable to starvation. Photo courtesy of Felton Davis. Licensed under CC BY 2.0.

Some species of animals naturally experience starvation for months. For example, hibernating bears (which do not eat food or drink water) can survive during the cold winter. Likewise, in their natural habitat or **aquaculture**, many species of fish can survive months of starvation, particularly during the times of breeding and migration. For example, the European **eel** exhibits extraordinary resilience to 1594 days of starvation. It is largely unknown why different species of animals have different resilience to prolonged starvation. (GW; JMF)

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Steam-volatile fatty acids:

see Volatile fatty acids (VFAs)

Steaming:

see Heat treatment

Stearic acid

Otherwise known as **octadecanoic acid**, $CH_3{\cdot}(CH_2)_{16}{\cdot}COOH$, shorthand designation 18:0. A saturated **long-chain fatty acid** found in many animal fats and some plant fats. Saturated long-chain fatty acids such as **myristic acid** (14:0), **palmitic acid** (16:0) and **stearic acid** (18:0) as triglycerides or mixed triglycerides give rise to what are called hard **fats**. (NJB)

Steatorrhoea

The passage of excess fat in the faeces, resulting in bulky, pale, foul-smelling, greasy stool. It is frequently a symptom of disease of the exocrine **pancreas** in which **lipase** is inadequate to hydrolyse dietary fat, or of biliary disease in which there are insufficient biliary components for the emulsification of digested dietary fat necessary for **absorption**. It may also involve malabsorption of

the **fat-soluble vitamins** A, D, E and K. (JAM)

Stereotyped behaviours

Repeated oral behaviours that are invariant and have no obvious purpose. They may be a single behaviour, such as cage gnawing, or may incorporate a sequence of behaviours, such as figure of eight tracing in caged animals. They are restricted to captive animals and are associated with the release of **endorphin**s, endogenous morphine-like compounds that soothe the animal. Stereotypies may be hard to reverse or extinguish, as they are usually acquired over a considerable period of time. This may give rise to incorrect conclusions about their environment; for example, rehoused circus elephants in zoos often have stereotypies, such as swaying, learnt when in the circus but then incorrectly attributed to their zoo environment. However, in other animals, zoo environments have been seen to readily cause stereotypies if they are too far removed from the animal's natural environment, for example pacing in polar bears.

Steroids

Steroid hormones are produced by the **adrenal** cortex and by tissues of the reproductive tract in both sexes. The adrenal cortex synthesizes as many as 50 different steroid molecules, which can be classified as **glucocorticoids**, mineralocorticoids and androgens. The glucocorticoids are involved in adaptation to stress. The glucocorticoids cortisol and corticosterone are 21-carbon steroids involved in **gluconeogenesis**. The mineralocorticoids are 21-carbon steroids necessary for maintaining normal Na^+ and K^+

balance. The mineralocorticoid **aldosterone** is the most potent in this class. Sex steroids are hormones produced by the adrenal cortex, ovaries and testes. Small amounts of testosterone (the male sex hormone) are produced in the adrenal gland but other tissues produce the bulk of testosterone. The androgen precursor dehydroepiandostrone and the weak androgen androstenedione are also produced in the adrenal cortex. The sterol **cholesterol** is the starting compound in the biosynthesis of **oestrogen** and **progesterone** (the female sex hormones) and of testosterone. Oestrogen is produced by the follicile and has effects on the central nervous system, the mass of uterus and secondary sex characteristics such as the **mammary gland**s. Progesterone is produced by the corpus luteum, placenta and adrenal gland and facilitates the preparation of the uterus for implantation of the fertilized **egg**. It is involved in the maintenance of pregnancy and in mammary development. Testosterone maintains the function of the male reproductive tract, spermatogenesis, accessory glands and mating behaviour. (NJB)

Steroids, anabolic

Androgenic (masculinizing) and oestrogenic (feminizing) **hormone**s produced by the testes of the male (testosterone and dihydrotestosterone) and ovaries of the female (**oestrogen** and **progesterone**). In steers and heifers, these hormones have an impact on **growth** by changing the relative rates of **protein synthesis** and protein **catabolism** in a coordinated manner among organs, so that the difference is greater, resulting in enhanced growth. Like other steroid hormones, they bind to

intracellular receptors, travel to the nucleus, bind to DNA and result in the gene-directed production of protein. The commercially produced hormones, oestradiol, zeranol, trenbolone **acetate** (TBA) and melengestrol acetate (MGA), enhance growth and decrease the proportion of **carcass fat** and have therefore been used in meat animal production. (DMS)

See also: Growth promoters

Key reference

Meyer, H.H.D. (2001) Biochemistry and physiology of anabolic hormones used for improvement of meat production. *Acta Pathologica Microbiologica et Immunologica Scandinavica* 109, 1–8.

Steroids, sex

Hormones produced in the testes and ovaries and released into the bloodstream. They promote sperm and ova production, the development of the reproductive tract, secondary sex characteristics and sexual behaviour. There are three general classes of sex steroids: the androgens, the **oestrogen**s and the progestins. The structures of these classes are derived from the same compound, cholestane ($C_{27}H_{48}$), which is referred to as the asteroid nucleus. The testis and the ovary produce the androgens, androstenedione and testosterone. In the Leydig cells of the testis, androstenedione is converted to testosterone ($C_{19}H_{28}O_2$). Androstenedione is also produced by ovarian thecal cells. It is converted by granulosa cells to oestrone or testosterone and subsequently to 17β-oestradiol ($C_{18}H_{24}O_2$). Several other hydroxylated and methylated derivatives of oestrone and 17β-oestradiol are also found. In regard to progestins, pregnenolone is

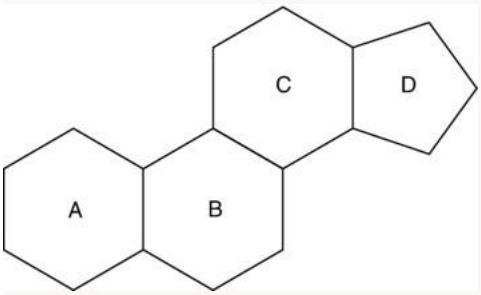
produced both in the ovaries and in the testes and converted to **progesterone**. Other hydroxylated forms of progesterone ($C_{21}H_{30}O_2$) are also found in testes and ovaries. (DMS)

Key reference

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Sterols

Sterols are based on the four-ring (A, B, C and D) structure of the cyclopentanoperhydrophenanthrene nucleus. If this nucleus has one or more hydroxyl (OH) groups and no carbonyl (C=O) or carboxyl (COOH) groups, it is a sterol. A number of steroids such as **cholesterol**, **bile** acids, adrenocortical hormones, sex hormones and the various forms of **vitamin D** and its **metabolite**s all have structures related to the phenanthrene (rings A, B and C) but vary in the groups added to the rings, in the unsaturation of the rings or in the addition of side chains. (NJB)



Stinging nettle (*Urtica dioica*)

A herbaceous perennial plant with straight stems of 0.5–1 m, which often grows naturally in gardens and wet places and in shady areas. Its creeping roots grow rapidly to fill the surrounding environment.

The nettle has a quadrangular stem covered with webs and its leaves are pointed and jagged (Zargari, 1997). Its flowers are bright green.



Stinging nettles (*Urtica dioica*). There are about 30 species of *Urtica*, mostly in temperate climates. Most possess stinging hairs on the stems and leaves. *Urtica dioica* is a herbaceous perennial. Photo courtesy of Leonora Enking. Licensed under CC BY-SA 2.0.

The aerial part of the plant stings the human body's skin, but nettle leaves, roots and juice can be used for food and medicine. The chemical compounds in nettle plants include **tannin**, mucilage, **formic acid**, phytosterone, **nitrate**, **potassium**, **calcium**, **iron** compounds and a type of **glucoside** producing inflammation of the skin. The nettle stem has a coloured substance called urticine. This plant has been used since ancient times to cure colds. Its other claimed therapeutic properties include strengthening digestion, stopping bleeding, reducing **blood sugar** and hair loss and enhancing **milk** secretion (Zargari, 1997; Grauso

et al., 2020). Today, dried nettle leaves are used to extract chlorophyll for the food industries and the formulation of medicines; the dry leaf contains 7.5% chlorophyll (Zargari, 1997; Halder and Sharma, 2017). Feeding the powder and extract of nettle leaves and roots to poultry at levels of more than 1% may lead to improved growth of internal organs, increased liver enzymes, reduced **lipid peroxidation**, reduced stress, improved antioxidant status and improved **immunity**. The compounds to which these benefits are attributed are **histamine**, acetylcholine, **serotonin**, quercetin, rutin, carotene, beta-sitosterol, vitamins C and K, calcium and **flavonoid** compounds. It is possible that these compounds will have a future role in anti-inflammatory, antibacterial, antiviral and immune system medication (Grauso *et al*., 2020; Pliego *et al*., 2022). (AS; BH-G; CJCP)

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Stomach

The shape and relative size of the stomach varies greatly amongst species. The stomach is divided into four regions: the oesophageal, cardiac, fundic and pyloric regions. The oesophageal region is the only part of the stomach lacking secretory cells. This region occupies a large fraction of the stomach of the horse but is very small in the relatively larger stomach of the pig, in which the cardiac region occupies the major part.

The secretory cells produce **hydrochloric acid** (HCl), **enzymes** and mucus. HCl is secreted by the **parietal cell**s in the cardia. **Hydrogen** ions are secreted into the lumen by a process requiring **adenosine triphosphate** (ATP). **Chloride** ions originate from **blood plasma**. The concentration of HCl in most farm animals is about 0.02–0.03 M and can lower the pH of stomach contents to 2.0 or less. The low pH established by HCl is bactericidal and may kill pathogenic bacteria entering with the food. The low pH also activates **pepsin** from its inactive pro-form, pepsinogen, and denatures dietary proteins, making them more susceptible to degradation by pepsin. Finally, minerals such as **calcium** carbonate and phosphates are dissolved. The secretion of gastric juice is controlled by the hormone, **gastrin**, which is secreted in response to the arrival of food in the stomach. In young **suckling** animals a more specific enzyme, **rennin**, is secreted rather than pepsin; its action is to clot **milk** protein.

The gastric epithelium is protected against attack by HCl and pepsin by mucus, which contains various mucopolysaccharides and mucoproteins. The latter also contain the intrinsic factor that aids the absorption of vitamin B_{12} in the **ileum**.

There are two types of stomach, one in simple-stomached, non-ruminant animals and one in ruminants, which have four stomach compartments: the **rumen**, **reticulum**, **omasum** and **abomasum**. The latter is the only true gastric stomach and corresponds to the stomach of non-ruminants.

In non-ruminants the function of the stomach is to store food after a meal, mix it with acid, mucus and pepsin and release it at a controlled steady-state rate into the **duodenum**.

The food is stored in the proximal stomach (cardia and fundus) where little contraction or mixing occurs. This means that the volume of the stomach in this area can easily be increased during a meal. **Amylase** from **saliva** as well as active enzymes in the food, e.g. **phytases**, may still be active when the food is located in this region.

In the distal stomach, the antrum and pylorus, there is intense slow-wave activity. Strong waves of **peristalsis** begin at about the middle of the stomach and migrate towards the pylorus, through which only particles smaller than about 2 mm can pass.

The rate of **gastric emptying** is under both nervous and hormonal control and is regulated to match the rate of **digestion** in the **small intestine**.

Some non-ruminant species have a forestomach; for example, birds have a crop, which serves as a storage organ in which microbial **fermentation** may occur together with a continued action of salivary amylase on **starch** degradation. The true stomach, in which HCl and pepsin are secreted, is called the **proventriculus**. In avian species, pepsin is ready for secretion at

a high level at the first meal after hatching; this meal can be of the same composition as that eaten by adults and is digested efficiently. The proventriculus is followed by the **gizzard**, which has very strong muscular walls that grind the food. The gizzard compensates for birds' lack of teeth by physically reducing **particle size**, often with the help of small stones that are swallowed.

In ruminants, the rumen, reticulum and omasum can be considered as forestomachs to the abomasum. The reticulum moves ingested food into the rumen or omasum and regurgitates ingesta during **rumination**. The rumen acts as a fermenter with a large population of microorganisms. The omasum has a role in controlling passage of **digesta** into the abomasum, the true stomach. (SB)

See also: Gastrointestinal tract

Stomach ulcers

Stomach ulcers occur commonly in pigs and are also seen in young foals. Abomasal ulcers occur commonly in cattle. In pigs, the aetiology is uncertain but the condition is associated with finely ground **pelleted feed**, especially when it contains a high proportion of **wheat**. The more finely ground the feed, the higher is the pH of the gastric contents and the more fluid their consistency. The pars oesophagea of the stomach appears to lack protection from the acid. *Helicobacter*, found to be associated with the condition in human beings, has recently been found in pigs with **gastric ulcers** but the condition has not been produced experimentally. In young foals, gastric ulcers are associated with inadequate long fibre in the diet. Abomasal ulcers in cattle are also

of uncertain cause but stress and a high proportion of **cereal** in the diet are commonly thought to be factors. Some prevention of gastric ulcers may be afforded by feeding fibrous material. Stomach ulcers cause signs of abdominal pain, blood loss leading to melaena, and occasionally fatal peritonitis following perforation. (WRW)



Stomach, or gastric, ulcers are often the result of a diet with inadequate fibre. Photo courtesy of Zappy's Technical Solutions. Licensed under CC BY 2.0.

See also: Gastric ulcers

Stone and stick chewing

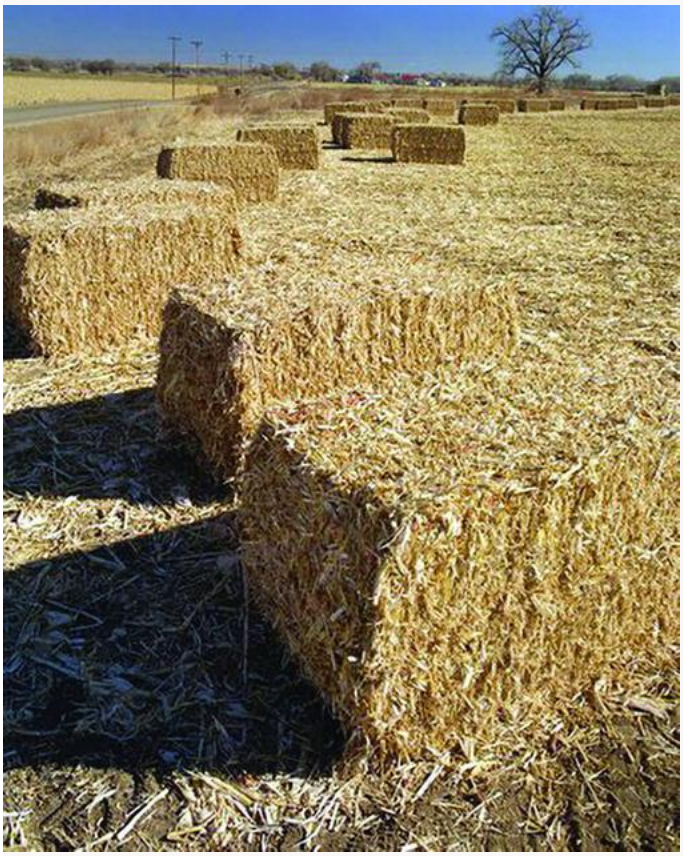
The chewing of stones is a common behaviour in pigs kept on land with limited plant cover; it is also common in dogs. Walkers throw stones and sticks for dogs to retrieve. This behaviour may lead to splinters entering the buccal mucosa and both sticks and stones lead to **tooth** damage and wear. (CJCP)

Storage polysaccharides

Polysaccharides used as energy reserves by living organisms. Major examples include **starch** in most higher plants, **fructans** in certain plants and **glycogen** in animals and bacteria. Starch is

present in all green plants and in most of their tissues. It accumulates in leaves in the light, where it is used for energy in the dark, and in storage and seed tissues, where it is used during **germination**. About 15% of higher plants produce fructans as a storage polysaccharide. Glycogen typically makes up 5% of liver weight and 1% of **skeletal muscle** weight in animals. (JAM)
See also: Carbohydrates

Stover
The dry stems and leaves of tall **cereal** plants (**maize**, **millet**s and **sorghum**) after removal of the **grain**-bearing structures (ear or cob). Stover is either stored for feeding later or grazed *in situ*. In the tropics it is often the major feed resource for ruminant livestock during the **dry season**.



Corn stover, in large square (as opposed to round) bales. Photo courtesy

of Idoha National Laboratory. Licensed under CC BY 2.0.

Stover is low in **crude protein** (20–30 g kg^{-1} dry matter (DM)) and high in fibre (cell walls 700–800 g kg^{-1} DM, consisting of **hemicellulose**, **cellulose** and **lignin**), limiting intake and **digestibility**, especially when it is the major component of the diet. The most nutritious fraction is the leaf, with stems often being of little value. The **nutritive value** of stover can be improved by physical treatment (such as grinding to reduce **particle size**) or chemical treatment (for example by the addition of **urea** to break down ligno-cellulose bonds and add **nitrogen**). **Supplementation** with a nitrogen-rich feed (such as urea, **oilseed** residue or legume **straw**) also improves the intake and digestibility of these materials. As a component of energy-rich diets, stover can provide the fibre necessary for efficient **rumen** function. (TS)

Straw

The dry cut stalks of **cereal** and **legume grain** crops, harvested after the grain has ripened and been harvested. Whereas the term **stover** is applied to the stalks from tall grain crops, straw refers to the shorter residues of **barley**, **oats**, **rice**, **rye** and **wheat**, and of legumes such as **pea**, **lentil**, **chickpea**s and faba **bean**. Straw is either removed from the field at harvest for threshing or remains in the field, after cutting with a combine harvester, usually to be baled before storage. In intensive livestock production systems, the level of inclusion depends upon the production purpose. In extensive systems, especially those in predominantly cropping areas, straw is

often the major or sole component of the diet. Straws are high in fibre (cell walls 700–800 g kg^{-1} dry matter (DM), consisting of **hemicellulose**, **cellulose** and **lignin**) and low in protein (**crude protein**, 20–38 g kg^{-1} DM). The techniques used to upgrade stover are generally successful with straw. (TS; GMcLD)

Striped catfish (*Pangasianodon hypophthalmus*):
see Catfish

Structural polysaccharides
Nearly all plants and microbes use **carbohydrates** as major structural materials. Structural polysaccharides in plants include **cellulose**, **pectic substance**s, β-D-**glucans**, **hemicellulose**s and other heteropolysaccharides of diverse **sugar** composition. Animal **connective tissue** includes several polysaccharides, including hyaluronic acid, chondroitin **sulphate**s, heparins, dermatan sulphate and **keratin** sulphate. Bacterial cell wall polysaccharides include **peptidoglycan**, **lipopolysaccharide**s, teichoic acids (polyol phosphates) and heteroglycans, frequently containing **amino sugars** or **uronic acid**s in the repeating **oligosaccharide** units. Fungal cell wall **polysaccharide**s include **chitin**, β-D-**glucans** and glycoproteins with a high proportion of **mannose**. Algal cell walls contain alginic acid, **galactan**s and sulphated galactans, e.g. **carrageenan**s. (JAM)
See also: Dietary fibre

Stunting
Stunted growth occurs in farm animals as a result of an inadequate

supply of nutrients, infection or genetic factors. It is characterized by delayed and retarded early growth of muscles and bone tissue, often caused by an inadequate supply of energy, protein and the minerals that are important for bone growth. Stunting usually occurs at an early age, in which case the growth retardation is likely to be permanent. The critical phase when stunting is most likely usually precedes the period of most rapid accretion of body tissues during pre-natal life. Small maternal size is also a risk factor. In rodents, substances that block dopaminergic neurotransmission retard brain development and are implicated in stunting. An infectious stunting syndrome is recognized in poultry, usually caused by enteric or respiratory tract viruses, including the avian influenza virus. The disease is characterized by growth retardation, variability in size, **leg weakness**, **diarrhoea** and increased mortality. Despite the association with enteric viruses, the growth retardation is believed to be due to disorders of the **metabolism**, rather than absorption or digestion. (CJCP)

Sturgeon

A **fish** of the family Acipenseridae, characterized by: a heterocercal tail; lack of adult teeth; four barbels in front of an inferior, protrusible mouth; a largely cartilaginous skeleton; and five rows of bony scutes or plates on the body. All species are either freshwater or anadromous. Some species can attain 4–6 m length and approach 500 kg in weight. There are two genera of sturgeons: *Acipenser*, consisting of 16 species distributed around the northern hemisphere; and *Huso*, with two species, kaluga (*H. dauricus*) and beluga (*H. huso*), confined to the Adriatic and Caspian basins and

the Amur river. Several species are prized for flesh and for the caviar derived from the roe. In the past the large swim bladder was used in isinglass production.



A concrete tank crowded with young sturgeon. Photo courtesy of USFWS/Southeast. Licensed under Public Domain Mark 1.0.

All species are long-lived (over 20 years) and have slow **growth** and **reproduction** rates. Consequently most wild populations have been drastically reduced. Two principal countries of sturgeon culture are Russia and the USA (California). Russia produces about 100 million fingerlings, largely of the hybrid (called bester) between the beluga and the sterlet (*A. ruthenus*) for stocking purposes. California cultures a few hundred tonnes annually of the white sturgeon (*A. transmontanus*), indigenous to western North America, primarily for commercial markets.

Ovulation and spermiation of broodstock are synchronized with the use of carp pituitary injections. Sperm is collected in hypodermic syringes by exerting pressure on the abdomen of the male, and the eggs are removed by Caesarean operation. After fertilization the eggs are mixed with silt to remove adhesiveness. The eggs of white sturgeon hatch in 5 days at 16°C. The young attain 500 g in the first year, 2 kg in 2 years, 4–5 kg in 3 years, and are marketed at about 6 kg in 3.5 years. Production of good-quality eggs from domestic females remains a problem, and wild females are still used for much **egg production**. (RHP)

Subacute ruminal acidosis (SARA)

A disease of cattle derived from the accumulation of acid end-products of **fermentation** in the rumen. It commonly affects 20% or more of early and mid-**lactation** dairy cows. This is usually the result of feeding a diet with too little fibre with particles of 1.8 mm long or more. As well as too little physically effective fibre, the acid accumulation may be due to feeding of large quantities of rapidly digested concentrate feed. Young grass, for example during spring, also has little physically effective fibre and is associated with low **milk** fat concentrations and a rapid decline in yield, suggesting that cows are experiencing SARA.

The proportion of time when the **rumen** pH is less than 5.6 is used to diagnose SARA. This, together with the presence of **lipopolysaccharide**s (LPS), causes damage to rumen epithelial cells, regulated by tissue necrosis factor (TNF) and mitogen-activated protein kinase (MAPK). Severe reductions in pH, which are typical in acute ruminal acidosis (ARA), cause apoptosis. Once

the LPS has breached the epithelial barrier, **cytokines** are released which trigger an inflammatory response. Acute-phase proteins, such as haptoglobin and amyloid phase A, are released. With inadequate fibre, cows ruminate less, with fewer pH buffers therefore added in **saliva**. The inadequate fibre intake results in low milk fat concentrations in their milk. Affected cows reduce their **feed intake** considerably. The disease is commonly associated with **lameness**, in particular **laminitis**, which suggests that cows with SARA are in pain. Although SARA is highly prevalent in dairy cows, the condition cures itself, as the reduction in feed intake dramatically reduces acid end-products and the cow's appetite eventually returns. Prevention measures include ensuring adequate physically effective fibre in the diet, feeding pH buffers and mixing concentrates with forage in a **total mixed ration**. (CJCP)

Substrates
Substances that undergo chemical reactions in **metabolism** (usually carried out with the aid of a catalyst or enzyme) and are converted into products. Thus, a substrate is changed during the reaction whereas the enzyme is not. (NJB)

Succinate
A four-carbon **dicarboxylic acid**, $HOOC{\cdot}CH_2{\cdot}CH_2{\cdot}COOH$. Because it is an intermediate in the **tricarboxylic acid** cycle, carbon from succinate, $^{-}OOC{\cdot}CH_2{\cdot}CH_2{\cdot}COO^{-}$, can be found in almost all compounds in the body. (NJB)

Sucking
The act of imbibing a liquid or air through rapid inspiration. In horses, inspiration of air in 'wind sucking' is a **stereotyped behaviour** similar to crib-**biting**. Sucking invokes coordinated neurohormonal reflexes resulting in **milk** ejection and synthesis, and the restriction of ovulation in many mammalian species, most notably the sow and cow. A reflex action in the sucking baby ruminant forms a channel (the oesophageal groove) that directs milk away from the **rumen** and directly into the **abomasum**. (KDS; CJCP)

Suckle
The act of withdrawing **milk** from the **mammary gland**. To nurse; to provide milk to a **suckling**. (KDS)

Suckling
In mammals, the act of nursing, of providing **milk** to the suckling animal by wrapping the mouth around the nipple to extract milk by squeezing and **sucking** the **mammary gland**. The sucking action creates a vacuum around that teat, which encourages milk expression. Suckling is also used to define an animal that has not been weaned, as in suckling pig, usually a baby animal that is dependent on milk withdrawn from the mammary gland as its principal source of nourishment. (KDS; CJCP)



Calf suckling its mother's teat. Photo courtesy of Geoff Penaluna. Licensed under CC BY 2.0.

Sucrase
A glycolytic enzyme (invertase; α-D-fructofuranoside fructohydrolase; EC 3.2.1.26) that hydrolyses the disaccharide, **sucrose**, into its constituents, **glucose** and **fructose**. Sucrase is attached to the **brush border** of epithelial cells in the **small intestine**, in particular the **jejunum**. (SB)

Sucrose
Common or table **sugar**. A non-reducing **disaccharide** of **glucose** and **fructose**, α-D-glucopyranosyl β-D-fructofuranoside, $C_{12}H_{22}O_{22}$, molecular weight 342. Sucrose occurs in many plants and is produced commercially from **sugarcane**, **sugarbeet** and **sorghum**. (JAM)
See also: Carbohydrates

Sugar
A general term applied to the simplest **carbohydrates**, **monosaccharide**s and **disaccharides** that are soluble in water and 80% **ethanol**. A 'simple sugar' usually refers to a

monosaccharide, which consists of a single polyhydroxy **aldehyde** or **ketone** unit. 'Sugar' also refers to the disaccharide **sucrose**, common or table sugar. (JAM)

Sugarbeet

The species *Beta vulgaris* (family Chenopodiaceae), to which the root crop sugarbeet belongs, also includes mangels and **fodder beet**. Although morphologically different these are generally classified according to their dry matter (DM) and **sugar** content, mangels having the lowest and sugarbeet the highest content. A temperate crop, sugarbeet is grown throughout Europe principally for sugar production, though some roots are either ensiled or fed directly to livestock. Yields vary with variety, location and management practices but fresh weight yields of over 50 t ha^{-1} are common. The crop is harvested from September to January with DM yields increasing over this time, but sugar content tends to decline from early December. Sugarbeet has a relatively high DM content (230 g kg^{-1}) similar to **potato**es and twice that of other common root crops such as **turnip**s or **swedes**. **Crude protein** and fibre levels are low, both about 50 g kg^{-1} DM, with **ash** content about 30 g kg^{-1} DM. The fibre component is highly digestible (> 850 g kg^{-1} DM), comprising mainly primary cells and containing a high level of **pectic substance**s. The high **nitrogen-free extract** (870 g kg^{-1} DM) comprises mainly sugars, of which the most important is **sucrose** (150–200 g kg^{-1} DM). Sugarbeet is high in **calcium** but low in **phosphorus**, **manganese**, **zinc** and **iodine**.



Sugarbeet is grown throughout Europe and has a high content of sugar. It is used for the production of sugar or fed to livestock (fodder beet). Photo courtesy of Gilles san Martin. Licensed under CC BY-SA 2.0.

Sugarbeet contains **betaine**, a tertiary **amine** formed by the **oxidation** of **choline**, and young leaves may contain 25 g kg^{-1}. It is this amine that is responsible for the 'fish-like' aroma frequently associated with commercial sugar extraction. Within the ruminant this is normally metabolized to **trimethylamine**, which is what gives the fish **taint** to **milk** produced by cows that have been offered excessive amounts of sugarbeet products. To reduce milk taint, it is recommended that sugarbeet should be offered immediately after milking. If sugarbeet is introduced too rapidly, the high **carbohydrate** content of the roots can lead to **lactic acidosis** resulting from rapid **fermentation**. If this occurs with high-yielding cattle, the accompanying depression of appetite can result in **ketosis**. **Rumen** impaction can also occur. As these roots are hard, it is common practice to chop or pulp them prior to

feeding. Sugarbeet has caused toxicity in horses and is therefore not recommended.

Commercial extraction of sucrose from beets (a relatively simple process in which the beets are washed, grated and then soaked in hot water to remove sugar) produces two highly valuable **by-product**s: sugarbeet pulp and **molasses**. In addition, while the tops removed at harvest can be used as a livestock feed, < 5% of this material is actually utilized.

Beet pulp is the residue from the sugar extraction process. It has a high water content (80–85%) and, while it can be fed directly (as pressed pulp), it is usually pre-dried to about 90%. The residue consists mainly of cell wall **polysaccharide**s: as these are highly digestible the product is readily consumed by all classes of ruminant livestock. The incorporation of sugarbeet pulp into rations stimulates fibre degradation in the rumen, enhancing intake, especially when poorer-quality feeds such as cereal **straw** are offered. It is consequently widely used for dairy cattle, with beneficial effects on milk fat content. It is incorporated in the diets of **fattening** cattle and is a major component of supplementary **feed block**s for sheep. The high fibre content makes it a less attractive feed for pigs and poultry. The feed is well tolerated by horses but it is recommended that the material is soaked in water prior to feeding, to prevent impaction. A further use of sugarbeet pulp is as an absorbent to limit effluent losses during ensilage of crops that are low in dry matter.

After crystallization and separation of the sugar from the water extract, a thick dark brown viscous liquid (molasses) remains. Yield

is generally about 300 kg t^{-1} sugar. Molasses contains 700–750 g DM kg^{-1}, 50% of which is sugars. The DM has a low crude protein content, mostly present as **non-protein nitrogen**, including betaine. At low temperatures, molasses is difficult to handle and not easy to mix into feeds on the farm. The use of heated tanks helps to permit accurate metering through calibrated pumps. Molasses can have a laxative effect and is therefore not used at high levels in the diet.

A number of industrial fermentations use molasses as the feedstock: the spent molasses (along with any residual **microbial protein**) is partially evaporated and sold to the feed industry as condensed molasses solubles. This product is less viscous and has lower sugar levels and higher protein and ash contents than molasses. Molasses is used at inclusion levels of 5–10% in the manufacture of pellets and cubes, not only to improve **palatability** but also to help to bind the product. In addition, being a rich source of sugars, molasses is used as an additive to **silage**. Molasses is also combined with beet pulp and the material sold as molassed sugarbeet feed. Although classed as an energy **supplement**, molasses degrades in the rumen more slowly than starchy feeds such as rolled **barley** and therefore has a significantly lower impact on rumen fermentation.

Sugarbeet tops comprise the leaves plus part of the upper root and are high in sugars. They are also an excellent source of carotene, a precursor of **vitamin A**. The tops may also contain, depending on the degree of soil **contamination**, considerable levels of ash. Despite the introduction of single-operation

harvesting systems, only 5% of this valuable feed is utilized, the rest being ploughed in. The tops also contain oxalic acid plus soluble sodium **oxalate** and insoluble calcium and **magnesium** oxalates. Soluble oxalates are largely detoxified in the rumen to carbonate and **bicarbonate**. Oxalate **poisoning** can be manifested as scouring, **hypocalcaemia**, haemolysis, renal failure and crystallization of oxalate in the brain, causing nervous disorders, paralysis and, in extreme cases, death. The risk appears to be reduced if the leaves are wilted first (up to 1 week). However, oxalate is still present after **wilting** and so other toxins may be involved. A further problem is the possibility of **nitrite** poisoning, where nitrates present in the leaves of beet tops are reduced in the rumen to nitrite. This combines with **haemoglobin** to form **methaemoglobin**, leaving the **blood** a characteristic brown colour and greatly reducing **oxygen** uptake. (FLM)

Sugarcane (*Saccharum officinarum* L)

A tropical or subtropical perennial **grass**, almost unique in that its **carbohydrate** reserve is **sucrose** rather than **starch**. Nearly two-thirds of all **sugar** is produced from sugarcane, the remainder being from **sugarbeet**, which is grown in temperate areas. Sugarcane is widely cultivated: India, Brazil and Cuba account for 40% of cane sugar. Sugarcane is planted by burying short pieces of stem (three-node 'setts') in well-drained soil. When mature, at around 18 months, the plant is about 3 m tall, the sugar concentration is highest and the crop is ready for **harvesting**. At maturity, cane becomes tough and turns pale yellow. After harvesting, the crop regenerates ('ratoon crop') and again matures

in about 18 months. Two to three ratoon crops are grown before replanting is necessary due to loss of yield. Sugarcane is reasonably resistant to **drought**, but *c.* 1500 mm annual rainfall, evenly distributed, is optimal; some irrigation is often employed. Yields are 30–160 t ha^{-1} annually. Cane represents 60–70% of the weight of whole crop, the remainder being tops (20–30%) and leaves (*c.* 10%).



Sugarcane is grown in tropical or subtropical climates and is used for the production of sugar, with residues fed to livestock. Photo courtesy of Ton Rulkens. Licensed under CC BY-SA 2.0.

Milling of cane generates 10% sugar plus 70% water, 3% **molasses**, 2% filter-press mud and 15% **bagasse**. Traditionally sugarcane is grown in plantations with sugar mills as adjuncts. Tops and leaves are removed in the field and the tops may be used as ruminant feed. Bagasse is normally burnt in mill boilers, processed to paper, board or furfural; use as a ruminant feed is limited. Filter-press mud is used as a soil ameliorant. Molasses is

used for alcohol manufacture or livestock feeding. Traditionally, commercial sugarcane production has not been fully integrated with livestock production because the emphasis was on sugar production and its potential as animal feed was not recognized. Since the mid-1970s the use of sugarcane and its **by-product**s in animal feeding has been developed in a number of countries.

Sugarcane tops

The composition of sugarcane tops depends on the point at which the top is cut from the cane and other factors (variety, age at harvest, growing conditions). In Mauritius, the average composition of tops containing 29% dry matter (DM) was (% in DM): **ash** 8.5; **crude protein** 5.9; **crude fibre** 33.5; **ether extract** 1.7; **nitrogen-free extract** 50.3. The **digestibility** of **organic matter** in sheep and cattle was 56%. Others have reported the structural components of tops to be (% in DM): **neutral detergent fibre** 63–67%; **acid detergent fibre** 37–43%; acid-detergent **lignin** 4.6–5.0%. Freshly cut tops provide **maintenance** level feeding for cattle, but for production levels they require supplementing with protein. Smallholder dairy-cow keepers in Mauritius offer tops to cattle at double the appetite rate; this facilitates selection by the animals of the more nutritious growing points and rejection of less digestible leaf. Similarly, trials with African hair sheep showed that intake of chopped tops increased 60% when the amount offered was two to three times the expected intake. Sugarcane tops can be ensiled. In Mauritius, sugarcane tops mixed with 1–5% molasses and 1% ammonium **sulphate** produced well-preserved and palatable **silage**.

Molasses

The composition of sugarcane molasses depends on the method of production. The total sugar percentage and the ratio of sucrose to **reducing sugars** are, respectively: A-molasses, 68, 60:40; B-molasses, 57, 50:50; blackstrap or final molasses, 47, 40:60; high-test molasses, 78, 30:70. The type of molasses is unimportant in ruminant diets but for pigs and poultry high-test and A-molasses are the most suitable. Molasses are used in five ways: (i) in dry feeds as a binder and to reduce dust and improve **palatability** (< 15% of dry feed); (ii) as an additive to improve **fermentation** during ensiling of grass (5% of grass); (iii) as a carrier for **urea** in liquid supplements and **feed block**s for ruminants; (iv) as a substitute for **grain**s in diets for ruminants (e.g. molasses lot feeding of cattle) and, to a lesser extent, pigs and poultry; and (v) to improve the palatability and acceptability of processed feeds, e.g. in horse feeds.

Bagasse

Sugar-mill bagasse is of low feeding value, containing 45% **cellulose**, 35% **hemicellulose** and 10% lignin. **Rumen** dry matter degradability is very low (*c.* 30%). High-pressure steam treatment (13 kg cm^{-2}, 200°C, 6 min) solubilizes the hemicellulose and improves rumen degradability to 80%. Steam-treated bagasse supplemented with urea and rumen bypass nutrients has given rapid **growth** rates in beef cattle. **Hydrolysis** with **sodium** hydroxide is also effective but the method is costly.

Chopped sugarcane

Whole sugarcane, after **chopping**, may be used as a dry-season

forage for ruminants, if economics permit. Although DM **digestibility** is acceptable (62%), **supplementation** with minerals (sodium, **phosphorus**, **sulphur**), **nitrogen** (as urea or ammonium **sulphate**) and rumen bypass nutrients (e.g. **rice** polishings) is necessary to achieve satisfactory growth rates in cattle. Rice polishings may be replaced by restricted feeding of forage from tree **legumes** (*Leucaena* or *Gliricidia*). Chopped sugarcane must be fed within hours to avoid fermentation of the sugar, which also makes ensiling difficult without the use of suitable additives (e.g. **ammonia**). However, the case for ensiling is debatable, as sugarcane can be harvested in the dry season and, as a 'standing crop', does not deteriorate. Supplemented whole sugarcane for lactating cattle has given disappointing **milk** yields.

Sugarcane juice

Farm-scale fractionation of sugarcane to produce juice as a feed for non-ruminants, and fibrous residue as a feed for ruminants, has proved more profitable than feeding whole sugarcane to ruminants. The juice is extracted by passing the stalks through a crusher which removes 60–80% of the sugars (sugar mills extract up to 97% of sugars). Consequently, farm-scale bagasse is of a higher feeding value to ruminants than sugar-mill bagasse. Farm-scale cane juice contains 15–23% total solids, 80% of which are soluble sugars, mainly sucrose. Sugarcane juice ferments within 8–12 h but can be preserved for 3–7 days with **formaldehyde**, ammonium hydroxide and sodium benzoate. For growing pigs, suitable supplements to cane juice include **soybean** meal (200 g per day) or **groundnut** cake (300 g per day) with a mixture of

sweet potato vines and water plants (for minerals and vitamins). Cane juice is not a suitable substitute for grains in the diets of **broiler chicken**s or **laying hen**s, because of the low-energy density of the juice, as well as stress and **cannibalism** caused by feathers sticking together when splashed with juice. Use of cane juice for **ducks** and geese shows much more promise. (EO)

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Sulphates

Sulphates, $\cdot SO_4^{2-}$, are normal constituents of food. In **metabolism**, **cysteine** is the primary source of sulphate. Sulphate is incorporated into glycoproteins via an ATP-like intermediate (adenosine 3′-phosphate-5′-phosphosulphate) or 'active sulphate'. Sulphate is attached to **galactose** or *N*-acetylgalactosamine or *N*-acetylglucosamine in **connective tissue**s and other cell surfaces as chondroitin sulphate, **keratin** sulphate, heparin, heparan sulphate and dermatan sulphate. Sulphate is used to conjugate drugs so as to facilitate their urinary excretion. (NJB)

Sulphur (S)

A non-metallic element with an atomic mass of 32.066. The earth's crust contains approximately 0.05% S as the free element or in combined states as sulphides and **sulphate**s. Sulphur is absolutely required in biological systems; it functions in numerous organic forms and as inorganic sulphate and sulphide. The table lists some of the active organic forms of sulphur found in animal tissues.

Organic forms of sulphur found in animal tissues.

Organic form	Comments
Adenosine-5′-phosphosulphate	'Active sulphate'
Adenosine-3′-phospho-5′-phosphosulphate	'Active sulphate
Biotin	A member of the B-vitamin complex
Chondroitin sulphate	Mucopolysaccharide containing β-D-glucuronic acid and *N*-acetylgalactosamine
Coenzyme A	Enzyme co-factor
Cystathionine	Intermediate in conversion of methionine to cysteine
Cysteic acid	Precursor of taurine
Cysteine	Amino acid
Cystine	Amino acid
Fibrinogen	Blood clotting factor

Organic form	Comments
Glutathione	A natural reducing agent made of glycine, cystine and glutamic acid
Heparin	Anticoagulant factor in blood
Homocysteine	Amino acid
Lipoic acid	A member of the B-vitamin complex
Metallothionein	Heavy metal-binding peptide
Methionine	Amino acid
Sulphated proteoglycans	Mucopolysaccharide in extracellular matrix of connective tissue
Taurine	Amino acid
Thiamine	Vitamin B_1

Most of the S in the body is in proteins as the amino acids **cystine**, **cysteine** and **methionine**. Another sizeable portion is in the form of sulphated proteoglycans in **connective tissue**s. Other important organic forms are the vitamins **thiamine**, **biotin** and lipoic acid, **enzyme** co-factors, and clotting and anticoagulant factors in **blood**.

Sulphur is consumed in the diet in both organic and inorganic forms. The organic forms comprise the largest portion, which includes the sulphur amino acids. For the most part, the smaller forms of S are absorbed intact. The sulphate and sulphide forms of

S are readily absorbed, and **absorption** seems to be regulated by a transport mechanism dependent on **vitamin D**. The absorbed inorganic S is also readily excreted in the urine as inorganic sulphate and/or sulphate esters. The rate of sulphate excretion is proportional to the concentration in plasma, where sulphate constitutes the fourth most abundant anion. The normal value for plasma sulphate is approximately 100 mg l^{-1}.

Although some inorganic forms of S are used in the synthesis of sulphur-containing compounds in the body, the dietary requirements for S for most animals can be supplied solely through the sulphur amino acids in proteins. However, it has been shown that by adding inorganic sulphate to a low sulphur amino acid diet, the **growth** rate of chicks and **laboratory animal**s can be improved. Very little response to added sulphate was seen when the animals were fed adequate concentrations of sulphur amino acids. Thus, the US National Research Council recommends 1500 mg S kg^{-1} diet for beef cattle, 2000 mg kg^{-1} for lactating dairy cattle and 1600 mg kg^{-1} for growing heifers, dry cows and mature bulls. There is no dietary S recommendation for pigs or poultry, but 1500 mg S kg^{-1} diet is recommended for horses and 1400–2600 mg kg^{-1} for sheep. S is added to **urea/molasses supplement**s for beef cattle to ensure that the nitrogen:sulphur ratio is about 14:1, and meets the requirements of **rumen microorganism**s. Sulphur (10–16% in a **salt** or molasses block) is also used to help prevent **cyanide poisoning** in cattle grazing forage **sorghum** crops. In the rumen, the added S converts cyanide to thiocyanate.

The severity of S toxicity greatly depends on the form ingested.

Elemental S is the least toxic form, whereas **hydrogen sulphide** is extremely toxic. Lactating cattle have been shown to tolerate daily doses of 20 g of sulphur dioxide or **sodium** metabisulphite, but 50 g per day reduced food intake. The severity of S toxicity also depends on whether the rumen microorganisms can produce hydrogen sulphide from the sulphur source. The combination of sulphur and **molybdenum** to form thiomolybdate in the rumen can reduce **copper** availability, which could lead to copper deficiency. The maximal tolerable concentration of S for cattle is 4000 mg kg^{-1} diet. (PGR)
See also: Thiomolybdates; Thiosulphates

Sulphur amino acids
A collective term for amino acids that contain sulphur. **Methionine** $CH_3{\cdot}S{\cdot}CH_2{\cdot}CH_2{\cdot}HCNH_2{\cdot}COOH$, **cysteine** $HS{\cdot}CH_2{\cdot}HCNH_2{\cdot}COOH$ and **cystine** $HOOC{\cdot}HCNH_2{\cdot}CH_2{\cdot}S\text{-}S{\cdot}CH_2{\cdot}HCNH_2{\cdot}COOH$, are all found in protein. It also includes a number of their derivatives. In the normal **catabolism** of methionine, four sulphur-containing amino acids are produced in sequence: L-**homocysteine** $HS{\cdot}CH_2{\cdot}CH_2{\cdot}HCNH_2{\cdot}COOH$, L-cystathionine $HOOC{\cdot}HCNH_2{\cdot}CH_2{\cdot}S{\cdot}CH_2{\cdot}CH_2{\cdot}HCNH_2.COOH$, L-cysteine $HS{\cdot}CH_2{\cdot}\ HCNH_2{\cdot}COOH$ and the β-aminosulphonic acid **taurine** $NH_2{\cdot}CH_2{\cdot}CH_2{\cdot}SO_3H$. L-Cysteine is in turn the source of sulphur for **sulphate**. (NJB)

Sulphuric acid
A strong inorganic acid, H_2SO_4, with molecular weight 98.08 and density of 1.84 at 20°C. In the concentrated form (98%) it is a

colourless, odourless and highly corrosive liquid (pH < 1) widely used in industry. Combined with **hydrochloric acid** in the AIV method, it is used to aid pH reduction when ensiling forages. (FLM)
See also: Acid treatment

Sunflower (*Helianthus annus*)
An **oilseed** crop of considerable potential for livestock and poultry production since it grows in many parts of the world. The main producers are Europe (France, Russia, Romania and Ukraine), South America, China and India. Sunflower is grown for oil production, leaving the extracted meal available for animal feeding. Globally the meal is third in importance after **soybean** and canola/rapeseed meals. Sunflower seed surplus to processing needs and seed unsuitable for oil production may also be available for feed use. A related species, **Jerusalem artichoke** (*Helianthus tuberosus*) is of some importance in human and animal nutrition.



A field of sunflowers in France. Photo by AF Vincent. Licensed under CC BY-SA 2.0.

Nutritional features

The seeds contain approximately 380 g oil kg^{-1}, 170 g **crude protein** kg^{-1} and 159 g **crude fibre** kg^{-1} and are a good source of protein and lipids. Composition and **nutritive value** of the meal vary considerably, depending on the quality of the seed, method of oil extraction and extent of dehulling before extraction. As a result the meal should be purchased with a guaranteed analysis or analysed before inclusion in diets, particularly for pigs and poultry.

The crude fibre content of whole (hulled) sunflower meal is around 300 g kg^{-1} and with a complete decortication (hull removal) the fibre content is around 120 g kg^{-1}. Sunflower meal contains about 360 g crude protein kg^{-1} (see table), which is not well balanced in its content of **lysine**, threonine and **tryptophan** for non-ruminant feeding. **Energy value** varies substantially with fibre level and residual oil content. However, the energy value of sunflower meal is lower than that of canola or soybean meal, with a **metabolizable energy** (ME) value of about 13 MJ kg^{-1} dry matter (DM) for cattle. Higher levels of hulls included in the final meal lower the energy content and reduce the **bulk density**.

The oil is highly valued for the human market, owing to its high content of **polyunsaturated fatty acid**s. **Calcium** and **phosphorus** levels compare favourably with those of other plant **protein source**s. Sunflower meal tends to be lower in **trace element**s compared with soybean meal, but it is high in B vitamins and β-carotene (see table). In contrast to other major oilseeds and oilseed meals, sunflower seeds and meals appear to be relatively

free of **antinutritional factors**.

Typical composition of sunflower seed meal, air-dry basis

Component	Amount	Component	Amount
Dry matter (g kg^{-1})	920	**Trace minerals** (mg kg^{-1})	
Crude fibre (g/kg)	265	Cobalt	4.03
Neutral detergent fibre (g kg^{-1})	410	Copper	35.2
Acid detergent fibre (g kg^{-1})	287	Iodine	0.1
Crude fat (g kg^{-1})	21.0	Iron	221.6
Linoleic acid (g kg^{-1})		Manganese	34.0
Crude protein (g kg^{-1})	285	Selenium	0.5
CP bypass for ruminants (%)	16	Zinc	100.9

Component	Amount	Component	Amount
ME for ruminants (kcal kg^{-1})	2440	**Vitamins** (IU kg^{--1})	
ME for ruminants (MJ kg^{-1})	10.2	Beta-carotene (mg/kg)	0.33
NEG for ruminants (kcal kg^{-1})	1390	Vitamin A (IU/kg)	550
NEG for ruminants (MJ kg^{-1})	5.8	Vitamin E (IU/kg)	13.18
NEL for ruminants (kcal kg^{-1})	1500	**Vitamins** (mg kg^{-1})	
NEL for ruminants (MJ kg^{-1})	6.3	Biotin	1.35
DE for pigs (kcal kg^{-1})	2150	Choline	2503
DE for pigs (MJ kg^{-1})	9.2	Folacin	0.5

Component	Amount	Component	Amount
ME for poultry (kcal kg^{-1})	1320	Niacin	213.0
ME for poultry (MJ kg^{-1})	5.6	Pantothenic acid	10.1
Amino acids (g kg^{-1})		Pyridoxine	13.6
Arginine	25.4	Riboflavin	3.5
Glycine + serine	25.7	Thiamin	36.4
Histidine	7.7		
Isoleucine	13.1		
Leucine	19.3		
Lysine	11.6		
Methionine (Met)	7.1		
Met + cystine	12.4		
Phenylalanine (Phe)	13.9		
Phe + tyrosine	21.3		
Threonine	11.5		
Tryptophan	3.8		
Valine	15.4		

Component	Amount	Component	Amount
Major minerals (g kg^{-1})			
Calcium	2.0		
Phosphorus (total)	4.1		
Phosphorus (non-phytate)	10.3		
Chloride	1.8		
Magnesium	7.2		
Potassium	15.9		
Sodium	0.4		

CP = crude protein, DE = Digestible Energy, met = methionine, ME = Metabolizable Energy, NEG = Net Energy for liveweight gain, NEL = Net Energy for lactation, phe = phenylalanine

Livestock and poultry feeding

Sunflower meal has been shown to be suitable as the sole source of supplemental protein in diets for dairy cows and beef cattle provided that the dietary energy and fibre levels are formulated correctly, and at lower levels in diets for growing stock. The oil content of sunflower meal adds to its value as a useful feed source for dairy cows. Lactating cows often respond to **supplementation** of the diet with **fat**. Sunflower meal is not recommended for young calves but can be utilized by older calves and cows. Limited

findings suggest that whole sunflower seed can be fed to dairy cows as an alternative to other oilseeds and that it can be used without any processing of the seeds. There appears to be no advantage in cracking or rolling sunflower seeds prior to feeding. The size of the seed results in cows **chewing** and breaking down the product during **digestion**. Feeding sunflower seed in a mixed diet eliminates any issues of feed preference or **palatability**.

Limiting factors for the inclusion of sunflower meal in pig diets are its high level of fibre, lower content of energy than other protein feedstuffs and its relative deficiency in several amino acids, including **lysine**, threonine and **tryptophan**. In practice these features indicate that sunflower meal should be avoided as a protein source for starting pigs and used only for older animals as a partial replacement for other protein sources and with appropriate supplementation with amino acids and formulation to maintain a correct amino acid balance in the diet, as well as a correct level of energy. Research studies have shown that the inclusion of sunflower meal as a complete replacement for soybean meal in diets for piglets and growing pigs resulted in lower **feed intake** and growth and poorer **carcass** quality (soft **backfat**). Sows and adult boars have lower lysine requirements and sunflower meal can be used as the sole supplementary protein source, provided that the total diet provides the required content of available lysine.

The factors that limit the use of sunflower meal in pig diets apply also in **poultry feeding**. As a result it can only ever be used at low levels in the diet of growing **meat** birds that have high protein and **energy requirement**s and is more suitable for

inclusion at higher levels in the diets of growing pullets and laying and breeding stock. As with pigs, the diets have to be formulated correctly to ensure the appropriate levels of energy, protein and amino acids. Reducing the bulkiness of the diet by **pelleting** has been shown in some studies to increase **feed intake**, **liveweight** gain and **feed conversion ratio**.

Dehulled sunflower meals have higher ME values than non-dehulled meals, since they contain more protein and less fibre. The use of exogenous enzymes (pectinase, protease, **phytase**, **glucanase**, **xylanase**, **cellulase** and **amylase**) to counter the negative effects of sunflower fibre has been researched, but with inconsistent results. Sunflower **silage** contains a similar protein concentration to grass **hay**, up to 12%. (RB)

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Superoxide

A reactive **oxygen** species (ROS) (really superoxide anion, $\cdot O_2^-$). It is produced after molecular oxygen (O_2) takes up an electron in reactions catalysed by NADPH oxidase and by the Complex IV of the mitochondrial electron transport system. Through a series of one-electron uptake reactions, superoxide is converted sequentially into **hydrogen peroxide**, the hydroxyl radical and water, i.e.:

(NJB; GW)

$$\overset{e^-}{\longrightarrow} O_2 \overset{e^-}{\longrightarrow} \cdot O_2^- \overset{e^-}{\longrightarrow} H_2O_2 \overset{e^-}{\longrightarrow} \cdot OH \overset{e^-}{\longrightarrow} H_2O$$

Supplement

A feed ingredient, such as an **oilseed** meal, or a mixture of ingredients, that is added to a **forage** feed to rectify one or more of the specific nutrient deficiencies in the forage. (JMW)

Supplementation

The provision of additional feed to animals, usually livestock at pasture, in an effort to provide additional nutrients either to boost productivity or to maintain the animals alive. The feed is mostly of the concentrated type, in the form of pellets for ease of handling, but the term may also refer to provision of conserved forages to grazing livestock, at pasture, in a building or on a concrete pad. Usually the cost of supplements is greater than the basal feed for the nutrients that they provide, hence supplements must be provided judiciously. When supplements are provided the intake of basal feed declines in a process known as substitution. If substitution rates are less than 1, the total intake of the animals is increased; if more than one, it is decreased. Supplements should be directed to animals most needing them, for example heavily lactating cows, or stock grazing in areas with **mineral deficiencies**, especially **copper** and **zinc**. (CJCP)

Surface area of animals

The surface area of animals is important in nutrition because heat loss from the body and (assuming a constant body **temperature**)

heat production by the body are related more closely to surface area than to body weight. In general, the surface area of a solid is proportional to the square of its linear dimensions and to the two-thirds power of its volume or, if density is constant, to the two-thirds power of its weight (W). The basic mathematical principle is the same for animals and the measured surface areas of animals tend to increase as $W^{0.67}$. However, animals are not simple geometrical shapes and even amongst animals of the same weight, there are differences in surface area between species, between young and old, and between obese and lean. Furthermore, an animal's effective surface area can be altered substantially by changes in posture. In **cold environments**, animals tend to reduce their effective surface area by curling up. In hot conditions, they tend to sprawl, with limbs, ears and tails extended, maximizing their effective surface area for both sensible and **evaporative heat loss**. In comparing the adults of different species of very different sizes, **metabolic rate** varies approximately with the ¾ power of body weight, $W^{3/4}$ ($W^{0.75}$), and this is called **metabolic weight**. (MFF)

Sweat

A clear watery liquid secreted by the eccrine glands in the skin of most species. It contains significant amounts of **sodium**, **chloride**, **bicarbonate** and **urea**. Sweat functions to wet the skin and permit evaporative cooling and is secreted when other heat-loss mechanisms are inadequate to prevent a rise in body **temperature**. (MFF)

Swede (*Brassica napus*)
An important temperate root crop grown for both animal **feed** and human consumption. Swedes provide a good level of energy in an easily fermentable form. They are low in dry matter (DM) but can be used to replace winter forage or concentrate. Swedes should be chopped before being fed to young stock and can be stored in clamps over winter. They **taint** milk if fed just before milking. The DM of swede is 110 g kg^{-1} and the nutrient composition (g kg^{-1} DM) is **crude protein** 95, **crude fibre** 90, **ether extract** 10, **ash** 60 and **neutral detergent fibre** 233, with MER 13.5 MJ kg^{-1}. Swedes can be included in the diet of beef cattle and ewes at 20% of the total diet, or for lambs, weaner and grower pigs at 15% and dairy cattle at 10%. (JKM)

Sweet potato (*Ipomoea batatas* (L) Lam)
A creeping plant with perennial vines and adventitious roots on which swollen tubers are formed. The tubers are highly digestible and palatable, and an excellent source of **energy**.



Sweet potatoes are high in energy. Photo courtesy of Jeepers Media. Licensed under CC BY 2.0.

Although mainly grown as human food, surplus and cull tubers are used fresh or dry in livestock feed. Sweet potato leaves are an excellent feed for ruminants, being high in both **protein** and **calcium**, and highly digestible (see tables). Pigs can also graze the vines. Fresh tubers can replace up to half the **cereal** in pig rations. Dried tubers can be mixed with **molasses** and **urea** up to a level of 50% of the concentrate for dairy cattle. Dried tubers have about 90% of the feeding value of **maize** for pigs and can constitute up to 60% of the ration. Fresh tubers are relatively bulky and are better utilized by mature pigs. Sweet potato is high in energy, and a high-protein meal is recommended as a **supplement**. Of particular note, free **amino acid**s contribute to approximately 29% of total amino acids, whereas **asparagine** accounts for about 18% of total free amino acids in sweet potatoes. It is also recommended that dietary intake be restricted to avoid the production of over-fat carcasses. The **metabolizable energy** content of tubers for pigs is 15.07 MJ kg^{-1} dry matter. However, pigs raised on rations containing sweet potato produce carcasses with hard **fat**. The protein in tubers has a high **biological value**. Sweet potato meal can be included up to 50% in poultry feeds, provided that adequate **protein supplement**s are available. Cooking is reported to increase the **nutritive value** of sweet potato tubers. Sweet potato leaves can be harvested with only a limited effect on tuber production. The leaves are difficult to dry but can be made into **silage** after **wilting**. Sweet potato vines and leaves were found to be an excellent **milk** replacer for goat kids, allowing households to increase **milk** offtake from does. Vines and leaves have a dry

matter **digestibility** of 70%. (LR; GW)

Typical composition of sweet potato products (% dry matter).

	DM (%)	CP	CF	Ash	EE	NFE	Ca	P
Fresh leaves	10.8	19.4	10.2	25.9	3.7	40.8		
Fresh vines	8.7	21.9	15.0	18.0	3.4	41.7	1.79	0.24
Fresh tubers	59.0	5.1	2.3	3.5	1.1	88.0		
Fresh peelings	11.7	6.3	0.3	4.6	1.3	87.5		
Dried tuber meal	87.1	4.6	3.0	3.9	0.3	81.9		

CF, crude fibre; CP, crude protein; DM, dry matter; EE, ether extract;

NFE, nitrogen-free extract.

Typical digestibility (%) and ME content composition of sweet potato products.

	CP	CF	EE	NFE	ME (MJ kg^{-1})
Ruminant					
Leaves	80.0	55.0	84.0	86.0	10.01
Fresh tubers	37.5	79.3	51.6	95.5	13.58
Dried tubers meal	14.0	37.0	74.0	90.0	11.35

ME, metabolizable energy.

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Swimming crab (*Portunus trituberculatus*)

One of the most typical and numerous crustaceans, belonging to the order Decapoda, containing about 6000 species placed in 47 families (Bowman and Abele, 1982). Crab tissue contains excellent nutritional components, such as high-quality proteins, lipids and essential amino acids (Naczk *et al*., 2004). The swimming crab, *P*.

trituberculatus, was officially discovered on the coasts of East Asia and was named in 1876 by Edward J. Miers. It is also called gazami crab, horse crab, or Japanese blue crab (Edwards, 1983). It is the most widely fished crab species in the world and makes a significant contribution to the world's crab fishery production (Davis *et al*., 2011). The total catch of this species reported by the Food and Agricultural Organization (FAO) was 125,300 t in 2016 and China and Korea were the largest producers. Farmed *P. trituberculatus* production in China was 116,251 t in 2018, based on a report from the *China Fishery Statistical Yearbook* (Fisheries Bureau, 2019).

Frozen 'trash' fish is considered a traditional feed in rearing swimming crabs, due to its good nutritional value and **palatability**. However, due to the overexploitation of marine fishery resources and environmental pollution, the commercial supply of frozen trash fish has been progressively reducing. There has been much research in formulated feed using terrestrial plant materials to replace frozen trash fish in China (Que *et al*., 2012). Studies on the effects of feeding on the nutritional composition of *P. trituberculatus* have made great progress. For example, the best dietary protein and lipid levels in feedstuff has been determined: 51% protein and 5% lipid levels for juvenile *P. trituberculatus* (Huo *et al*., 2014). Shao *et al*. found no significant difference in the hepatopancreas and gonad quality of crab fed with natural and formulated diets (Shao *et al*., 2013). The formulated feed was demonstrated to be better in the accumulation of **phospholipid**s in *P. trituberculatus* muscle and could replace the frozen trash fish

as feed. Such replacement could reduce the dependence on wild fishery resources and thereby guide producers towards the production of high-quality swimming crabs for human consumption (Wang *et al*., 2021). (QS)

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Swine:

see Pig

Synthetic diets

Diets composed of pure sources of nutrients, such as **starch**, **cellulose**, **casein**, **amino acid**s, **urea**, **fatty acid**s and **mineral** elements. Also called purified diets. (JMW)

T

Tail biting

This occurs in intensively housed pigs, in which pigs take the tail of a conspecific into their mouth and attempt to chew on it. If blood is

drawn, it may lead to an outbreak of **cannibalism**, in which the animal is targeted by a number of individuals. Tail biting also occurs in stressed dogs, in this case their own tail. Such dogs also engage in lip licking. (CJCP)



Tail biting occurs in stressed animals and is particularly common in dogs and pigs. Photo courtesy of Taro. Licensed under CC BY 2.0.

Taint

Abnormal, usually unpleasant, odour or **taste** of food. Taints in animal products may be due to odoriferous materials (such as fish meal) in the animal's diet or may be produced in the **metabolism** of an animal given a normal diet. Amongst the latter are **boar** taint caused by 3-methylindole (**skatole**) and 5-α-androst-16-en-3-one (androsterone), both of which are odoriferous compounds in pig **adipose tissue**. There is variable susceptibility to boar taint in humans. Diet-related taints in cows' **milk** include those from **silage**, **sugarbeet** (which can give a fishy taint), garlic, wild **onion** and other weeds such as stinking mayweed. Contamination

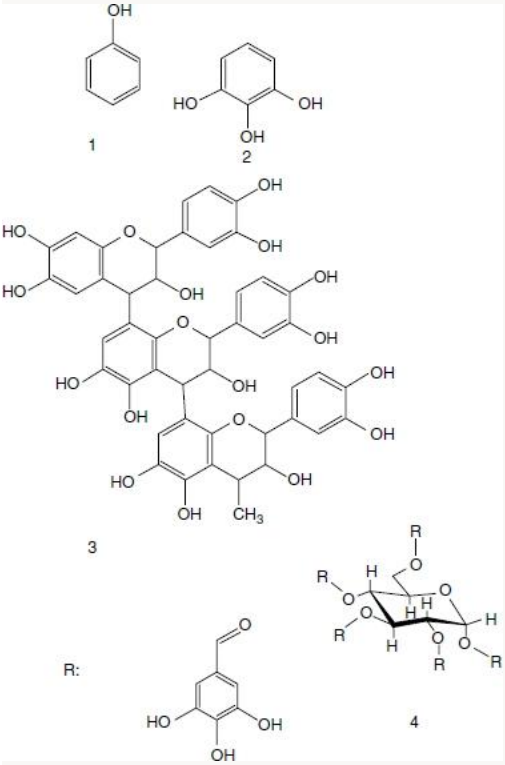
of milk with some disinfectants (e.g. phenolics) can cause off-flavours. (JMF)

Tallow
Fat rendered from animal carcasses, especially of cattle and sheep. Usually solid at room temperature. Beef tallow is hard and typically contains, as a percentage of total **fatty acid**s, 26% **palmitic**, 17% **stearic**, 43% **oleic** and 4% **linoleic acid**s. (JRS)
See also: Animal fat

Tambaqui (*Colossoma macropomum*)
Like **pacu**, a native of the Amazon and Orinoco rivers of Brazil and mainly cultivated in Central and South America. These large, nearly round migratory **fish** may reach 1 m in length and weigh 20–30 kg. They have a set of large **teeth** and molars (like those of humans) which can crack open the tough shells of many seeds and fruits. For farmed fish, a market size of 1–2 kg is attained in 18–20 months at **water temperatures** ranging from 22°C to 28°C. Tambaqui do not reproduce in a natural way in captivity and **spawning** must be induced by **hormone** injection. (SPL)

Tannins
A group of complex **polyphenolic compound**s (see figure) found in most plant species, mainly in the leaves and seeds. Phenols are aromatic compounds with substituent hydroxyl groups on the aromatic ring (see figure). Polyphenolic compounds have a number of substituent hydroxyl groups. Not all polyphenolic compounds are tannins but all tannins are **polyphenol**s. The

structural complexity of tannin molecules confers varying degrees of activity towards other molecules and thus determines their reactivity in biological systems. One of the easiest methods of quantitation is to cause tannins to react to produce colours and then determine these by colorimetric or spectrophotometric methods. However, the spectral properties of reaction products of different tannins vary and cause inaccurate quantitation. This method often also inaccurately predicts the biological reactivity of the tannins.



Structure of some phenolic compounds and tannins. (1) Phenol. (2) Pyrogallol; (1,2,3-trihydroxy benzene). (3) Representation of a (tri) flavonoid. (4) Representation of a hydrolysable tannin (pentagalloyl-glucose).

Tannins exist predominantly (but not exclusively) as two main types: the hydrolysable tannins, based on a central **glucose** molecule substituted with phenolic moieties (see figure), and the

condensed tannins, based on oligomers of flavonoids. The major difference between the two types is that the ester linkages in hydrolysable tannins undergo **hydrolysis** readily to produce relatively small molecules, such as pyrogallol, while condensed tannins are much more resistant to biological and chemical degradation. Hydrolysable tannins thus tend to produce toxic effects in animals that ingest them whereas condensed tannins are much more stable. The reactions of tannins are pH dependent. They react vigorously, especially with proteins, to reduce the function of proteins such as enzymes. Tannins react with proteins in the gut, whether these are dietary, endogenous or microbial. Often these effects are detrimental to animal performance and nutrient utilization. However, tannins can have beneficial effects in animals by reducing **bloat**, increasing uptake of some nutrients, complexing with dietary protein to increase the rumen undegradable protein (this is subsequently dissociated from tannins in the **abomasum** and can be digested there and in the **small intestine**), reducing **methane** production, and reducing intestinal parasites and pathogenic bacteria. These beneficial effects may account for the fact that **ruminant animal**s can often be seen to choose to consume plants that contain tannins, even though alternative plant material is available. Tannins also **chelate** mineral elements strongly; this can reduce mineral absorption and increase endogenous losses from the gut.

Hydroxylated polymers such as polyethylene glycol (PEG) bind strongly with tannins and reduce their adverse effects. (TA)

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Tapioca:

see Cassava

Taste

Chemoreception of ingested food or **feed** and imbibed liquids by the tongue, otherwise known as gustation, with the aim of facilitating the selection of nutritious food, feed or liquids and avoidance of potentially harmful items. The four main tastes are: sweet in response to soluble carbohydrates; **salt** (mainly NaCl and to a lesser extent KCl) to control **electrolyte** balance; bitter to avoid toxins; and sour to regulate acid/base balance in the body. Metallic and **monosodium glutamate** tastes also exist, but generally all tastes result from combinations of the four main tastes. The different tastes are perceived by sensors at specific locations on the tongue, for example sweet and salt taste on the tip of the tongue in humans.



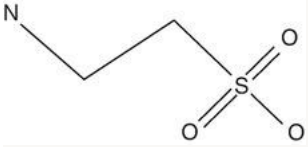
Sweet and salt taste buds are located on the tip of the human tongue. Photo courtesy of Animantis. Licensed under CC BY 2.0.

In contrast, in cattle the sweet taste is towards the back of the tongue, perhaps because more lengthy **mastication** is required to release soluble carbohydrates from fibrous feed than food eaten by humans. Food and feed flavours interact, with some potentiating specific flavours in a process known as flavour enhancement. Other flavours may be antagonistic to each other in a process known as mixture suppression; for example, the taste of an artificial sweetener thaumartin is dulled by salt. Intake rate is affected by the taste of food or feed, with sweet tastes generally enhancing it and bitter and strong salty tastes reducing it. For important nutrients taste perception is acute; for example, cattle, which through their evolution were commonly **sodium** deficient, can detect differences in sodium contents of a feed of as little as 1g Na kg^{-1} dry matter. In **ruminant animal**s regurgitated feed boli provide an opportunity for sensing rumen conditions, through taste receptors. During **subacute ruminal acidosis**, for example, the increased acidity of rumen contents will be detected by the taste receptors, and the end result is a marked reduction of **feed intake**. Taste perception begins at an early age, *in utero* in fact. The taste of the feed or food eaten by the mother influences how

receptive **newborn animal**s are to particular tastes. Aversion to a taste may be conditioned by coupling it with aversive consequences, such as sickness. This process can be used to discourage animals from grazing toxic plants, by coupling the initial presentation with a drug inducing nausea, such as **lithium chloride**. Just one presentation can potentiate the aversion to the plants, and the taste aversion can be generalized to similar plants. (CJCP)

Taurine

An aminosulphonic acid ($H_2N{\cdot}(CH_2)_2{\cdot}SO_3H$, molecular weight 125.2). Taurine is an **organic acid** not found in protein. It is synthesized from **cysteine** and is used nutritionally for conjugation of **bile** acids, osmoregulation and an **antioxidant**. Biosynthesis of taurine is inadequate in feline species, so some taurine must be supplied in the diet to prevent retinal degeneration and cardiomyopathy. It is also essential for some juvenile **marine fish** and **shrimp** species, and supplementation can have positive effects on growth. Some juvenile **freshwater fish** also benefit from taurine supplementation if the diet is devoid of fish meal and has a low taurine concentration. (DHB; QS; CJCP)



See also: Non-protein amino acids

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Tea (*Camellia sinensis* (L.) Kuntze)
A small evergreen widely grown for its leaves, which are dried and constitute the tea of commerce. The inclusion of tea leaves or products in animal diets may have health benefits by their influence on the **gastrointestinal microflora** and by their **antioxidant** properties: catechins in tea are effective alternatives to **vitamin E** as antioxidants. The dry matter (DM) content of fresh tea leaves is 920 g kg^{-1} and the nutritive composition (g kg^{-1} DM) is **crude protein** 266, **crude fibre** 94.5, **ether extract** 30.4, **starch** and **sugars** 639, and **ash** 64. (JKM)
See also: Green tea

Teeth:
see Tooth

Temperature, body
In animals, body temperature is controlled by the **hypothalamus** and is usually taken per **rectum**, but **milk** temperature will also reflect that of the body. Body temperature varies with age, species, the time of day (highest late afternoon) and stage of the **oestrous cycle**. Raised temperature (pyrexia) may be a result of exercise,

pain, infection or heat stroke. Body temperatures above 41°C are considered dangerous in most mammals.

Average and range of body temperature (°C) in domesticated species

Species	Average	Range
Cattle	38.6	36.7–39.3
Sheep, goats	39.1	38.5–39.9
Pigs	39.2	38.7–39.9
Horses	37.7	37.2–38.2
Camel	37.5	
Dogs	38.9	37.9–39.9
Cats	38.6	38.1–39.2
Rabbits	39.0	38.5–40
Poultry	40.6	40–42
Small birds	41.0	40–42

Hypothermia may be caused by endotoxic shock, **starvation** or collapse. It is most often associated with neonates, where it may be a result of starvation over the first few hours of life, exposure to unsuitable environmental conditions or a combination of both. Piglets and lambs are particularly susceptible. (EM)

Temperature, environmental:
see Environmental temperature

Termamyl

Proprietary name for a microbial thermostable (up to 105–110°C) α-**amylase** (1, 4-α-D-glucan-glucanohydrolase; EC 3.2.1.1) purified from a selected strain of *Bacillus licheniformis*. Commonly used in industry and research for rapid and efficient *in vitro* digestion of **starch**. (SB)

Terpenes
A structurally diverse group that occurs throughout nature in various polymeric cyclic and linear forms, with many stereoisomers. The nomenclature is based on the fundamental unit of the unsaturated, branched-chain pentane isoprene; thus hemiprenes (C5), monoterpenes (C10), sesquiterpenes (C15), diterpenes (C20), etc. Terpenoids are classified into two groups: primary **metabolite**s of the plant kingdom (**carotenoid**s, terpenoid **quinone**s, etc.); and secondary metabolites with highly species-dependent distribution and often undefined function. (DLP)

Testa
Also called the seed coat, the hard outer layer of tissue surrounding the seed of flowering plants. Also involved in the control of seed dormancy. (ED)

Tetany, grass
A hypomagnesaemic disorder of cattle in early **lactation** when **magnesium** requirement is increased by the demands of lactation. Grass tetany is usually associated with the consumption of lush, high-quality pasture that is low in magnesium or contains

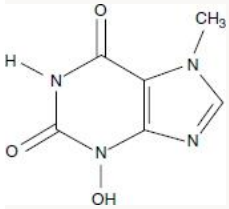
high concentrations of **potassium**, **nitrogen** or tricarballylic acids (which interfere with the absorption of magnesium across the rumen). As a result, magnesium concentrations in plasma, and especially cerebral spinal fluid, decrease and can reach levels that no longer support normal nerve function. In affected cows the plasma magnesium concentration often falls from a normal value of 1–1.1 mM magnesium to less than 0.5 mM. Animals become hyperexcitable and can go into uncontrolled muscle spasms (tetany) and **convulsion** leading to death. The syndrome is often accompanied by **hypocalcaemia** secondary to the low **blood** magnesium concentration. Treatment of animals with convulsions consists of intravenous administration of magnesium and **calcium** salt solutions, though the results are often disappointing. In mild cases, the animals can be treated with oral drenches containing magnesium salts. In housed animals, prevention is easily achieved by feeding higher amounts of magnesium (adding 20–30 g magnesium in a mineral form each day to the diet) but it can be difficult to ensure that grazing animals get sufficient supplemental magnesium. (JPG)
See also: Hypomagnesaemia

Tetrahydrofolate
5,6,7,8-Tetrahydropteroyl-glutamic acid, the fully reduced form of the water-soluble B **vitamin**, folic acid. In foods, folic acid is found as more than ten separate species, including folic acid, **dihydrofolate** and **tetrahydrofolate**. Tetrahydrofolate is involved in one-carbon **metabolism** and is found as the 5- or 10-formyl, 5-formimino, 5-methyl, 5,10-methenyl or 5,10-methylene

forms and as a number of **polyglutamate**s, the most prevalent form being the pentaglutamate. In metabolism, these one-carbon intermediates are critical to the *de novo* synthesis of **nucleic acid**s. (NJB)

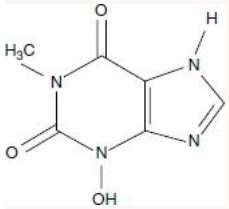
Theobromine

A xanthine **alkaloid** (3,7-dimethylxanthine; $C_7H_8N_4O_2$, molecular weight 180) similar to **caffeine**. It is either extracted from the dried ripe seed of *Theobroma cacao* or made synthetically. Theobromine is a diuretic and a **smooth muscle** relaxant. It has little stimulant activity on the central nervous system and hence is preferred over caffeine in the treatment of certain cardiac ailments. (KEP)



Theophylline

A **caffeine**-like **alkaloid** (1,3-dimethylxanthine; $C_7H_8N_4O_2$, molecular weight 180), isomeric with **theobromine** and first isolated from **tea** (*Camellia sinensis*) in 1885. It is synthesized from caffeine or other xanthine derivatives. Theophylline is used in many prescription drugs; it causes **smooth muscle** relaxation and possesses diuretic properties. (KEP)



Thermogenesis
The generation of heat in the body in the course of **metabolism**. (JAMcL)
See also: Heat production; Non-shivering thermogenesis

Thermoregulation
Thermoregulation in warm-blooded animals (homeotherms) is brought about by involuntary (reflex) and voluntary (behavioural) actions. The principal reflex actions are as follows.

Vasodilation or vasoconstriction of capillary vessels alters **blood flow** in the skin and subdermal regions. This effectively alters the insulation of the body.
Piloerection: piloerector **muscles** in the dermis cause fluffing up of the fur or feathers, trapping a greater depth of still air, which is a good thermal insulator.
Sweating makes liquid water available at the skin surface for evaporation, which is a very effective method of cooling because every gram of water vaporized absorbs some 2.2 kJ of **energy** (heat) from the evaporating surface.
Panting increases the airflow over moist internal surfaces in the respiratory tract. The humidity and **temperature** of air respired are raised from the levels in ambient air to saturation at deep-body temperature. It follows that respiratory **evaporative heat loss** increases in proportion to the volume of air breathed in and out.
Shivering is a form of increased **heat production** resulting from involuntary muscular activity that occurs in the cold.
Behavioural actions include seeking shelter, huddling and curling

up, which all limit heat loss. Standing in the wind promotes both convective and evaporative heat losses. The heat load of direct solar radiation may be avoided by seeking shade.



Shade seeking is an important thermoregulatory response to high temperatures. Photo courtesy of USDA government. Licensed under Public Domain Mark 1.0.

Adequate **water intake** is critical for the dissipation of excessive heat from animals exposed to elevated ambient temperatures. Under the conditions of **heat stress**, dietary **supplementation** with **fats** within physiological ranges can partially offset a reduction in the food intake of an animal, while generating metabolic water in the body. In addition, any excessive intake of dietary **protein**, which has the highest value of heat increment among **macronutrient**s and also promotes the loss of water via the urinary excretion of water-soluble nitrogenous **metabolite**s, should be avoided. However, diets should contain sufficient **amino acid**s, particularly **arginine** (the precursor of

nitric oxide as the major vasodilator), to facilitate the loss of heat via the flow of **blood** from internal organs to the skin, while ensuring an adequate flow of blood from mother to fetus in gestating dams or through the **mammary gland**s in lactating dams. Likewise, the ability of **skeletal muscles** to produce heat via contraction in animals exposed to low ambient temperatures depends on adequate nutrition to provide amino acids, **fatty acid**s, **carbohydrates**, **vitamins**, **minerals** and water. In animals (e.g. sheep and cattle) containing **brown adipose tissue** (which produces a large amount of heat in the mitochondria due to the presence of the uncoupling protein), the mass and physiological activity of this tissue may be promoted through dietary supplementation with **citrulline** or **rumen**-protected arginine. Furthermore, increasing the intake of dietary **fat** within physiological ranges can increase the availability of fatty acids for **heat production** by the skeletal muscle, liver, heart and kidneys of all animals under the conditions of cold stress. **Hypoglycaemia** is a life-threatening condition in neonates (particularly animals without brown adipose tissue, such as pigs) exposed to a **cold environment**, and they should be provided with adequate nutrients (including fats, amino acids and **glucose** or its sources). (JAMcL; GW)

See also: Climate; Environmental temperature; Evaporative heat loss

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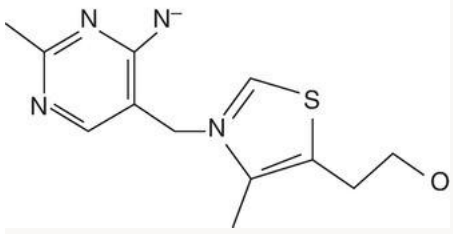
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Thiamine

Vitamin B_1, one of the water-soluble B vitamins. Thiamine is a **coenzyme** intimately associated with **metabolism** of **carbohydrates**, **fatty acid**s and some **amino acid**s and with two **metabolite**s in the **tricarboxylic acid** cycle. It is widely distributed in nature and found in numerous animal and plant foods. It is also produced commercially and sold as thiamine hydrochloride ($C_{12}H_{18}Cl_2N_4OS$) and as thiamine mononitrate ($C_{12}H_{17}N_5O_4S$).



Although thiamine is produced by bacteria in the intestine, the

site of microbial synthesis is distal to the site where the vitamin is digested and absorbed, so thiamine is required in the diet of all non-ruminant animals. Requirements are in the range of mg kg^{-1} diet. In ruminants, microbial synthesis in the rumen provides an adequate supply. Thiamine is absorbed by an energy- and **sodium**-dependent process. It is found in four distinct forms in cells: thiamine (T), thiamine monophosphate (TMP), thiamine diphosphate (TDP) and thiamine triphosphate (TTP). One **enzyme**, thiamine pyrophosphokinase, is involved in using ATP in each **phosphorylation** step T → TMP → TDP. Independent phosphatases are involved in dephosphorylating TTP, TDP and TMP. In tissues, T makes up about 3%, TMP 8%, TDP 88% and TTP 1% of the total thiamine. In **blood** serum, T and TMP are found in approximately equal amounts but only traces of TDP and TTP are seen.

The vitamin co-factor form of the vitamin is TDP. Thiamine as TDP is a co-factor for the enzyme pyruvic **dehydrogenase**, which is involved in the **decarboxylation** of pyruvic acid to acetyl-CoA and CO_2. TDP is the co-factor in the decarboxylation reactions involving α-ketoglutarate to form succinyl-CoA, and the decarboxylation of the ketoacids of the **branched-chain** amino acids **leucine**, **isoleucine** and **valine** to form the CoA forms of their decarboxylated **keto acid**s. Additionally, TDP is thought to be a co-factor in the **decarboxylation** reaction of the keto acid of **methionine**, and α-ketobutyrate which is derived from both methionine and threonine.

A deficiency of thiamine can be assessed by an oral **glucose**

load and measuring **blood** concentrations of lactic and pyruvic acids. As a metabolic deficiency progresses, the amounts of these products appearing in blood and excreted in the **urine** increase. Another approach to identifying a deficiency of thiamine is by measuring the activity of the erythrocyte **enzyme** transketolase, which requires TDP as a co-factor. This assay is most meaningful when it is tested with and without the addition of the enzyme co-factor TDP. As a deficiency progresses, the amount of cellular TDP available to support the activity of the enzyme decreases and the activity of the enzyme declines. In the laboratory test, direct addition of the co-factor (TDP) to the *in vitro* test results in a greater stimulation or recovery of **enzyme activity**, which is an indication of a deficiency. (NJB)

Thickeners and gelling agents

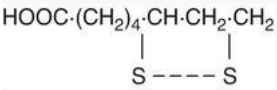
The following thickeners and gelling agents are listed in the Feedingstuffs (UK) Regulations 2000. (MG)

Alginic acid	E400
Sodium alginate	E401
Potassium alginate	E402
Calcium alginate	E404
Propylene glycol alginate	E405
Agar	E406
Carrageenan	E407
Locust bean gum	E410
Tamarind seed flour	E411

Alginic acid	E400
Guar gum	E412
Tragacanth	E413
Acacia	E414
Xanthan gum	E415
Pectins	E440
Microcrystalline cellulose	E460
Cellulose powder	E460(ii)
Methylcellulose	E461
Ethylcellulose	E462
Hydroxypropylmethylcellulose	E464
Ethylmethylcellulose	E465
Carboxymethylcellulose	E466

Thioctic acid

6,8 Thioctic acid, α-lipoic acid, acts as a **coenzyme**. As lipo**a**mide it receives the two-carbon acetyl unit from α-hydroxyethyl **thiamine** diphosphate, producing acetyllipoamide, an intermediate of the **pyruvate dehydrogenase** complex by which pyruvate is converted to acetyl-CoA. In the reaction, the disulphide form or lipoamide is converted to the disulphydryl form dihydrolipoamide, which must be oxidized to lipoamide by FAD bound to a **protein** which is part of the pyruvate dehydrogenase complex. Thioctic acid (lipoic acid) participates in other dehydrogenase reactions, such as the α-ketoglutarate dehydrogenase complex. (NJB)



Thiocyanates

Metabolic and **detoxification** products of **glucosinolate**s and **cyanogenic glycosides**. **Poisoning** occurs when free **cyanide** (HCN) is liberated from the glycoside. Thiocyanates and isothiocyanates inhibit **iodine** uptake by the thyroid gland, which becomes enlarged (**goitre**). This can be prevented by increasing the level of dietary iodine. Cyanide is readily detoxified and so acute toxicity occurs only if the detoxification rate is exceeded. All animal tissues contain an enzyme called rhodanase, which catalyses the conversion of cyanide to thiocyanate, which is subsequently excreted in the urine. This reaction is significant in the treatment of cyanide poisoning by injection of **sodium** thiosulphate and sodium **nitrate** (intravenously). Sodium thiosulphate reacts with cyanide and produces a **sulphate** product and the less toxic thiocyanate, while the nitrate converts **haemoglobin** to **methaemoglobin**, which has a greater affinity for cyanide than does cytochrome oxidase (the biochemical target for cyanide toxicity). Therefore, the methaemoglobin participates in stripping the cyanide from the enzyme. Treatment is usually impractical in farm situations because of the acute nature of cyanide poisoning. Chronic cyanide poisoning from moderate exposure to cyanogenic glycosides has occurred in some human populations. In tropical Africa where **cassava** and other foods containing cyanogens are dietary staples, a condition called tropical ataxic neuropathy occurs. Symptoms are

lesions of optic, auditory and peripheral nerves, elevated **blood** levels of thiocyanates and an increase in goitre. **Vitamin** B_{12} and **sulphur amino acid**s such as **methionine** supplementation have beneficial effects. Similar neurological disorders have been observed in livestock consuming chronic levels of cyanogenic forages. (KEP)

Thioglucosidase:
see Glucosidase

Thiomolybdates
Sulphur- and molybdenum-containing compounds that occur naturally in many farm animal feedstuffs. They have the chemical forms MoO_3S^{2-}, $MoO_2S_2^{2-}$, $MoOS_3^{2-}$ and MoS_4^{2-}. The tri- and tetramolybdate forms readily bind **copper** and render it unavailable for **absorption** from the gut. This is a special problem in **ruminant animal**s, where copper complexes can be formed with naturally occurring **sulphur** and **molybdenum** compounds in **feed** during ruminal **digestion**. (PGR)

Further reading

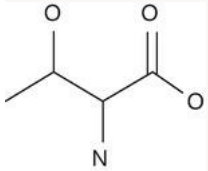
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Thiosulphates
In biological systems, thiosulphate ($S_2O_3^{2-}$) is a **by-product** of the **metabolism** of the amino acids **cysteine** and **cystine**. The **salts**

of thiosulphate, such as **sodium** thiosulphate, are often used as treatment for **copper** or **cyanide poisoning** in animals. Thiosulphate plus **molybdenum** forms **thiomolybdate**, which will complex with copper and reduce its availability for absorption. (PGR)

Thirst:
see Water deprivation; Water intake

Threonine
An essential amino acid ($CH_3{\cdot}CHOH{\cdot}CHNH_2{\cdot}COOH$, molecular weight 119.1) found in protein. Because threonine contains a hydroxyl group on the β-carbon atom, it, along with **serine**, is often referred to as a hydroxy amino acid. Threonine is sometimes a limiting amino acid in practical diets for growing animals. It is the second-limiting amino acid in **soybean** meal (after **methionine**) and in most cereal **grain**s (after **lysine**). The endogenous proteins that enter the gut have a high concentration of threonine and may account for as much as one-half of the total dietary requirement for threonine. Threonine in the body does not enter into **transamination** reactions. Instead, three different enzymes are involved in the initial reaction of threonine **catabolism** (a **dehydrogenase**, a dehydratase and an aldolase) and **glycine** is produced as a product in two of these three pathways. (DHB)



Thrombosis

The formation of a thrombus (a **blood** clot) in a blood vessel. Thrombosis is a relatively common condition in cattle. The usual site is the caudal vena cava but the cranial vena cava is sometimes involved. The thrombi often arise from liver abscesses, caused by rumenitis following **rumen** acidosis after feeding on large amounts of starchy feeds, e.g. rolled **barley**. Vena cava thrombosis commonly leads to pulmonary abscesses, which can cause fresh blood to be seen in the nose. This sequence of events was more frequent when 'barley beef' cattle were reared on diets consisting largely of ground barley. The condition is often fatal, the animal drowning in blood, but some live for several days or weeks after signs first appear. Treatment is of no avail, and cattle showing fresh frothy blood at the nose may be slaughtered. (WRW)

Thromboxanes

Lipid compounds biosynthesized by addition of oxygen at C-9, C-11 and C-15 of **arachidonic acid**, a 20-carbon unsaturated (T6, 20:4 $\Delta^{5,\ 8,\ 11,\ 14}$) **fatty acid** derived from **linoleic acid** (18:2 $\Delta^{9,\ 12}$). Cats cannot convert linoleic acid to arachidonic acid and so it is an essential dietary component. For thromboxane biosynthesis, arachidonic acid precursors must be located on the *sn*-2 position of **glycerol** in **phospholipid**s of cell membranes. The 20-carbon thromboxanes are synthesized in platelets via a cyclo-oxygenase-dependent pathway and upon release cause vasoconstriction and platelet aggregation. Their synthesis is specifically inhibited by aspirin, indomethacin, ibuprofen and other non-steroidal anti-

inflammatory drugs. (TDC)

Thymine
A **pyrimidine** base, 5-methyluracil, $C_5H_6N_2O_2$, found in DNA as the nucleoside thymidine. It is not found in RNA. (NJB)

Thyroid
A two-lobed **endocrine gland** located in the anterior neck that synthesizes and releases mainly 3,5,3′,5′-tetraiodothyronine, also called thyroxine or T_4. Although 90% of total secretion is composed of T_4, 10% of secretions also contain 3,5,3′-**triiodothyronine** or T_3. Less than 1% of secretion is made up of 3,3′,5′-triiodothyronine or reverse T_3. **Iodine** plays a central role in thyroid **hormone** synthesis, which involves the coupling of two iodinated **tyrosine** molecules. Hormone release is regulated by the hypothalamic–pituitary axis. Thyrotropin-releasing hormone (TRH) from the **hypothalamus** stimulates release of thyroid-stimulating hormone (TSH) from the anterior pituitary, which in turn causes the release of T_4 and T_3. Release of TRH in animals is decreased by a reduction in caloric intake and increased by exposure to cold. T_4 and T_3 also exhibit strong negative **feedback inhibition** on TSH release. More than 99.5% of T_4 and T_3 is bound to thyroid-binding **globulin** in plasma, and only free forms of the hormones are active. T_4 functions mainly as a prohormone for the production of T_3, which exhibits most of the physiological effects. Activation of the thyroid hormone receptor in cells specifically regulates gene transcription, causing a multitude

of metabolic effects. The major effects of thyroid hormones are to increase **metabolic rate**, heart rate, cardiac output, ventilation and total body **heat production**. (GG)

Thyroid antagonists
Compounds that interfere with the ability of the thyroid gland to produce thyroid **hormone**s, which can ultimately result in thyroid hormone deficiency. Such compounds are called **goitrogen**s; ultimately they can cause the thyroid to enlarge, a condition called **goitre**. (JPG)

Thyroid diseases
Thyroid diseases are **metabolic disorder**s arising from either the overproduction of thyroid hormones (hyperthyroidism), leading to excessive **metabolic rate**s, or inadequate thyroid hormone production (**hypothyroidism**), resulting in reduced metabolic rates. **Hypothyroidism** is often due to **iodine** deficiency or the presence of **goitrogen**s in the diet. (JPG)
See also: Goitre

Thyroxine:
see Thyroid

Tilapia
Freshwater finfish belonging to the family Cichlidae. Tilapia, or tilapiine fish, are grouped into three genera: *Tilapia*, *Sarotherodon* and *Oreochromis*, characterized by both their feeding and their reproductive habits. In general, tilapia of the genera *Sarotherodon* and *Oreochromis* are primarily omnivorous, feeding on

phytoplankton, periphyton or detritus, whilst members of the *Tilapia* genus tend to take coarser food, including macrophytes. *Tilapia* are **substrate** spawners whereas *Oreochromis* are maternal mouthbrooders and *Sarotherodon* are bi-parental mouthbrooders.



Tilapia are increasingly cultured in the tropics. Photo courtesy of Dunk. Licensed under CC BY 2.0.

Tilapia originated exclusively from the African continent (excluding Madagascar) and from Palestine (Jordan valley and coastal rivers) but they have been introduced into different habitats in various countries throughout the tropics. Tilapia culture, whether extensive, semi-intensive or intensive, has expanded worldwide and represents 10.24% (5.56 million tonnes) of farmed finfish (54.28 million tonnes); Nile tilapia (*Oreochromis niloticus*) (4.53 million tonnes) accounted for nearly 81% of this volume in 2018. Most *Oreochromis* species are euryhaline and offer an advantage in culture. Commonly cultured tilapia species are very adaptable and hardy, and are considered an ideal fish for culture in the tropics.

The highest **protein digestibility** in tilapia occurs at 25°C and the optimum dietary **protein:energy ratio** for *O. niloticus* juveniles is approximately 18 g DP MJ^{-1} DE. *O. niloticus* benefit from several daily feedings, with four or more feedings a day resulting in better growth than two. (RMG; QS)

Key reference

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Titanium dioxide

One of several indigestible **markers** that may be added to diets for the measurement of **digestibility** or the rate of passage of **digesta**. (MFF)

Toasting

The application of dry (usually radiant) heat to feed materials to improve either their chemical structure or their nutritional value. (MG)



Tobacco plant, *Nicotiana tabacum*. Photo courtesy of Marry Finn. Licensed under CC BY-ND 2.0.



Wild tobacco plant (*Nicotiana rustica*), otherwise known as Aztec tobacco. Photo courtesy of Magnus Manske. Licensed under CC BY-SA 3.0.

Tobacco

A plant from the Solanaceae family that has two economically important species: *Nicotianan tabacum* and *Nicotiana rustica*

Nicotiana tabacum is used to prepare cigars, cigarettes, pipe tobacco and chewable forms of tobacco and is mass produced in many continents and countries. *Nicotiana rustica* is mostly cultivated in Asian countries and is used as hookah tobacco; it has a higher nicotine content (Lieberei *et al*., 2007; Krist, 2020). Tobacco is a herbaceous annual plant with a stem of 30 cm to 2 m in height and relatively thick, soft oval leaves leading to distinct petioles. The leaves are alternate and have a wide spear shape; and the flowers are funnel-shaped and red or yellow. Its main root is firm, spiral

and of medium length, and the lateral roots are smaller. The flowers are placed on top of the stem and each one has five petals. The tobacco fruit is in the form of capsules with two to four chambers, oval in shape and dark to light brown in colour, which when it reaches maturity is fully opened and its seeds are exposed (Barth and Jehle, 2003). The origin of tobacco is South America. The first tobacco growers were the Indians of North and South America (Zargari, 1997). This plant was introduced to Spain in 1560 as an ornamental plant. The French ambassador in Lisbon, Jean Nicot, introduced the tobacco plant to France, and the plant was later named after him (Lieberei *et al*., 2007). The most used species of *N. tabacum* derive from a combination of two species, *Nicotiana sylvestris* + *Nicotiana tomentosiformis*. The global area under cultivation is more than 5 million hectares, producing about 6 million tonnes annually (Lieberei *et al*., Krist, 2020). The most important alkaloid of the tobacco plant is nicotine ($C_{10}H_{14}N_2$), and in addition it contains three other alkaloids ($C_{10}H_8N_2$, $C_{10}H_{12}N_2$ and anabazisine, a nicotine isomer). These are all produced in the roots and some (1–6%) is stored in the leaves (Lieberei *et al*., 2007; Krist, 2020). These compounds are mostly used to prepare cigarettes and insecticidal lotions (Zargari, 1997). In addition to the widespread use of the leaves of this plant, the seeds (about 400,000 ha^{-1}) are a useful by-product, containing 30–40% **oil** (60–70% **linoleic acid**, 10% **palmitic acid**). The refined oil is nicotine-free and can be consumed as edible oil (for example, salad oil) (Krist, 2020). In addition, tobacco oil contains an alkyd resin that is used in the preparation of painting colours (building paint

and road marking), printing ink and polishing materials (Mukhtar *et al*., 2007). It has been found that tobacco seed oil can be used as an economic and renewable raw material for biodiesel production (Veljković *et al*., 2006). The content of phytosterol compounds in seeds increases during **germination**; the highest values are of stigmasterol and campesterol compounds (Bush and Grunwald, 1972). The meal obtained after oil extraction contains 3.5% **nitrogen**, which can be used in animal **feed** and as an organic fertilizer (Krist, 2020). Bosticco and Bonomi (1963) found that its meal seed oil contained 8.31 g moisture kg^{-1}, 10.34 g **ash** kg^{-1}, 35.1 g **protein** kg^{-1}, 1.56 g **lipid** kg^{-1}, 17.05 g fibre kg^{-1}, 11.74 g **calcium** kg^{-1}, 11.60 g **phosphorus** kg^{-1}, 5.57 g **magnesium** kg^{-1}, **copper** 102 ppm, **cobalt** 3.4 ppm, **iron** 816 ppm, **zinc** 1.4 ppm and **manganese** 70 ppm. **Lysine** is considered its limiting amino acid. (AS; BH-G; CJCP)

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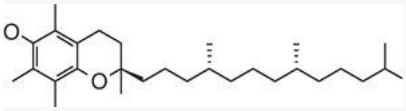
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Tocopherols

A group of compounds, each of which possesses **vitamin E** activity. They have a phenolic functional group at carbon 6 on a chroman ring (substituted six-member heterocyclic double rings) with either a 16-carbon phytanyl (tocopherols) or isoprenoid (**tocotrienol**s) chain attached to C-2 of the chroman ring. In addition to the hydroxyl group on carbon 6, either a CH_3 or H is attached to C-5, C-7 or C-8, leading to a total of four tocopherols and four tocotrienols (Table 1).



Structure of α-tocopherol.

Table 1. Tocopherols and tocotrienols

Tocopherols	C-5	C-6	C-7	C-8	Tocotrienols
α-tocopherol	CH_3	OH	CH_3	CH_3	α-**tocotrienol**
β-tocopherol	CH_3	OH	H	CH_3	β-**tocotrienol**
γ-tocopherol	H	OH	CH_3	CH_3	γ-**tocotrienol**
δ-tocopherol	H	OH	H	CH_3	δ-**tocotrienol**

The 16-carbon phytanyl chain in tocopherols is saturated and has three chiral carbons (C-2, C-4′ and C-8′) leading to a racemic mixture of eight stereoisomers in chemically synthesized tocopherols. In the case of α-tocopherol, this mixture is called allracemic (all-rac-) α-tocopherol. Variation in vitamin E activity of tocopherols depends on the orientation (*R* or *S*) at the chiral carbons and the number and position of methyl groups on the chroman ring. Table 2 lists the relative biological effectiveness of the four tocopherols and two of the four tocotrienes, in two different bioassays.

Table 2. Relative vitamin E activity of homologues of tocopherols and

tocotrienes in rats.

Form	Gestation/resorption	Haemolysis
α-Tocopherol	100	100
β-Tocopherol	25–40	15–25
γ-Tocopherol	8–19	3–18
δ-Tocopherol	~ 1	~ 1
α-Tocotrienol	21	17
β-Tocotrienol	4	1–4

α-Tocopherol is a slightly viscous, pale yellow **oil** with a melting point of 2.5–3.5°C and a boiling point of 200–220°C. It fluoresces when exposed to a wavelength of 296 nm, emitting **light** at 325 nm. The ultraviolet **absorption** maximum is at 294 nm. α-Tocopherol is soluble in organic solvents but poorly soluble in water. It is stable to heat and alkalis in the absence of **oxygen**, but slowly oxidizes upon exposure to atmospheric oxygen and rapidly oxidizes in the presence of ferric **salts**. Feed handling methods can result in loss of natural α-tocopherol. Drying forages in sunlight, treatment of **maize** with **propionic acid** and ensiling of high-moisture maize have been shown to result in substantial loss of α-tocopherol. In order to stabilize α-tocopherol, the C-6 phenolic hydroxyl group is shrouded by **esterification** to **acetate**. During extraction of tocopherols from plant or animal tissue, it is common to amend the extraction medium with a cation chelator and a reductant to protect the tocopherols, as they may come into contact

with oxygen during **sample** preparation. A common approach for quantifying α-tocopherol involves liquid **chromatography** with UV or fluorescence detection. α-Tocopherol is considered to be the most important natural **antioxidant** in cell membranes. Physicochemical studies have demonstrated that the polarity and structure of α-tocopherol account for the chroman group being located at the surface of a **lipid** bilayer membrane with the phytanyl tail serving to anchor the molecule in the interior lipophilic region of the membrane. The protective activities of α-tocopherol are related to oxidative damage, which is attributed to the presence of molecular oxygen in aerobic organisms and its **solubility** in tissues. Specific chemical species known as reactive oxygen species have been implicated in cells as strong pro-oxidants that participate in **fatty acid oxidation** reactions. Prominent reactive oxygen species are **superoxide** anion ($O_2 \cdot^-$), **hydrogen peroxide** (H_2O_2) and hydroxyl radical (HO·). During oxidation of **unsaturated fatty acid**s, peroxyl and alkoxyl radicals arise and propagate fatty acid oxidation. α-Tocopherol quenches free-radical-mediated fatty acid oxidation by donating a proton and an electron from its C-6 hydroxyl group to radical species, thus converting them to less oxidative stable species. In the process, α-tocopherol becomes α-tocopheroxyl radical, but this radical is much less reactive than the radicals that have been quenched. Since α-tocopherol is located in membranes and membranes are composed of predominantly unsaturated fatty acids that are inherently prone to oxidation, α-tocopherol's role as a premier tissue antioxidant is very logical. α-Tocopherol can be regenerated

from α- radical by reductions involving, for example, **ascorbic acid**, **glutathione** and ubiquinone. Providing high levels of α-tocopheryl **acetate** to livestock has not produced evidence of toxicity. (DMS)

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Tocotrienols

A group of compounds with a phenolic functional group at carbon 6 on a chroman ring (substituted 6-member heterocyclic double rings) with a 16-carbon isoprenoid chain attached to C-2 of the chroman ring. The number and location of methyl groups on the chroman ring determine the identity of α, β, γ and δ tocotrienols. Since the isoprenoid chain of tocotrienols has three C-C double bonds, there is only one chiral carbon (C-2). While the biological activity of the **tocopherols** varies from 1.49 IU mg^{-1} (for D-α-tocopherol, 2*R*, 4′*R*, 8′*R*) to 0.85 IU mg^{-1} (for 2*R*, 4′*S*, 8′*R*), the tocotrienols are about one-fifth as biologically active. (DMS)

Tolerance, immune:

see Immune tolerance

Tomato

Edible berry of the plant *Solanum lycopersicum* widely used in

human cuisine. A native of central and south America, the tomato is rich in **vitamin C** and a phytochemical, lycopene. (CJCP)

Nutrient composition of tomato products (g kg^{-1} dry matter).

		Nutrient composition (g kg^{-1} DM)						
	Dry matter (g kg^{-1})	Crude protein	Crude fibre	Ash	Ether extract	NFE	Ca	P
Skin and seeds, dried	933	248	276	66	220	190	1.8	2.6
Oil cake	–	370	283	74	68	205	1.6	5.9

DM, dry matter; NFE, nitrogen-free extract.

Tomato by-products

By-products of commercial **tomato** (*Solanum lycopersicum* L.) production and processing include waste fruit and tomato pomace (the residue of juice extraction), which may be pressed and dried. These materials have limited use for non-ruminants. Tomato cannery waste can be used as a feed ingredient in low-energy

poultry diets, i.e. broiler, breeder and laying hen rations, at < 20% of total diet. Tomato products may be fed to ruminants with no specific limitations. (JKM)

Tongue rolling

Otherwise known as tonguing and tongue lolling. A condition in which animals protrude their tongue and either roll it (most common in cattle), repeatedly retract and protrude it (common in dogs), or leave it hanging (also common in cattle). This repetitive behaviour is often a form of displacement behaviour, exhibited as a coping mechanism when the animal is under stress. It is particularly common in cattle restrained in individual stalls. This form of oral dyskinesia has a similar aetiology to lip smacking and **bruxism**. It is associated with **bar biting** in cattle. (CJCP)

Tooth

A hard structure embedded in the jaw, collectively used for biting food, defence and grooming. Teeth are specialized for different purposes in many animals: incisors for cutting food, canines for grasping food and in defence, premolars to chew food and transition it to the rear of the buccal cavity, where there are molars, which grind the food into a form in which it can be swallowed to enter the **gastrointestinal tract**. Because the jaw of animals grows in size as the animal ages, two sets of teeth are common: deciduous and permanent teeth. Dentition is commonly described by a formula for one half of the jaw, with the upper jaw first, followed by the lower jaw; for example, 3123/3123 would indicate that the half upper and lower jaws each had three incisors, one

canine, two premolars and three molars.

Teeth may be worn down over time, particularly if the animal is eating feed with an abrasive texture, such as when sheep graze on stony pastures. In this case the wear on sheep's teeth may necessitate removing the animal to more benign pastures. Excessive wear is also seen in **ewes** folded on root crops and in upland areas.



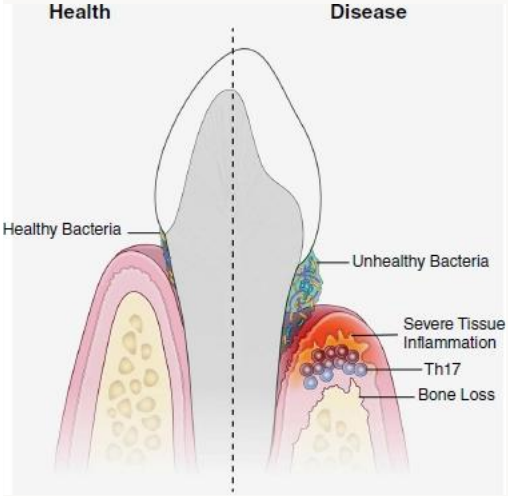
Excessive lengthening of the lower incisor teeth in a rabbit. Photo courtesy of Kalumet. Licensed under CC 3.0

The nutrients primarily required for the growth and maintenance of teeth are **calcium** and phosphorus. Prolonged dietary deficiency of one or both of these will cause weakening and premature loss of teeth, although the effects of the deficiency on

bone, for which adequate dietary supplies of calcium and phosphorus are also required, will probably be noticed before the effects on teeth. (CJCP; JMF)

Tooth disease

The buccal cavity, as the point of entry of air, food and water into the body, is particularly exposed to diseases. These are often manifested in the periodontal region, due to its exposure to ambient conditions.



Causes of periodontal disease. Image courtesy of National Institutes of Health. Licensed under Public Domain Mark 1.0.

Three main types of disease prevail: infections, mineral disorders of the **teeth** and physical damage. Infections favour this site of colonization of the body because of the ability to transmit the disease during communal feeding; however, the bacteriostatic properties of salivary **antibodies** and other compounds, such as agglutinins, help to prevent disease. Foot-and-mouth disease is one example of a disease readily transmitted between grazing animals. The gums, with their exposed state, are also prone to inflammation, as in gingivitis, and vascular disorders, such as the localized

hypoxia that accompanies lead **poisoning** and is manifested as a blue coloration or 'lead line'. **Mineral** disorders commonly affect the teeth, due to their mineralized nature, and the status of many minerals in animals can be assessed by chemical analysis of teeth. **Fluorine toxicity**, or fluorosis, is accompanied by a yellowing of the teeth and is common near **aluminium** smelters. Physical damage is mainly to the teeth, and tooth loss (a temporary problem in young cattle progressing from milk teeth to permanent teeth) is a common source of morbidity in sheep grazing stony pastures. Sheep grazing short mountain pastures suffer excessive tooth wear and become 'broken-mouthed', at which time they can only satisfactorily graze on lush lowland pastures, where they are unlikely to consume small stones that will further damage their teeth. Free-range pigs can also suffer tooth damage when stone **chewing**.

The periodontal region is subject to a number of abnormalities, such as over- or undershot jaws, a problem (particularly in ruminants) where the lower jaw fails to meet the hard pad in the upper jaw. (CJCP)

Total body water

The sum of extracellular and intracellular water. Total body water (TBW) is usually measured by the dilution of isotopically labelled water. The label may be **deuterium** (^{2}H), tritium (^{3}H) or ^{18}O. Each of these gives a slight overestimate (up to 5%) of total body water because there is some exchange of isotope with substances other than water. (MFF)

Total digestible nutrients (TDN)
The total digestible nutrient value of a feed is calculated as: digestible **crude protein** + digestible **crude fibre** + digestible **nitrogen-free extract** + 2.25 × digestible **ether extract**. In contrast to **digestible energy** (DE), which is based on **energy value**s of nutrients, TDN is based on mass, with a correction factor for **lipids**. (JvanM)
See also: Efficiency of energy utilization; Energy systems

Total mixed ration (TMR)
A method of feeding cattle in which feed ingredients are mixed in a wagon into a feed that is completely mixed, so that each cow is consistently consuming an appropriate diet. The mixing is achieved by paddles or rotating arms in a wagon. Care must be taken to ensure adequate mixing when adding **micronutrient**s. The main benefit of feeding TMRs is to ensure slow **digestion** of high-energy ingredients, thereby reducing the risk of acidosis in the rumen. (CJCP)

Toxins:
see Poisoning. *See also*: Aflatoxins; Algal toxins; Alkaloids; Aspergillosis; Botulism; Bracken fern; Carcinogens

Trace elements
Trace elements are the metallic elements required in the diet in trace amounts (between 1 and 100 mg kg^{-1} diet) for **growth** and **maintenance**. They include **copper**, **iron**, **manganese** and **zinc**. Other trace elements that show beneficial effects in some

animal species include **silicon**, **chromium** and **fluorine**. Dietary elements required in concentrations of < 1 mg kg^{-1} diet are generally referred to as **ultra-trace element**s. (PGR)

Trans fatty acids

Unsaturated fatty acids in which one or more double bonds are in the *trans* configuration, in contrast to the all-*cis* configuration that predominates in nature. They are formed naturally from dietary **unsaturated fatty acid**s by ruminal bacteria, thus occurring in small amounts (<5%) in ruminant **fats**. Diverse *trans* fatty acids are formed by the industrial hydrogenation of unsaturated vegetable **oils**. *Trans* unsaturation increases the melting point compared with the *cis* analogue. (DLP)

Transamination

The process whereby the α-**amino nitrogen** ($X{\cdot}CHNH_2{\cdot}COOH$) of many amino acids can be removed and then transferred to the α-**keto acid** ($X{\cdot}CO{\cdot}COOH$) precursor of an amino acid to form the amino acid. The transamination reaction is dependent on the **vitamin** B_6 (**pyridoxine**) co-factor pyridoxal 5′-phosphate and forms pyridoxamine 5′-phosphate, which is the **nitrogen**-carrying intermediate in transamination reactions. By transamination, an inappropriate pattern of amino acids from the diet can be modified to produce an amino acid pattern that more closely meets its metabolic needs. Nitrogen supplied in a simple compound such as ammonium citrate can be taken up as **glutamate** and used as a source of α-amino nitrogen for dispensable amino acid biosynthesis. This biosynthesis of dispensable amino acids is

dependent on the production of the α-keto acid precursors of the amino acids (i.e. **pyruvate**, α-ketoglutarate, **oxaloacetate**, etc.) which are usually derived from the **catabolism** of **carbohydrates** such as **glucose** and **glycerol**. Transamination is also, for many amino acids, the first step in the process of catabolism. (NJB)

Transferrin
A glycoprotein that provides the primary means for inter-organ transport of non-haem **iron**, binding up to two iron atoms in the +3 (ferric) **oxidation** state. It is present in **blood** in the diferric, monoferric and apo- or iron-free forms. In adult animals the majority of serum transferrin is iron-free (about 70%), helping to prevent the accumulation of toxic (not **protein**-bound) iron. Diferric transferrin binds to cell-surface **transferrin receptor**s and is internalized into cells by receptor-mediated endocytosis. (RSE)

Transferrin receptor
A glycoprotein present in the membrane of many cell types that is required for the internalization of **transferrin** (Tf) **iron**. The transferrin receptor (TfR) is a 90,000 dalton glycoprotein that dimerizes: each TfR monomer binds one Tf molecule. Iron-loaded Tf binds much more tightly to the TfR than does the iron-free form of Tf, thus assuring iron uptake. TfR is brought into the cell (endocytosed) in membrane-bound vesicles called endosomes. The endosomes containing TfR with Tf bound to it become acidified; this is required for release of iron from Tf and its delivery to the

cytosol. Under these conditions of low pH the iron-free Tf binds well to TfR and is brought back to the cell surface and released to find more iron. Iron-deficient cells increase their expression of TfR to acquire more iron; conversely, in iron overload, TfR expression is reduced. Cells can contain from several thousand TfR to several million, as on immature red **blood** cells that are actively making the iron protein, **haemoglobin**. Genetic inactivation of the TfR gene is lethal to the embryo in part because TfR represents the only way to deliver iron into immature red blood cells. As red cells mature they lose their TfR, leading to the formation of a serum form of TfR which is thought to be a good **indicator** of body iron status. High serum TfR suggests iron deficiency. Recently a second TfR, TfR2, was discovered. TfR2 also allows for internalization of iron. TfR2 is highly expressed in liver and the inability to reduce its expression in iron overload may lead to damage to tissues such as liver. (RSE)

Transit time

Transit time is a measure of the time required for a dietary component to pass through the whole digestive tract or a part of it. The transit time through the **stomach** is strongly influenced by feed composition, in particular the physical structure, because particles above a certain size cannot pass through the pylorus. Furthermore, **gastric emptying** rate is under nervous and hormonal control and is regulated to allow adequate **digestion** of food material in the upper part of the **small intestine** before more material enters. Thus, non-absorbed **lipids** trigger the release of **cholecystokinin** (CCK) from receptors in the

duodenum and also of gastric inhibitory polypeptide from receptors in the **jejunum**; both hormones inhibit gastric emptying.

In the **small intestine**, digesta are propelled by peristaltic contractions associated with the migration of myoelectric complexes from duodenum to **ileum**. These complexes are composed of a quiescent phase whose duration varies according to feeding and time of day, a phase of irregular spiking activity lasting 50–80 min and a phase of regular spiking activity lasting 3–5 min. The myoelectric complexes migrate at a decelerating speed from about 20–30 cm min^{-1} in the first part of the small intestine to about 5 cm min^{-1} in the distal parts.

Transit processes in the **large intestine** are less well documented. The **caecum** acts more or less as a mixing reservoir, and the slow transit through the **colon** is based on peristaltic waves.

Dietary fibre reduces transit time in the stomach and small intestine but increases transit time in the large intestine, resulting in a general increase throughout the whole digestive tract. The transit time or passage rate can be studied by the use of **markers**. **Chromic oxide** or rare-earth minerals that bind strongly to fibre compounds that are not degraded are commonly used. Also native dietary fibre compounds such as **lignin** or insoluble **ash** can be used. Simultaneous electromyographic and radiological observations are also useful methods.

The transit time varies between species and generally increases with complexity of the digestive tract. In chickens and turkeys,

markers appear in the faeces 2–2.5 h after ingestion and are almost completely excreted after 24 h. In pigs, average transit time throughout the digestive tract is about 24 h. In ruminants, the transit time is considerably higher, due to a **retention time** in the **rumen** of typically 50–80 h when foods are highly lignified, or 30–50 h for more readily digested foods such as immature pasture herbage or concentrates. (SB)
See also: Motility

Trehalase
A glycolytic enzyme (α, α-**trehalose** glucohydrolase; EC 3.2.1.28) that hydrolyses the **disaccharide** trehalose (abundant in **algae** and **fungi** as well as in the haemolymph of insects) into its constituent, **glucose**. Trehalase is attached to the **brush border** of epithelial cells in the **small intestine**. (SB)
See also: Carbohydrates

Trehalose
A **disaccharide**, $C_{12}H_{22}O_{11}$, molecular weight 342, of two glucopyranose residues joined at their anomeric carbons (carbon 1) and a novel non-mammalian autophagic activator of rapamycin target **protein** pathway. Trehalose is an important reserve **carbohydrate** in **yeasts**, lichens and **algae**. It occurs in insect **eggs**, larvae and pupae and is the major **blood sugar** in some mature insects. It is an autophagy inducer through the mTOR independent pathway; it can induce autophagy in a variety of neurodegenerative diseases and increase the clearance rate of aggregation-prone proteins (such as α-synuclein, mutant

Huntington protein and prion protein) (Zhang *et al*., 2014). Previous studies have elucidated the neuroprotective effects of trehalose. It prevents the loss of dopaminergic neurons and enhances the clearance of abnormal protein aggregation, being regarded as a potential drug for Parkinson's disease (Tien *et al*., 2016). Moreover, oral administration of trehalose not only reduced the accumulation of **ubiquitin**-positive protein and the formation of polyglutamine in the striatum of mice with Huntington's disease, but also prolonged lifespan and improved motor function (Debnath *et al*., 2017). Trehalose has also been reported to inhibit neural tube defects and the apoptosis of Schwann cell after sciatic nerve injury (Xu *et al*., 2013). An *in vitro* mechanism study using rats indicated that the regulations of trehalose in autophage and apoptosis were via the AMPK-ULK1 pathway. Trehalose protects injured motor neurones by enhancing autophage and inhibiting apoptosis, demonstrating the essential role of trehalose in the prevention and treatment of **brachial plexus root avulsion (**BPRA) (Li *et al*., 2021). (QS; JAM)

See also: Carbohydrates

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Triacylglycerol lipase

An enzyme that hydrolyses triacylglycerols to **free fatty acid**s and **glycerol**. In the digestion of dietary fats, triacylglycerol lipases are secreted from the tongue (specific for **medium-chain triacylglycerol**s), the **stomach** and the **pancreas**. In **adipocyte**s, triacylglycerol is hydrolysed to glycerol and **fatty acid**s by a hormone-sensitive **lipase**. In **blood**, triacylglycerols in **chylomicron**s and very-low-density **lipoprotein**s are converted to glycerol and **fatty acid**s by **lipoprotein lipase**. (NJB)

Triacylglycerols

Esters of **glycerol** and **fatty acid**s, also called triglycerides. The alcohol groups on a single glycerol of most naturally occurring triacylglycerols do not contain the same fatty acid residue and thus are mixed **acylglycerol**s. They are the main form of **fat** in feedstuffs and the major **energy** reserve in higher animals.

(JAM)

Tricarballylate
A **metabolite** of transaconitic acid, an **organic acid** of lush, growing plants. Tricarballylate, produced in the **rumen**, can bind **magnesium** and other cations to form a stable complex preventing **absorption** of the bound cations. Tricarballylate may be a cause of **hypomagnesaemia** in grazing ruminants. (JPG)
See also: Tetany, grass

Tricarboxylic acid (TCA) cycle
Also called the Krebs cycle or the **citric acid** cycle, a series of reactions that participate in both anabolism (the biosynthesis of molecules from smaller components and requiring energy) and **catabolism** (breakdown of complex molecules into smaller components and releasing energy). The TCA cycle is especially associated with the cristae in the matrix of the mitochondria within the cells of the animal body. These reactions form a cycle, the first step in the catabolism of acetyl-CoA being its combining with oxaloacetic acid to form citric acid. In the ensuing nine steps in the breakdown of citric acid, two moles of CO_2 are produced, and, in the last step in the TCA cycle, oxaloacetic acid is produced. The catabolism of acetyl-CoA produces 2 CO_2 and 12 ATP. The following is the sequence of reactions that comprise the TCA cycle: **oxaloacetate** + acetyl-CoA → citrate → cis-aconitate → isocitrate* → CO_2 + α-ketoglutarate* → + CO_2 + succinyl-CoA → CoASH + ATP + **succinate**** → fumarate → **malate*** → oxaloacetate. In steps marked *, NAD → NADH + H^+, and in steps marked **, FAD

→ $FADH_2$. The energy trapped in the reduced co-factors is recovered as ATP when the reduced co-factors are oxidized by the electron transport chain. In the electron transport chain, the electrons carried by the reduced co-factors NADH and $FADH_2$ are used to reduce O_2 to H_2O in a process whereby the energy in the reduced co-factors is used to synthesize ATP from ADP + P. The catabolism of acetyl-CoA in the TCA cycle results in 3 NAD → 3 NADH + 3 H^+, 1 FAD → $FADH_2$ and ATP produced in a single substrate → product reaction. Each NADH is equivalent to 2.5 ATPs and each $FADH_2$ equivalent to 1.5 ATPs for a total of 10 ATPs (7.5 + 1.5 + 1 = 10). In catabolism, CO_2 is produced from the carbon in the substrates and the energy in the substrates is captured ultimately as ATP. In anabolism, non-glucose carbon can be converted to glucose carbon in a process called **gluconeogenesis** and non-amino acid carbon can be converted to dispensable amino acid carbon. In catabolism, the TCA cycle is the metabolic pathway by which the acetyl-CoA produced from the catabolism of **fatty acid**s and some amino acids, or the acetyl-CoA produced from glucose or amino acids via pyruvate, is converted to CO^2. The TCA cycle is also the pathway by which carbon from amino acids which produce oxaloacetate, α-ketoglutarate, fumarate or succinate in their catabolism is converted to malate. The latter exits the mitochondria into the cytoplasm for conversion into **pyruvate**, which enters the mitochondria for **oxidation** to acetyl-CoA. The role of the TCA cycle in anabolism is in gluconeogenesis and in **lipogenesis**. In gluconeogenesis, compounds that become intermediates in the TCA cycle (i.e. **oxaloacetate**, fumarate,

succinate and α-ketoglutarate) can be converted into glucose carbon. Thus, aspartate, **glutamate** and parts of **arginine**, **histidine**, **glutamine**, **proline**, **isoleucine**, **methionine**, **valine**, **tyrosine**, **phenylalanine**, threonine and **propionate** are carbon sources for the synthesis of **glucose**. Because pyruvate can be converted to oxaloacetate, parts of amino acids that are converted to pyruvate are also gluconeogenic. Thus, **alanine**, **cysteine**, **glycine**, **serine** and threonine are sources of glucose carbon. In lipogenesis, citrate leaves the mitochondrion into the cytoplasm and is converted into acetyl-CoA, which is the two-carbon precursor used in the biosynthesis of **long-chain fatty acid**s. In this process aspartate, **glutamate** and parts of **arginine**, **histidine**, glutamine, proline, isoleucine, methionine, valine, tyrosine, phenylalanine, threonine and propionate are carbon sources for the synthesis of **long-chain fatty acid**s and **cholesterol**. (NJB; GW)

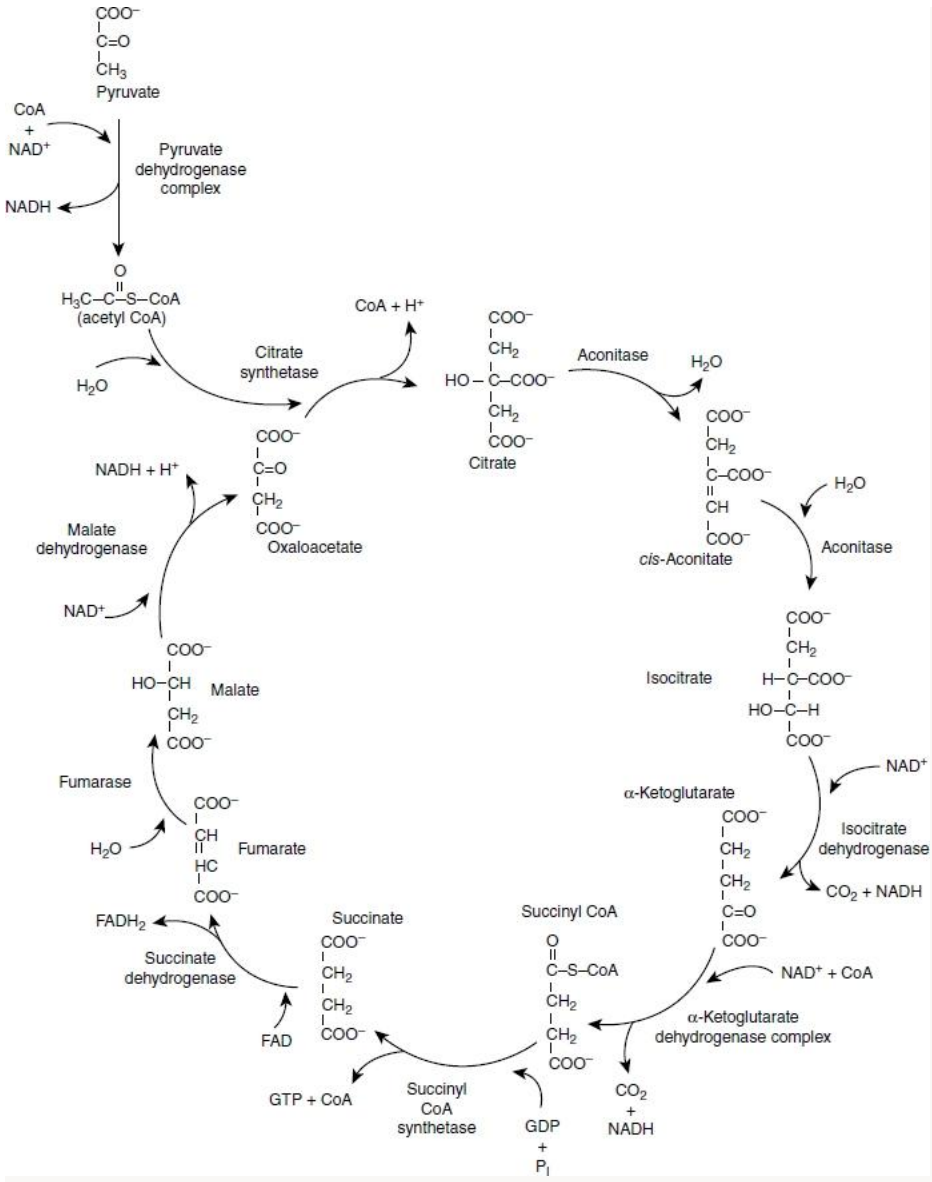


Diagram of the TCA cycle.

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Trichothecenes

Trichothecenes are **mycotoxin**s produced by several species of *Fusarium* fungi. More than 100 trichothecenes are known; the

most important are T-2 toxin, HT-2 toxin, diacetoxyscirpenol (DAS), 15-monoacetoxyscirpenol (15-MAS) and **vomitoxin** (**deoxynivalenol** or DON). The name trichothecene derives from the fungus *Trichothecium roseum*, from which the compounds were first isolated. Trichothecenes have neurotoxic, cytotoxic and immunotoxic effects. They are potent inhibitors of **protein synthesis**. Cytotoxic effects include inflammation and necrosis of epithelial tissue, especially of the oral and gastrointestinal tracts. Feed refusal and **vomiting**, especially with DON, are common signs. Neurotoxic effects include posterior paralysis (pigs) and incoordination. Thymic involution and impaired antibody production are immunotoxic effects. Specific trichothecene-induced disorders include mouldy **corn** toxicosis in cattle (T-2), alimentary toxic aleukia in humans (T-2), **bean** hull **poisoning** in horses, and stachybotryotoxicosis. The production of trichothecenes in grains is stimulated by low **environmental temperatures**. (PC)

Triglycerides:
see Triacylglycerols

Triiodothyronine
Also called T_3, 3,5,3′-triiodothyronine, $HO{\cdot}C_6H_3I{\cdot}O{\cdot}C_6H_2I_2{\cdot}CH_2{\cdot}CH(NH_2){\cdot}COOH$ is a **thyroid** hormone derived from thyroxine (T_4,3,5,3′,5′-tetraiodothyronine, $HO{\cdot}C_6H_3I_2{\cdot}O{\cdot}C_6H_2I_2{\cdot}CH_2{\cdot}CH(NH_2){\cdot}COOH$). These hormones are produced in the thyroid gland and are unique in that they contain **iodine**. They are transported in the blood bound to

thyroxine-**binding protein**. T_3 has its effect by binding to receptors on target cells. These hormones are required for growth and normal development and to maintain the basal **metabolic rate**. (NJB)

Trimethylamine
A colourless liquid, $(CH_3)_3{\cdot}N$, with a fishy ammoniacal odour. In animals it is a product of the microbial degradation of **choline** $(CH_3)_3{\cdot}N^+{\cdot}CH_2{\cdot}COH$ and **betaine** $(CH_3)_3{\cdot}N{\cdot}CH_2{\cdot}COOH$. (NJB)

Trimethyllysine
$(CH_3)_3{\cdot}N{\cdot}CH_2{\cdot}CH_2{\cdot}CH_2{\cdot}CH_2{\cdot}CHNH_2{\cdot}COOH$. Trimethyllysine is produced by **methylation** of protein-bound **lysine** by ***S*-adenosylmethionine**. When protein is degraded, trimethyllysine is released and becomes available for the synthesis of **carnitine**. (NJB)

Tripeptidase
A **peptidase** that specifically hydrolyses tripeptides. Tripeptidases are located together with dipeptidases and **aminopeptidase**s in the epithelial cells in the **small intestine**, mainly in the **jejunum**. (SB)
See also: Protein digestion

Triticale
A hybrid **cereal** derived from **wheat** (*Triticum* spp.) and **rye** (*Secale* spp.). It combines the desirable characteristics of wheat (**grain** quality, productivity, baking properties, disease resistance)

with those of rye (vigour, hardiness). Triticale is grown commercially mainly for animal feeding in Central and Northern Europe and North and South America. Spring varieties are an alternative source of forage to oats and **barley**; winter varieties are grown mainly as a spring pasture for ensiling or harvesting for grain. Winter triticale may also be planted in mixtures with barley or **oats** to produce a high-quality **silage** crop with late-season grazing. **By-product**s include triticale meal, rolled triticale, quick triticale flakes and triticale bits. Recent varieties of triticale are comparable to wheat in terms of protein content but there is a high degree of variability (110–185 g kg^{-1} dry matter) among varieties. **Protein quality** is higher than in wheat, due to the higher concentration of **lysine** and sulphur-containing amino acids, but triticale is deficient in **tryptophan**. Triticale contains **antinutritional factor**s (**trypsin inhibitor**s, alkyl resorcinols) which have been implicated in poor **palatability** and performance in pigs. Triticale should not contribute more than half the total grain fed in the diet of farm animals. (ED)

Further reading

Zhu, F. (2018) Triticale: nutritional composition and food uses. *Food Chemistry* 241, 468–479.

Trough:

see Drinker; Feed trough

Trout

A term most commonly used to denote any of several species of Salmonidae in the genera *Salmo* (e.g. brown trout, *Salmo trutta*),

Salvelinus (e.g. brook trout, *Savelinus fontinalis*) and *Oncorhynchus* (e.g. **rainbow trout**, *Oncorhynchus mykiss*). The term has also been applied to fish other than Salmonidae, such as the Australian family Galaxiidae, and certain Sciaenidae (drums) of the genus *Cynoscion* ('seatrouts'). (RHP)



Brook trout. Photo courtesy of USFWS/Southeast. Licensed under CC BY 2.0.

True digestibility

A calculated value for the digestibility of a dietary component after correction of the determined **apparent digestibility** for endogenous losses. For example, the digestibility of **amino acid**s is based on the collection of ileal **digesta**, which contain not only undigested proteins (amino acids) but also un-reabsorbed endogenous amino acids. Part of this endogenous loss can be regarded as a basal (minimal) loss; part is induced by the diet. After correction for the estimated basal loss of amino acids, the 'true' digestibility is obtained. **True protein** digestibility is now often referred to as 'standardized digestibility'. (SB)

True metabolizable energy

True metabolizable energy, often abbreviated to TME, is used to characterize the **energy value**s of feeds for poultry. Apparent **metabolizable energy** (AME) is measured directly as the difference between ingested and excreted energy. Because the excreta contain uric acid, the measured value is higher in a bird that retains more of the dietary nitrogen than in one that retains less and excretes more. TME is calculated by subtracting from AME the energy that would have been expended if all the dietary N had been excreted as uric acid (34.4 kJ g^{-1} N), i.e. if no protein were deposited. TME is thus more independent than AME of the use to which dietary energy is put. (SB)

True protein

The actual protein content of a material, exclusive of the **non-protein nitrogenous compound**s present in it that form part of the **crude protein**. Early workers in animal nutrition proposed methods for measuring true protein but none were acceptable, due to technical difficulties. Accurate measurement of true protein would entail extraction with a protein precipitant, such as 10% trichloroacetic acid, to remove non-protein N compounds, followed by acid, alkaline or enzymatic **hydrolysis**. The resultant hydrolysates are analysed for amino acid using high-performance liquid **chromatography** (the most popular method), gas chromatography, or ion-exchange chromatography. The true protein content of the material could then be obtained from the sum of the component amino acids – provided that allowance is made for water lost when amino acids combine in **peptide** linkage.

Note that N analysis of the extracted material would not provide a measure of true protein as, without knowing its amino acid composition, the percentage of N in the protein is not precisely known. (CBC; GW)

Trypsin
A pancreatic enzyme classified as an **endopeptidase**. It has a specificity for cleavage at the site of basic amino acids such as **arginine** and **lysine**. Trypsin is secreted as the inactive **zymogen**, **trypsinogen**, which is activated by **enterokinase**. Trypsin in turn converts inactive chymotrypsinogen to **chymotrypsin**, its active form. **Trypsin inhibitor**s are found in a number of plants, especially **legume** seeds. (NJB)

Trypsin inhibitors
A widely distributed group of plant proteins that inactivate animal **serine** proteases. They can be classified into two groups. Those of the first group have either a single domain (single- or double-headed, *c*. 8 kDa, heat and pH stable) Bowman-Birk inhibitory structure (ranging from 14 amino acids in **sunflower**s to, more commonly, 60–70 amino acids as in some **legumes** and **wheat**), or two domains (e.g. **barley** and legumes), allowing simultaneous and independent binding of two trypsin molecules. A specific inhibitor, threonine, is highly conserved and provides optimal inhibition of trypsin. This increases pancreatic trypsin and **chymotrypsin** secretion. Those of the second group are Kunitz inhibitors (18–24 kDa, heat and pH labile; growth inhibition twice that of Bowman-Birk inhibitors) whose activity can vary 1000-fold.

They increase pancreatic trypsin secretion. Inhibitors with similar *in vitro* inhibition patterns can have different *in vivo* effects. Dietary sources of trypsin inhibitors inhibit certain cancer cells, inhibit proteases from mammalian inflammation-mediating cells and can suppress **superoxide** anion radical secretion from immunocytes. Inhibitor-resistant duodenal **pancreatic juice** tryptic activity is evident after eating raw **soybean**s. Sources include Leguminosae (**beans**), Poaceae (**cereal**s), Chenopodiaceae (**spinach**), Solanaceae (**potato**es), Convolvulaceae (**sweet potato**es), Asteraceae (lettuce, sunflowers), Amaranthaceae (**amaranth**us), Brassicaceae (radish) and Cucurbitaceae (squash). (JDO)
See also: Antinutritional factors

Trypsinogen
The inactive precursor of **trypsin**, secreted from the **pancreas** via the pancreatic duct into the lumen of the **duodenum**, where it is activated by a specific cleavage of an *N*-terminal polypeptide, first by **enterokinase** and progressively by activated trypsin, which assures a rapid and complete activation. Spontaneous activation of trypsinogen in the pancreas is prevented by the presence of a potent trypsin inhibitor. (SB)

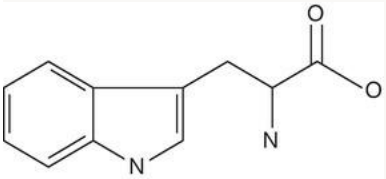
Tryptamine, 5-hydroxy:
see Serotonin

Tryptophan
An essential amino acid ($C_8NH_6{\cdot}CH_2{\cdot}CHNH_2{\cdot}COOH$, molecular

weight 204.2) found in protein. Tryptophan is sometimes limiting in practical diets fed to non-ruminants. When evaluated in terms of g tryptophan per 16 g nitrogen (i.e. percentage of **crude protein**), **maize** and **rice** are low in tryptophan whereas **soybean** meal is rich in this amino acid. **Gelatin** is virtually devoid of tryptophan.

The main catabolic pathway of tryptophan involves several **oxidation** reactions that result in the synthesis of 2-amino 3-carboxymuconate semialdehyde (ACS). This compound is primarily converted to acetoacetate and then CO_2, but some of the flux goes toward quinolinic acid, which is a precursor for the synthesis of nicotinic acid mononucleotide, and ultimately NAD. Feline species have little capacity to make quinolinic acid from ACS and therefore tryptophan does not reduce their **niacin** requirement.

An estimated 3% of the tryptophan catabolic flux involves hydroxylation followed by **decarboxylation** to form **serotonin**, a vasoactive **amine**. Serotonin synthesis occurs primarily in enterochromaffin cells of the **intestinal mucosa**, with a lesser quantity being synthesized in the pineal gland of the brain. Some of the brain serotonin is converted to **melatonin** in the pineal gland. (DHB; GW)



Tube feeding:
see Force feeding

Tubers:

see Cassava; Jerusalem artichoke; Potato; Sweet potato, Yam

Tumeric: see Turmeric

Turbot (*Scophthalmus maximus*)
A highly valued **flatfish**. Landings of wild turbot have declined, generating an interest in commercial turbot cultivation. An industry emerged in the 1980s based on managed broodstocks that are manually stripped of gametes, with 10 days of hatchery incubation at about 10°C for the approximately 1 mm diameter eggs, larviculture using enriched **rotifers** and *Artemia* diets from about 3 days after hatching, and continuous illumination in large rearing tanks at the higher temperature of about 18°C. Time to market size depends on rearing temperature, nutrition and market demand, but may be 2–3 years. (KP)



Turbot is a highly valued flatfish but availability is declining. Photo courtesy of Peter van der Sluijs. Licensed under CC BY-SA 3.0.

Turkey
The turkey (*Meleagris gallopavo*) was originally domesticated by the Native Americans. The wild turkey contains five subspecies. Its territory included all of Mexico, except the extreme southern and

western parts, and the USA south of the Great Lakes and from the Atlantic coast west to Arizona.

The wild turkey is a poor flyer but it can run very fast and, once airborne, can glide for long distances. Settlers in North America consequently found them quite easy to shoot and destroyed entire flocks. By 1900, only small populations of the once great flocks still existed. Since then, protective measures by the US Government have resulted in a population explosion to the extent that wild turkeys can now be found as far north as Canada.



Male wild turkey (*Meleagris gallopavo*) strutting. Photo courtesy of Frank Schulenburg. Licensed under CC BY-SA 4.0.

The domestication of the modern turkey owes much to European influence. It is thought that the first turkeys were brought to Europe by Spanish explorers early in the 16th century. A Yorkshireman, William Strickland, is credited with introducing the domesticated turkey to England. They soon became the favoured meat of royalty and nobility. The domesticated European turkey re-

crossed the Atlantic with the early European settlers. A further significant importation was of a broad-breasted strain imported from England in the 1920s.

The North American turkey industry proceeded to develop much faster than that of Europe, which suffered shortages of feedstuffs, during and after World War II. Since the 1960s, there has been interchange of genetic material and the genetic stock is now very similar on both sides of the Atlantic.

Breeding programmes

The original domesticated turkeys were coloured bronze, the dominant feather colour being black with the tips of the feathers overlain with iridescent red-green bronzing and some feathers having terminal edging and barring in white.

Because of difficulty of removing all the small, developing black feathers, which then spoilt the appearance of the carcass, the white-feathered turkey now completely dominates the industrial market. However, alternative premium markets have been developed using black- or bronze-feathered birds, using the black feathers to identify them as having a traditional farm-produced background.

The breeding programmes are based around breeding specialized lines selected strongly for **reproduction** to provide the parent female, and crossing these with males from lines which have been selected strongly for **growth** rate and breast conformation. In all lines, fitness and mobility are of overriding concern, because it is important for the birds to survive a full breeding season. The relative concentration on reproduction or

growth rate differs according to the market for which the commercial cross offspring are destined.

The turkey market

The growing of turkeys was initially to produce oven-ready birds for the festive markets, i.e. Thanksgiving and Christmas. Since then the production of turkeys has grown rapidly around the world. The main market now is for **meat**, in the same way that pigs, cattle and sheep are cut up into joints or further processed. In some countries the most valuable meat is breast meat. In others it is the dark meat. As a result, an international trade in turkey meat has developed.

Turkeys can be killed at a wide range of ages from 10 to 24 weeks, depending on the intended market. The **meat yield** increases with age. The breast meat is the **muscle** that has the latest peak in growth rate. **Fat** deposition increases from about 14 weeks of age. The females have an earlier growth profile than males. The most common age for killing is 16 weeks for females and 21 weeks for males.

The meat flavour increases with fat deposition, which increases with age. It is important not to overcook turkeys as it can result in dry meat. As a rule of thumb, when the juices run clear after a fork pierces the skin between the thigh and breast, the turkey is adequately cooked.

Turkey nutrition and feeding: commercial growing

Different breeds have been developed for different markets, with varying speeds of growth. The males grow considerably faster than the females. However, it is not normal to formulate different feeds for different breeds or sexes. Instead, the age schedule for feeding

the different diets is modified, with the slower-growing breeds going on to the lower-protein diets earlier than the fast-growing breeds. Similarly, the females will go on to lower-protein diets earlier than males. No difference has been demonstrated between the sexes in terms of diet requirements earlier than 8 weeks of age.

The turkey is a high-protein, low-fat animal and as such has a higher amino acid percentage requirement in its diet than the **broiler chicken**. The turkey's amino acid requirements reduce with increasing age. The more normal system is to change the **feed formulation** every 3 or 4 weeks as age increases, as is shown in Table 1. The recommendations are expressed as g amino acid per megajoule (MJ) of **metabolizable energy** (ME) to allow for variations in desired nutrient density. The range of the most commonly used ME levels used is also shown.

Table 1. Important nutrients for growing turkeys (g MJ^{-1} ME)

Age (weeks)	Lysine	Methionine	TSAA	Threonine	Calcium	Available P	Range of ME (MJ kg^{-1})
0–4	1.57	0.57	1.02	1.06	1.14	0.64	11.7–12.2
4–8	1.34	0.53	0.94	0.86	1.04	0.58	11.9–12.8
8–12	1.1	0.46	0.83	0.75	0.94	0.53	12.1–13.4

Age (weeks)	Lysine	Methionine	TSAA	Threonine	Calcium	Available P	Range of ME (MJ kg^{-1})
12–16	0.89	0.4	0.71	0.58	0.86	0.49	12.2–13.6
16–20	0.75	0.36	0.64	0.48	0.78	0.46	12.3–14.0
20–24	0.65	0.32	0.57	0.42	0.74	0.41	12.5–14.0

TSAA, total sulphur amino acids

The optimum density will depend on ingredient costs, primarily the ratio of the cost of protein-rich ingredients to energy-rich ingredients. Fat is particularly important to the latter category, being of higher **energy value** than protein or carbohydrate.

The recommended amino acid contents of diets advised by commercial breeding or feed companies are noticeably higher than indicated by published research work. The latter are obtained from work in small pens and at low stocking dens ities. Commercial recommendations allow for adverse factors affecting **feed intake** that are usually experienced by turkeys in commercial conditions. An example of commercial amino acid recommendations is shown in Table 1. With its rapid growth rate, it is important that the turkey

consumes sufficient minerals for normal bone development. Particularly important are **calcium** and available **phosphorus**. Example levels used are also shown in Table 1.

Turkey nutrition and feeding: breeding stock

It is not necessary for future breeding stock to grow to maximum potential. It is normal to feed a lower-protein diet than for commercial birds during rearing. The nutrient recommendations given by a major primary breeder for turkey parent stock during rearing are shown in Table 2.

Table 2. An example of dietary specifications (g MJ^{-1} ME) for turkey breeding stock diets at different bird ages

Age (weeks)	Protein	Lysine	Methionine	TSAA	Threonine	Calcium	Available P	Range of ME (MJ kg^{-1})
0–4	25–26	1.55	0.56	1.01	0.94	1.45	0.73	11.6
4–6	21–23	1.15	0.45	0.78	0.74	1.35	0.68	11.6
6–10	16–18	0.9	0.38	0.65	0.61	1.25	0.62	11.6
10–16	12–14	0.65	0.29	0.5	0.42	1.1	0.55	11.6

Age (weeks)	Protein	Lysine	Methionine	TSAA	Threonine	Calcium	Available P	Range of ME (MJ kg^{-1})
16–29	10–12	0.45	0.25	0.42	0.29	1	0.5	11.6
29 to end of lay: females	16.5–18.5	0.8	0.4	0.66	0.57	2.8	0.38	11.8
29 to end of lay: males	9–12	0.45	0.25	0.42	0.29	1	0.5	11.6

TSAA, total sulphur amino acids

It is very desirable, for maximum fitness, to grow future breeding males slowly after selection (which normally takes place when they are around 17–20 weeks of age). This is usually achieved by feeding a low-protein, high-energy diet *ad libitum*. However, some organizations will feed controlled quantities of feed to

regulate growth rate.

The turkey breeding hen has a high feed consumption relative to its egg output. For this reason, the calcium content of its diet, which is necessary for shell quality, is lower than in chicken diets. The hen is sensitive to **environmental temperature**. High temperatures reduce feed intake and increase the tendency of the hen to go broody. For this reason, it is normal to feed different turkey breeding diets according to the season of the year and the local **climate**. Higher-density diets are fed when the season or local climate is hot.

The use of drugs to prevent diseases and the addition of **antioxidant**s and other additives will vary according to local circumstances. To minimize the risk of digestive upsets, it is advised that changes in the ingredients used between diets or batches is kept to a minimum. Good pellet quality is important for turkeys. For this reason, when available, it is advised that a minimum of 15% **wheat** is included in all diets. Added fat levels should also be limited to the maximum that will allow good pellets to be produced.

Feeding practices

The day-old turkey (poult) should be given feed in the form of crumbles or pellets not larger than 2 mm. Early feed intake and growth are reduced if day-old turkeys are given feed in meal form but this can be counteracted in part by increasing the nutrient density of the first diet. The age at which the young turkeys move on to pellets depends upon the size of the pellet being presented. If it is 3 mm cut short, i.e. not much longer than 3 mm, it can be

introduced as early as 14 days of age. The larger the pellet, the older the turkeys must be before it is introduced. The optimum changeover age is also influenced by the type of feed on which the day-old poults were started. The changeover from meal to 4.5 mm pellets is difficult and may have to be delayed until 6 weeks of age. The optimum grist profile of the crumbles leaving the feed mill should approximate to 80% retained by 1.7 mm sieve and < 7% smaller than 1.18 mm.

It is important that the feed is easily accessible to the very young turkey. For the first few days, in addition to feed in tubular feeders, feed should be presented either on paper or in trays so that the poults walk on the feed. This encourages them to learn to eat. The tubular feeders should not have a rim higher than a poult's shoulders and the level of the feed should be kept high to enable the poult to see and reach it easily.

It is important that the poult learns to drink soon after arrival at the farm. To encourage early drinking the lights should be bright and often a light bulb is hung near the brooder in order to create a sparkling effect on the water surface, which induces the poult to peck at it and so learn to drink.

It is good practice to turn the lights out 3 h after placement. This prevents overeating, which is thought to be a factor in poults losing their balance and coordination and can result in death from overheating under the brooders. A programme of alternate periods of 3 h light and 3 h dark is sometimes practised for at least the first 36 h to improve survival and early growth rates.

The feed intake of turkeys is sensitive to the pellet quality, i.e.

the percentage of broken pellets and dust. Pellet quality is the responsibility of the feed mill, but it should be matched to the feed delivery system, both to the feed bins and to the feeders within the house. If older turkeys are given feed in meal form, feed intake is markedly reduced, resulting in reduced growth rates and also excessive feed wastage, as the turkeys will flick the meal out while looking for larger particles. The drinkers will also contain more feed material, resulting from the meal sticking to beaks during eating. There is circumstantial evidence that meal feeding increases the number of turkeys suffering from pendulous crops.

As the turkeys grow, the feeders and drinkers should be raised accordingly, with access being at around shoulder height. The type of feeder and **drinker** should enable the turkey to eat or drink standing at right angles to the feeder. The bird should not have to resort to feeding at an acute angle to obtain feed or water. To prevent wastage by the older turkeys, particularly the males, the feed should have a depth of at least 3 cm, and the distance between the feed level and the rim of the feeder should be great enough to prevent the birds from flicking the feed out and wasting it. The minimum feeder and drinker space increases with age and is greater for males than females. As an indication, for large males, one tube feeder or 120 cm of linear trough space is required for 40 males. Less drinker space is required: one bell-type drinker or 100 cm of linear trough space is required for 100 birds. Breeding birds have similar requirements. If breeding males are being fed controlled quantities per day, they require more feeder space, about double that recommended for commercial males.

Specially designed feed **supplement**s for feeding the poults during transit and even in the hatchery have been developed with the aim of reducing early mortality. The use of whole wheat feeding has become more common in recent years and there are several systems for feeding it. One system adds the wheat on top of the **pelleted feed** in the vehicle at the feed mill prior to delivery. By the time it is delivered to the birds, it is mixed with the pellets. The quantity of wheat added is calculated from the feed formulation. If the feed formulation is using 50% wheat, 15% wheat is left in the formulation that is pelleted, to aid pellet quality, and the remaining 35% wheat is added as whole grain. Other systems require two bulk bins: one for the pellets, the other for the wheat. There may be two separate feed bins within the house to allow the birds free choice of wheat or pellets. The better system involves weighing out prescribed quantities of each into a central hopper from which the mixture is delivered into the house. The quantities of wheat can be pre-determined or, in the most sophisticated system, calculated by computer according to the flock weight and the target intake of **lysine** for that weight. Whole-wheat feeding results in better **litter** quality and is reported to give a fitter bird. There is a clear cost saving resulting from the wheat not incurring **milling** charges. (CN)

Turmeric (*Curcuma longa*)

A herbaceous plant, with a height of 1–1.5 m and swollen rhizomes from which the aerial stem emerges. The leaves are without petioles along the stem, but a complete leaf is formed at the end of the stem. The flowers are spiked and enclosed in two bracts and are

yellowish green in colour. Each flower has three sepals. Inside the calyx, there is one fertile stamen and five non-fertile stamens, and around the pistil there is an ovary with three chambers (Zargari, 1997).



Turmeric plant. Photo courtesy of Collen Taugher. Licensed under CC BY 2.0.

Turmeric has an essential **oil** composed of **valeric acid**, caprylic acid, sabinene, cineol, borneol, tourmerol, curcumone and a resinous substance in the rhizome called curcumin ($C_{21}H_{20}O_6$) (Zargari, 1997). Curcumin is present in concentrations of 1% to 5%, and is claimed to have anti-inflammatory properties by acting as an antioxidant, anti-diabetic effects by increasing **insulin** secretion, anti-lipid effects by increasing the **intestinal absorption** of **fatty acid**s, anti-**obesity** effects by reducing **lipogenesis**, and anti-

hypertensive effects (Memarzia *et al*., 2022). In laboratory and domestic animal models, it appears that turmeric oleoresin can increase the expression of genes related to the recruitment of neutrophils, proteins that regulate the production of cytokines, as well as the processing and secretion of antigens. It may be an alternative to antibiotics, but the low bioavailability of curcumin in animals is problematic (Kiczorowska *et al*., 2017). (AS; BH-G; CJCP)

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Turnip (*Brassica rapa*)

A temperate root crop widely grown for feeding cattle and sheep. It may be used from July to December to provide **green feed** when **grass** growth or quality is declining. Root turnips are usually grown in more northerly areas of Europe and take 8 weeks from sowing to feeding, yielding grey-white fleshy tubers, which are very palatable but have laxative properties when fed at high levels. Turnips are usually fed by strip **grazing**. Intakes by cattle should

be restricted to 30–35 kg per day. Turnips can be included in the diets of dairy and beef cattle at < 50% of the total diet, calves at < 20%, lambs at 25% and ewes at 75%. The dry matter (DM) content of turnips is 105 g kg^{-1} and the nutrient composition (g kg^{-1} DM) is **crude protein** 115, **crude fibre** 105, **ether extract** 10, digestible **crude protein** 85, **neutral detergent fibre** 254, **ash** 65, **starch** 7 and **sugar** 550, with MER 12.5 MJ kg^{-1}. (JKM)

Turnover

A concept used to describe dynamic aspects of **metabolism**. It represents the molecular flow or flux of a **metabolite**, and has units of mol min^{-1}. Turnover describes the continuous synthesis and breakdown of an individual metabolite such as acetyl-CoA or of polymers such as proteins, fats and **glycogen**. Measurement of turnover is facilitated by the use of isotopic tracers. The rate of entry of a tracer into a molecular pool such as **glucose** or **protein** can be measured and from this the turnover rate can be calculated and expressed as the fractional turnover rate (% per day). If the size of the pool is also measured, an absolute turnover rate (mol min^{-1}) can be calculated. (NJB)

Twin lamb disease

A form of **ketosis**, so called because ewes in late pregnancy with more than one fetus are particularly susceptible, although it can occur in single-bearing ewes and non-pregnant sheep, including rams. It is due to the toxic effects of **ketone**s produced in excessive quantities during rapid mobilization of **adipose tissue** when food supply is short and **energy requirement**s are high. An affected

animal staggers, collapses and if not treated dies within a few hours. It is also known as snow-**blindness**, because heavy snow prevents grazing and the early symptoms include apparent blindness in affected animals. Treatment is by rapid supply of energy-yielding **substrates**, the most common method being oral administration of **glycerol** by gavage. Over-fat animals are particularly susceptible. (JMF)

Twinning

The production of two offspring by the same female at the same time. Often defined at their birth, but strictly refers to the conception of two individuals when an embryo splits after fertilization, giving rise to identical twins, or when two ova are fertilized. The incidence of twinning in dairy cattle is approximately 2% and in beef cattle approximately 0.5%. Twinning is the norm in goats and is common in sheep, with a large variation between breeds. Twinning is unusual in horses and twin pregnancies tend not to be carried to term. (PJHB)

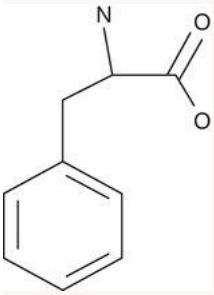
Tyramine

A pressor **amine**, $C_8H_{11}NO$, molecular weight 137, produced from **tyrosine** by L-aromatic amino acid decarboxylase, primarily by bacterial action. It is metabolized in gut tissue and liver by monoamine oxidase to the corresponding **aldehyde** and NH_3. Its biological actions are somewhat similar to those of adrenaline. If monoamine oxidase action is blocked or insufficient, tyramine accumulation in the organism can elevate blood pressure to dangerous levels. Tyramine production is increased during acute

rumen acidosis and tyramine accumulation may play a role in the pathogenesis of the acidosis. (JAM)

Tyrosine

An aromatic amino acid ($HO{\cdot}C_6H_4{\cdot}CH_2{\cdot}CHNH_2{\cdot}COOH$, molecular weight 181.2) found in protein. It is synthesized from **phenylalanine**. The hydroxylation of phenylalanine to form tyrosine is an irreversible reaction. Both phenylalanine and tyrosine are required for **protein synthesis**, but excess phenylalanine can meet the physiological need for tyrosine. Of the total requirement for aromatic amino acids (Phe + Tyr), about half is for phenylalanine and half is for tyrosine. Tyrosine is catabolized primarily through homogentisic acid to fumarate and acetoacetate. A smaller portion of tyrosine is metabolized to thyroxine, **norepinephrine**, **epinephrine** and melanin. (DHB)



See also: Thyroid

U

Ubiquinone
A lipid-soluble electron-transferring agents in the mitochondrial electron transport chain, also known as **coenzyme** Q (CoQ). Ubiquinones have a side-chain containing 6–10 isoprenyl units and can be synthesized in animal tissues. (JS)

Ubiquitin
A highly conserved, low-molecular-weight protein present in bacteria, plants and animal cells. Multiple ubiquitin residues are added to a protein that is destined to be degraded by a very large multi-subunit structure called the proteasome. Proteasomal degradation of proteins is a major pathway for cellular **protein degradation** in health and disease. The proteasome degrades damaged, improperly made or old proteins. It also degrades proteins that are targeted for elimination in response to specific physiological situations. This can include important regulatory molecules such as those that influence expression of specific genes. Proteasomal degradation of proteins is also important in the immune response in order for the body to recognize foreign proteins and make **antibodies** against them. In sepsis the body degrades many proteins, particularly those in **skeletal muscle** using the ubiquitin/proteasome system. Activity of the ubiquitin/proteasome system can be hormonally regulated. For example, during sepsis, cortisol increases the activity of this protein degradation system in skeletal muscle. (RSE)

Ulcer

An open sore accompanied by the disintegration of tissue. Ulceration in the **stomach** occurs when the barrier that normally prevents irritation and autodigestion of the **mucosa** by the gastric secretions is destroyed in consequence of some preliminary alteration of the epithelial surface. **Gastric ulcers** are often observed in pigs and foals and abomasal ulcers in calves and mature cattle appear to be increasing. The incidence of ulcers in the stomach can be attributed to the structure of the feed, stress, infection, or certain medications. In pigs, high stocking density and attributes of the feed (fineness of grinding, **pelleting**, **maize** starch, gelatinization and other, unknown, factors) appear to be the most common causes of stomach ulcers. These are primarily oesophagogastric ulcers, occurring in the pars proventricularis. The presence of the spiral bacterium *Helicobacter heilmanii* may be involved in the development of ulcers.

Ulcers may also lead to perforation of the stomach wall and to peritonitis as well as to haemorrhage into the stomach lumen, which is a common cause of sudden death in grower pigs and sows. (SB)

Further reading

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Ultra-trace elements

Those metallic and non-metallic elements required in the diet in very small amounts (between 50 and 1000 μg kg^{-1}) for **growth**

and **maintenance**. These include **selenium**, **molybdenum** and **iodine**. Other ultra-trace elements with beneficial nutritional effects in some animal species include **nickel**, **boron**, **lithium** and **vanadium**. Dietary elements required in concentrations < 1 mg kg^{-1} diet are generally referred to as **trace element**s. (PGR)

Ultrasound

Sound with frequency above the audible range (20 kHz to 1000 MHz). Ultrasound is widely used in biology and medicine for measuring and imaging body tissues. Simple ultrasound reflectance machines are used to measure the thickness of fat and muscle in meat animals. Ultrasonic scanning is used to provide detailed images of body tissues, especially when X-rays would be damaging. Ultrasound is transmitted into the body by the scanner and the reflected ultrasound waves from the internal tissues are detected and displayed as a real-time image on a screen. Ultrasound has a number of other applications in industry, biology and medicine, based on its diverse effects on gases, liquids and solids. (SPL)

Undegradable dietary protein (UDP)

Protein that is resistant to, or escapes, **hydrolysis** and degradation by **rumen microorganism**s. In ruminants, **metabolizable protein** (MP) requirements are met by a combination of effective rumen degradable protein (ERDP), which microorganisms use to produce microbial **crude protein** (MCP), and UDP. MCP synthesis alone may not be sufficient to meet the MP requirements of productive animals, and in such situations UDP levels must be sufficient to make up the requirement. UDP can be maximized by

including protein food sources resistant to microbial degradation, such as fish meal or artificially protected **soybean**. However, the ERDP (and thus UDP) of feeds in the rumen is not constant. ERDP is affected by the rate at which feed passes through the rumen. Increasing the **feed intake** by increasing the proportion of highly digestible food increases the rate at which it passes through the rumen. This reduces the length of exposure of the food to rumen microorganisms and therefore its degree of **digestion**.

For the most effective use of protein-containing feeds there is a need to classify feedstuffs by the rumen degradability of their protein, but there are no simple reliable methods for measuring this. It can be determined directly *in vivo* in fistulated animals, or estimated by incubating test samples of food in dacron bags within the rumen (the ***in sacco*** method). *In vitro* methods using isolated enzymes, microorganisms, or infrared reflectance spectroscopy are being developed. (JKM)

Underfeeding:
see Undernutrition

Undernutrition
Deficiencies or imbalances in the dietary intakes of energy and nutrients (amino acids, carbohydrates, fatty acids, vitamins, minerals and water). During the period of undernutrition, animals mobilize **body fat** and **protein** to meet their requirements for energy and amino acids. In certain regions of the world, grazing animals without **feed supplement**s can experience undernutrition during the winter or **dry season**s when **forage** is

limited and has low nutritive quality. Depending on their biology and **metabolism**, underfeeding may be imposed on some species during a certain phase of production, such as gilts or **sows** during pregnancy to improve embryonic survival and **lactation** performance. Maternal and child undernutrition remain a major health concern in developing nations, but undernutrition may also occur in subpopulations (for example: the elderly; pregnant women with severe **vomiting**; and individuals with burns and infections) in both developed and developing nations. Severe undernutrition results in wasting, **stunting**, underweight, reduced productivity and characteristic metabolic diseases or disorders. In humans, **marasmus** and kwashiorkor are caused primarily by a severe deficiency of dietary energy or protein, respectively. Undernutrition contributes to about 50% of all annual deaths in children under 5 years of age worldwide. Long-term undernutrition and inanition lead to **starvation** and eventual death. (GW)

Unsaturated fatty acids
Unsaturated fatty acids with one or more double bonds C=C making up the **fatty acid** chain. Unsaturated fatty acids can be monounsaturated (having one double bond) such as **oleic acid** (18:1) or polyunsaturated (having two or more double bonds) such as **arachidonic acid** (20:4). (NJB)

Uptake:
see Absorption

Uracil

A **pyrimidine** base, $C_4H_4N_2O_2$, found in RNA as the nucleoside uridine. It is not found in DNA. (NJB)

Urea

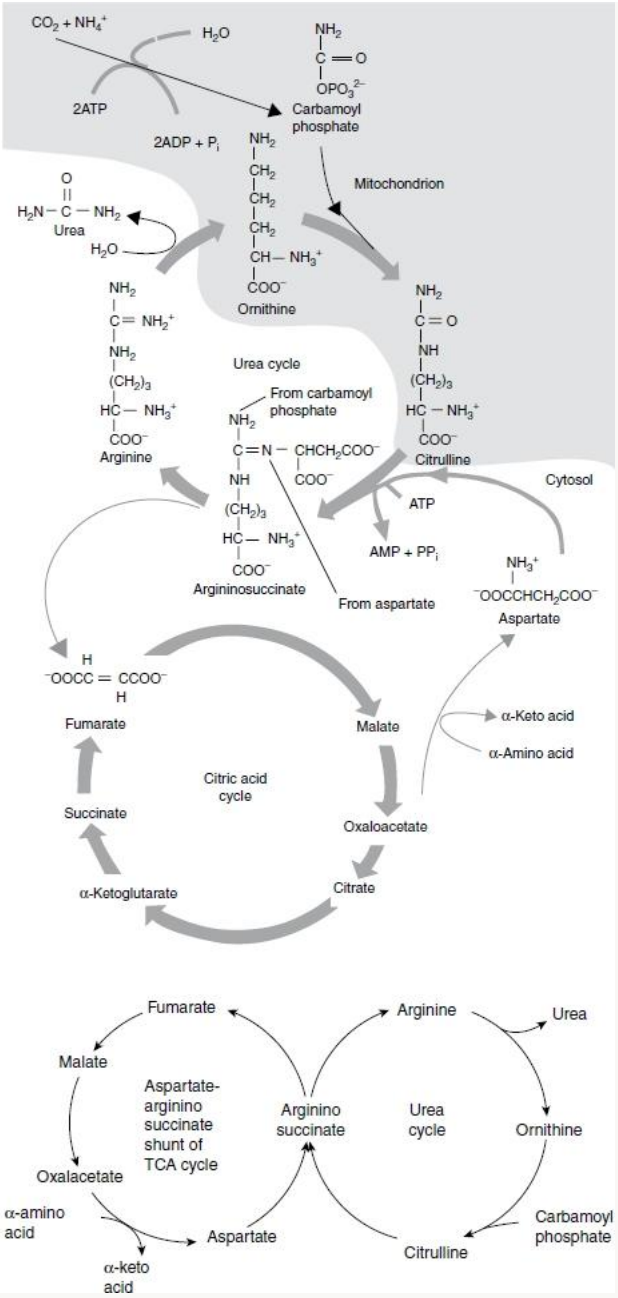
A nitrogenous end-product of amino acid **catabolism**, $CO{\cdot}(NH_2)_2$, excreted in **urine**. Variable proportions of the total production of urea are excreted into the intestinal tract in both ruminants and non-ruminants. In **ruminant animal**s, urea secreted into the rumen via **saliva** is used as a **nitrogen** source by rumen bacteria; and under conditions of limited dietary nitrogen intake it can add substantially to the nitrogen economy of the animal. In some cases the microbial nitrogen outflow from the rumen can exceed the dietary nitrogen intake. In non-ruminants, most of the **amino acid** synthesis by intestinal microflora occurs distal to the site of amino acid **absorption** and so **microbial protein** is not a major source of nitrogen for body functions, because most is excreted in the faeces. Urea is synthesized primarily in the mammalian liver and, to a much lesser extent, in **enterocyte**s of post-weaning mammals by enzymes of the **urea cycle**: the immediate nitrogen precursors are ammonium and aspartate. This aspartate is a **substrate** for argininosuccinate synthase, and is ultimately derived from ammonium and **oxaloacetate** via **glutamate dehydrogenase** and glutamate-oxaloacetate transaminase. (NJB; GW)

Reference

Wu, G. (1995) Urea synthesis in enterocytes of developing pigs. *Biochemical Journal* 312, 717–723.

Urea cycle

A sequence of reactions in which 1 mol **ammonia** (NH_3) and 1 mol HCO_3^- (derived from CO_2 and H_2O) are converted into 1 mol **urea** in the liver of all mammals. This pathway requires carbamoylphosphate synthase-I (CPS-I), **ornithine** carbamoyltransferase (OCT), argininosuccinate synthase (ASS), argininosuccinate lyase (ASL) and **arginase**, as well as **adenosine triphosphate** (ATP), **bicarbonate** and *N*-acetylglutamate (NAG) (synthesized from **glutamate** and acetyl-CoA by NAG synthase). CPS-I, OCT and NAG synthase localize in the mitochondrion to generate **citrulline** (a neutral **amino acid**) from ammonia, bicarbonate and ornithine, whereas ASS, ASL and arginase are cytosolic enzymes to convert citrulline into **arginine** and then urea plus ornithine. Ammonia **detoxification** via urea synthesis requires large amounts of ATP (4 mol ATP mol^{-1} urea), and is essential to survival, growth and development.



The urea cycle.

The relationship of the urea cycle to the TCA cycle.

The first step in urea biosynthesis occurs in the matrix of the mitochondrion. In this step, 1 mol ammonia combines with 1 mol HCO_3^- to form carbamyl phosphate. This reaction is carried out by CPS-I. The next step is the combination of carbamyl phosphate with ornithine to form citrulline. This step is carried out by the enzyme OCT. The second transport requirement for urea biosynthesis is the entry of ornithine into the mitochondrial matrix, followed by its conversion into citrulline and the exit of citrulline

from the matrix into the cytosol. The next step in the cycle is the synthesis of argininosuccinate from citrulline and aspartate by ASS, which utilizes two ATP equivalents and the second **nitrogen** for urea comes from aspartate. This aspartate is eventually formed from ammonia and **oxaloacetate** via **glutamate dehydrogenase** and aspartate transaminase. The third reaction of the cycle is carried out by ASL, which cleaves argininosuccinate to arginine and fumarate. Fumarate is reduced to **malate**, which enters the mitochondrion via the malate shuttle. Within the mitochondrion, malate along with glutamate is converted into aspartate for the synthesis of the next molecule of urea. The movement of aspartate out of the mitochondrial matrix occurs via the transporter, citrin. To complete the cycle, arginine is cleaved by arginase to yield urea and ornithine. Once ornithine is transported into the mitochondrial matrix via ornithine carrier 1, ornithine can again be used to form citrulline.

$NH_3 + HCO_3^- + 2ATP \rightarrow$ carbamyl phosphate + 2ADP

Carbamyl phosphate + ornithine → citrulline

Citrulline + ATP + aspartate → argininosuccinate + AMP + PPi

Argininosuccinate → arginine + fumarate

Arginine → urea + ornithine

Enterocytes of the **small intestine** in post-**weaning** mammals, as well as colonocytes and ruminal epithelial cells, also have a functional urea cycle to generate urea from extracellular and intra-mitochondrially derived ammonia. Urea synthesis in the small intestine is the first line of defence against the potential toxicity of ammonia that is: (i) produced by extensive intestinal degradation

of **glutamine** (a major fuel for enterocytes); and (ii) derived from the diet and luminal microorganisms. Interestingly, some **fish** synthesize urea from ammonia in their **skeletal muscles** as a mechanism for consuming bicarbonate and reducing body pH if the fish live in an alkaline environment, but directly excrete ammonia if the fish live in fresh water.

In ruminants, urea in the circulation enters the lumen of the rumen through **saliva** and uptake from the arterial **blood** across rumen epithelium via facilitative urea transporters. Within the rumen, **urease** (a bacterial enzyme) rapidly hydrolyses urea to form ammonia and CO_2. A large proportion of the urea-derived ammonia is utilized for synthesis of free amino acids, small peptides and proteins by ruminal bacteria, archaea and fungi, whereas **protozoa** consume those microbes to obtain amino acids. These nitrogenous products of ammonia flow into the lumen of the **abomasum** and thence into the lumen of the small intestine for digestion and absorption. Once absorbed, free amino acids and small **peptide**-derived amino acids are used for **protein synthesis** or they undergo **metabolism** in tissues, and their nitrogen is ultimately transformed into urea in the liver. Some of this urea nitrogen is again recycled into the **gastrointestinal tract** via saliva and from the arterial blood into the rumen, as described previously. The proportion of urea transferred from the liver to the gastrointestinal tract ranges from 10% to 80% in ruminants and is affected by species and dietary protein content. For example, in ewe lambs fed diets containing 9.7%, 17.8% and 25.8% **crude protein**, 75%, 41% and 30% of the urea produced in

the liver is reutilized each day, respectively, via urea recycling. The urea recycling is an evolutionary advantage in ruminant nutrition and physiology, particularly when ruminants consume relatively low-protein (e.g. 10% crude protein) diets. Thus, urea (representing 15–25% of crude protein in diets) has been fed to ruminants as a **non-protein nitrogen supplement** for more than 100 years. Efficacy and safety of dietary supplementation with urea in the diets of cattle, sheep and goats depend on: (i) the dosage (usually ≤ 1% in a concentrate-rich diet; ≤ 2% in low-crude protein hay) (for cattle in 'store' condition about 30 g urea 100 kg^{-1} liveweight in a single dose can be toxic) and frequency; (ii) the percentages of dietary carbohydrates and crude protein, as well as their digestibilities in the rumen; and (iii) an adequate supply of **phosphorus**, **sulphur** and trace minerals.

When good or medium-quality **hay** is not available, low-quality **roughages** (such as wheat, oat, barley and rice straw; corn stover; and very mature, low-quality grass hay (≤ 6% crude protein and ≤ 48% TDN, dry matter basis)) can be ammoniated for feeding ruminants. The sources of ammonia may be: (i) urea, with the ratios by weight (g) among straw, water and urea being 100:40:4.5; (ii) ammonium bicarbonate, with the ratios by weight (g) among straw, ammonium bicarbonate and water being 100:12:40; (iii) urea plus lime, with the ratios by weight (g) among straw, urea, lime and water being 100:2.5:8:40; and (iv) anhydrous ammonia, with the ratio by weight (g, air-dry basis) of anhydrous ammonia to straw being 3:100. Ammoniating low-quality roughages can increase their digestibility in the rumen of ruminants (e.g. cattle) by

10–30%, and can enhance their **feed intake** by 15–20%. In addition, the ammoniation can augment dietary nitrogen content by 100–200%, which can beneficially boost **microbial protein synthesis** in the rumen. (GW; NJB)

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Urease

An enzyme that catalyses the conversion of **urea** to ammonium and **bicarbonate** ($CH_4N_2O + 2H_2O + H^+ \rightarrow 2NH_4^+ + HCO_3^-$). It is found in **legume** seeds such as **soybean** and **jackbean**. Urease is not produced by higher animals but is produced by certain intestinal bacteria and is found throughout the digestive tract. Microbial urease is critical to the recycling of **nitrogen**, especially in ruminants, because it makes urea-N available for microbial use. (NJB)

Uric acid

A nitrogenous end-product of **amino acid** and **purine**

catabolism, $C_5H_4N_4O_3$. It is the main end-product of **nitrogen metabolism** in birds, in which it is excreted in combination with the faeces, but is also found in the urine of mammals. In the production of uric acid, one molecule of **glycine** provides two carbon atoms (C) and one nitrogen atom (N), aspartate one N, **glutamine** two N, **carbon dioxide** one C and the **folate** system two C. Because this form of nitrogen excretion draws on the folate one-carbon system it increases the demand for folate carbon, leading to a potential shortage of methyl groups for other processes such as **nucleic acid** biosynthesis. (NJB)

Urinary tract diseases

Cystitis is an inflammatory condition of the bladder which is usually caused by a bacterial infection. It is accompanied by frequent, painful urination. It is commonly associated with calculi within the bladder and also with stagnation of the urine so that bacteria ascending via the urethra can invade damaged mucosa. The urine may contain blood. Rupture of the bladder occurs most commonly in castrated male ruminants because of obstruction of the urethra by calculi (*see* Urolithiasis). The diameter of the urethra may be reduced by a high level of dietary **oestrogen**s, for example from grazing subterranean clover. After rupture, abdominal distension soon becomes apparent and death follows within 2–3 days. (ADC)

Urine

A pale yellow fluid derived from **blood** filtered by the kidney. Filtration takes place in the glomerulus of the kidney nephron. The

glomerular filtrate passes through the nephron to the collecting duct and is then stored in the bladder until it is discharged. The volume of urine produced per day is dependent on the amount of fluid consumed and the rate of evaporative water loss. With a constant fluid intake, more evaporative water loss results in less urine being produced. Urine is a complex fluid, its composition changing with the metabolic state of the animal. It contains **nitrogenous compound**s such as **protein**, **urea**, ammonium, **creatine**, **creatinine**, uric acid, **allantoin** and **amino acid**s. **Ketone** bodies, **citric acid** and volatiles such as phenols are also found, as well as **sulphate**, carbonate and the mineral elements **chloride**, **potassium**, **sodium**, **calcium**, **copper**, **magnesium**, **iron**, etc. Methylated and sulphated **detoxification** products are also excreted in the urine. The pH of urine can range from acid (pH 4–5) to basic (pH 8–9), depending on the diet and other factors. (NJB)

Urolithiasis

The formation of urinary calculi. **Urine** is normally supersaturated with regard to **calcium**, **magnesium** and phosphate and, in some species, also **oxalate** and urate. The **solubility** of calcium and magnesium is increased by chelation with **organic acid**s (e.g. citrate) but the potential for this chelation to take place decreases in acid urine. There are specific inhibitors of crystallization in urine, such as pyrophosphate. The latter is increased during increased dietary intake of orthophosphate but its urinary concentration is insufficient to account for all the inhibition of crystallization noted in normal urine. The identity of the other

inhibitors is unknown. Renal stones commonly consist of **calcium phosphate**, calcium oxalate and **magnesium** ammonium phosphate but uric acid and other crystals may also be found. Urinary infection with an organism capable of hydrolysing **urea** (e.g. *Proteus* spp.) favours the formation of an alkaline urine and crystals of magnesium ammonium phosphate. In some dry areas (e.g. South Australia), renal calculi of **silica** may be formed by grazing ruminants as a result of a low intake of water and the absorption of micro crystals of silica from the intestinal contents. Excessive urinary excretion of calcium and phosphate in primary **hyperparathyroidism** is associated with the incidence of renal calculi containing calcium phosphate. In housed lambs fed a high-concentrate diet at more than 1.5% body weight, urolithiasis begins. This is especially true when the diet is high in magnesium. The ingestion of relatively large quantities of **oxalate** and a high dietary intake of phosphate are also factors that may be involved in the incidence of urolithiasis. Depressed water intake, resulting in increased concentrations of the precipitating **salts** in the urine, is a major underlying cause of the condition. Another is the formation of a nucleating centre of desquamated epithelial cells which favours the deposition of crystals about itself. A deficiency of **vitamin A** or an excess of **oestrogen** may both exacerbate this phenomenon. (ADC)

Uronans

Polysaccharides in which the main **sugar** residue is **uronic acid**. The primary uronic acids are **glucuronic acid** in animals and **galacturonic acid** in plants. (JAM)

See also: Carbohydrates; Dietary fibre; Galactouronans; Pectic substances; Rhamnogalactouronans

Uronic acids

The most important type of acidic sugars, occurring almost exclusively as **hexuronic acid**s. **Oxidation** of the terminal alcohol group or non-reducing end of a **sugar** gives rise to a uronic acid. In biosynthetic sequences, hexuronic acids are intermediates in the conversion of hexoses into **pentoses** via oxidation and **decarboxylation**. In animal **metabolism**, D-**glucuronic acid** is conjugated with a wide variety of compounds (such as steroids, phenols, aromatic carboxylic acids and pharmaceutical agents), increasing their **solubility** and thus promoting their urinary excretion. D-Glucuronic and D-**galacturonic acid**s are also found in plant **gums** and bacterial cell walls. As the major sugar residue in **uronan**s and **pectic substance**s, galacturonic acid is widely distributed in the plant world, functioning as a **structural polysaccharide**, frequently in close association with **cellulose**, and as a **storage polysaccharide**. D-Mannuronic and L-glucoronic acids are found in **algae**; D-glucuronic acid is a component of proteoglycans; and L-iduronic acids are components of two of the glycosaminoglycans, dermatan **sulphate** and heparin. D-Glucuronic acid is also a component of heparin. Uronic acids are difficult to isolate from natural sources; the strong acidic conditions necessary to break glycosidic linkages cause decarboxylation and elimination reactions. (JAM)

See also: Carbohydrates; Dietary fibre; Galactouronans

Urophagia
Otherwise known as **urine** drinking. This is most commonly displayed in livestock, which may imbibe their own urine when they are short of elements in their diet, such as **sodium**. Males taste the urine of cows they suspect of being in oestrus. Humans have imbibed human or livestock urine for thousands of years, especially in India, where cow urine is believed to have medicinal properties. There is no scientific evidence, but the **urea** content may act as a diuretic and the minerals, mainly **sodium chloride**, may also be beneficial. Urine is sterile on leaving the body but may be quickly contaminated thereafter. (CJCP)

Utilization, energy:
see Energy utilization

Utilization, protein:
see Protein utilization

V

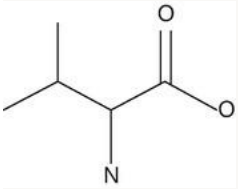
Valeric acid
Pentanoic acid, an odd-chain saturated **short-chain fatty acid**,

$CH_3 \cdot CH_2 \cdot CH_2 \cdot CH_2 \cdot COOH$, molecular weight 102.13. It may be produced by **fermentation** during **digestion** or from partial degradation of longer **odd-chain fatty acids**. (NJB)

Valine

An essential amino acid $(CH_3)_2 \cdot CH \cdot CHNH_2 \cdot COOH$, molecular weight 117.2, found in protein. Valine is one of the three **branched-chain amino acids** (with **leucine** and **isoleucine**). It is purely gluconeogenic, yielding **propionate** as an end-product of **catabolism**. The first two enzymatic reactions involved in valine catabolism use the same enzymes that catabolize leucine and isoleucine. The first reaction involves **transamination**, primarily in muscle. This produces the keto analogue, ketoisovaleric acid. This is then oxidatively decarboxylated, primarily in liver, by **branched-chain keto acid dehydrogenase** to the CoA derivative.

After **lysine**, which is first-limiting in low-protein **maize–soybean** meal diets, valine is among the next-limiting amino acids (along with one or more of **tryptophan**, threonine and **methionine**) for young pigs, chickens and turkeys in such diets. (DHB)



Vanadium (V)

A mineral element that has not yet been accepted as an essential nutrient or a requirement established for any avian or mammalian

species but, because of its involvement in **metabolism**, is classified as one of the 'occasionally beneficial elements' (Suttle, 2010). It is highly toxic and the maximal recommended dietary concentration for many species of animals is around 20 mg kg^{-1}. As a result, it has been studied mainly for its toxicological and pharmacological properties.

Vanadium exists in nature in four valency states; +2, +3, +4 and +5, and exists in biological systems primarily in the metavanadate (VO_3^-) or the orthovanadate ($(HO)_2VO_2^-$) configurations. As outlined in the review by Baloš *et al*. (2017), it is an essential element in various enzymes in algae, bacteria, fungi and lichens, but there are conflicting reports as to its essentiality for animals and data on natural vanadium deficiency are still scarce. Deficiency was first described in rats, deprivation tending to decrease **growth** while increasing **thyroid** weight. Diets low in **iodine** may amplify responses to dietary vanadium and those high in **goitrogen**s may have similar effects. Poor growth and reduced development of feathers of the tail and wing were reported in chickens fed diets containing less than 10 μg V kg^{-1}. Other reported effects of a low dietary vanadium content are a reduced level of **iron** in **blood** and abnormal bone development. As reported by Suttle (2010), female goats given a diet containing <10 μg V kg^{-1} (DM basis) had a higher **abortion** rate, lower **milk** production and fewer offspring than control goats given a diet with 2 mg V kg^{-1} DM.

Sources

Vanadium is abundant in soils, particularly in the finer clay

fractions (65–200 mg V kg^{-1} DM), but only a small fraction (< 10%) is extractable and levels in pasture and crops are usually low (< 0.1 mg kg^{-1} DM) (Suttle, 2010). Natural foodstuffs contain vanadium mainly in the form of vanadyl (VO^{2+}). Since grazing animals cannot avoid consuming soil when they forage and contamination of herbage varies from approximately 2% in summer to 10% or more of DM intake in winter, **soil ingestion** is a major source of vanadium intake for pastured animals. Free-range hens may also ingest significant amounts of soil vanadium. It is possible that levels in the environment may be increasing due to the combustion of vanadium-rich **oils** and use of vanadium-rich dietary phosphate **supplement**s, which contain on average 135 mg V kg^{-1} DM and as much as 185 mg V kg^{-1} DM. In Minnesota, however, the prolonged use of phosphatic fertilizers has not increased the V content of soils or **maize** crops (Suttle, 2010).

Metabolism

Animals generally absorb very little vanadium; for instance, sheep absorb only 1.6% of their dietary vanadium, whether the diet contains 2.6 or 202.6 mg V kg^{-1} DM (Suttle, 2010). Simulated soil-ingestion studies with sheep have shown that the ingestion of soil containing 4.9 or 8.3 mg V kg^{-1} DM for 41 days raised kidney vanadium from undetectable levels (< 0.2 mg kg^{-1} DM) to means of 0.65 or 1.85 mg kg^{-1} DM. Ingested soil vanadium is therefore partially absorbed. Reported concentrations of vanadium in animal organs and tissues range from 10 to 200 μg kg^{-1} fresh sample (muscle to testes, respectively). Vanadium content in the chicken

ranges between 0.018–0.038 mg kg^{-1} in liver, 0.101–0.180 mg kg^{-1} in kidney, 1.3–6.3 mg kg^{-1} in bone and 0.002–0.003 mg kg^{-1} in egg yolk (DM basis) (Baloš *et al.*, 2017). The low concentration in animal tissue may be explained by the fact that both the natural intake of vanadium and the rate of absorption are very low. Intravenously administered dioxo-vanadium is metabolized differently than the orally dosed element, raising questions as to the physiological significance of *in vitro* studies with vanadium. The reactivity of vanadium depends on the wide range of **oxidation** states that the element can enter; movements between the tetravalent and pentavalent state are the major contributor to its reduction–oxidation potential in mammalian tissues. Vanadium is readily transported across membranes by non-specific anion channels and binds to proteins such as **transferrin** and **lactoferrin**. It can substitute for phosphate, mimicking the effects of cyclic AMP. As peroxo-vanadate, vanadium influences **free-radical** generation and mimics **insulin** (Suttle, 2010). This latter effect has led to vanadium being proposed as a **supplement** in the management of human type 2 **diabetes**. In addition, certain vanadium compounds have been shown to be potentially effective against malign tumours including cancer, endemic tropical diseases (e.g. trypanosomiasis, leishmaniasis and amoebiasis), bacterial infections (tuberculosis and pneumonia) and HIV infections (Rehder, 2016). So far, no vanadium compounds appear to have been approved as pharmaceuticals for clinical use in relation to these diseases.

Toxicity

Species vary widely in their susceptibility to vanadium toxicity, with poultry the most and sheep the least susceptible of farmed species (Suttle, 2010). The maximum tolerable level for poultry has been set at 10 μg V kg^{-1} diet (NRC, 2005), and the toxicity level at 100–800 mg kg^{-1} diet. Other studies suggest that poultry can tolerate up to 25 mg V kg^{-1} diet and possibly up to 50 mg V kg^{-1} diet without significant decreases in weight gain and health (Baloš *et al*., 2017). Albumen quality in eggs is particularly sensitive to vanadium supplementation, with as little as 6–7 mg kg^{-1} DM added as **dicalcium phosphate** lowering egg albumen content. Hen body weight and **egg production** were both reduced during 140 days on a diet containing 50 mg added vanadium kg^{-1} as **calcium** orthovanadate, while supplementation with 100 mg kg^{-1} DM caused up to 56% mortality without specific pathology. Toxicity has been investigated in relation to its presence in phosphates at high concentrations in the form of calcium orthovanadate (Baloš *et al*., 2017). Toxicity tends to increase as the valency of the vanadium source increases, depending on the chemical form of the vanadium source, the period of dosing, the length of exposure and the size of the dose. Bones and kidneys are major target organs for vanadium, with an increased content in the liver. **Enzyme** inhibition and cell damage are considered the most likely mechanism of vanadium toxicity. The vanadium cation competes with ions of Ca, Mn, Zn and Fe for ligand-binding sites and interacts with phosphate ions in a range of metabolic processes. Growth suppression, mortality, enteritis and cystitis have been recorded in weanling pigs given a

diet with 200 mg V kg^{-1} DM for 10 weeks, but lambs tolerated a dietary level of 200 mg added vanadium kg^{-1} for at least 84 days; higher levels (400 and 800 mg kg^{-1} DM) caused immediate **diarrhoea** and **anorexia**. Dietary factors such as high **iron**, **sulphur** amino acid and **vitamin C** concentrations reduce the toxicity of vanadium, and ruminants may be protected by the reduction of vanadium in the rumen. The World Health Organization (WHO, 2006) classified vanadium pentoxide (V_2O_5) as a possible **carcinogen** for humans, based on data from animals. (RB; PGR)

See also: Ultra-trace elements

References and further reading

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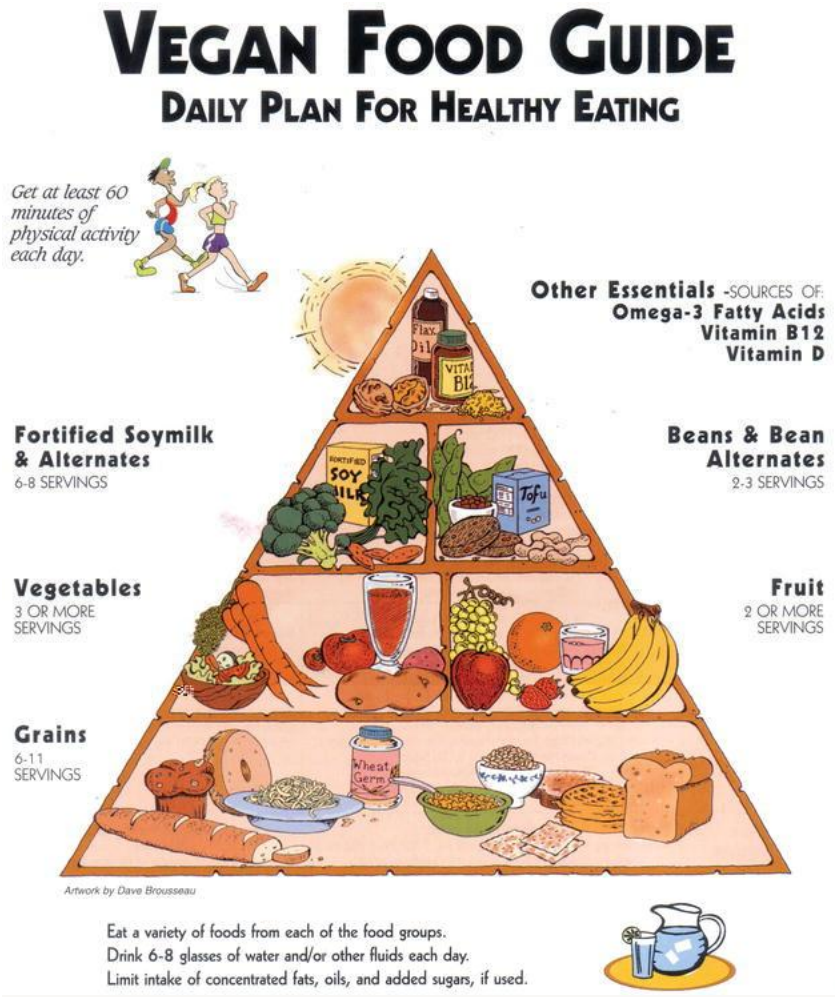
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Vasoactive intestinal peptide (VIP)

A 28 amino acid polypeptide that is released from nerve endings, primarily throughout the **gastrointestinal tract**. This neurocrine substance acts through a cyclic-adenosine monophosphate (cAMP)-mediated intracellular pathway to cause the relaxation of **smooth muscle** in both intestine and blood vessels. VIP regulates intestinal **motility** and **blood flow**, and it may also stimulate pancreatic and intestinal secretions. (GG)

Veal calves:
see Calf

Vegan
An increasingly popular philosophy, at least in the Western world, which includes the avoidance by humans (but also some other animals, especially companion animals) of consuming (or otherwise using) all products derived wholly or in part from animals, including meat (from terrestrial and aquatic animals), dairy, eggs, honey and leather. The term was initiated by The Vegan Society in 1944. Also known as strict **vegetarian**. (CJCP)



The Vegan Food Guide. Courtesy of Becky Striepe. Licensed under CC BY-NC-ND 2.0.

Vegan dog and cat food

Cats and dogs evolved from carnivorous species, although dogs are now considered omnivores. However, many companion animal guardians are increasingly concerned about the health implications of diets rich in meat, milk or eggs (Kassam and Kassam, 2022), the environmental impacts of **meat production** (Crippa *et al.*, 2021; Xu *et al.*, 2021), the **welfare** of 'food' animals (Knight *et al.*, 2022) and global food security and food justice (Knight, 2022). Hence, the vegan food sector is rapidly growing. Surveys have indicated that around 35% (Dodd *et al.*, 2021) to 46% (Knight and Satchell, 2021) of those feeding conventional or raw meat-based pet foods

would be interested in feeding an alternative diet. Accordingly, manufacturers are rapidly developing vegan pet foods. Nutritionally complete vegan pet foods use a combination of plant, mineral and synthetic ingredients to ensure all nutritional needs of the target species are met. Attention must be given to ensuring adequate quantities of some amino acids (**taurine**, **carnitine**, **methionine**, **lysine** and **tryptophan**), **vitamins** (e.g. vitamins A, B_3, B_9 and B_{12}), minerals (e.g. **calcium**, **iron**, **zinc** and **copper**) and certain **fats** (Knight and Leitsburger, 2016).

Can vegan cats and dogs be healthy? In the first large-scale study of such animals, 187 of 1026 cat guardians were feeding plant-based diets (Dodd *et al*., 2021). These cats were more commonly reported to be in very good health and were reported to have fewer gastrointestinal or **liver** disorders, and more ideal **body condition** scores (usually this indicates reduced body weight, as excessive body weight is one of the most common health problems among cats). In a survey of 1369 cats fed meat-based (1242) or vegan diets (127), the proportions of cats considered unwell were 42% (meat-based diets) and 37% (vegan diets) (Knight, 2022). Among the unwell cats, the average number of cases of disorder per cat were 1.61 (meat-based diets) and 1.30 (vegan diets). Again, the healthiest dietary choices for cats appear to be nutritionally sound vegan diets.

With respect to the dogs, Knight *et al*. (2022) examined the health outcomes of 2536 dogs fed conventional meat (1370), raw meat (830) or vegan diets (336). The proportion of dogs considered unwell were 49% (conventional meat), 43% (raw meat) and 36%

(vegan). The inference was that conventional meat diets produced health outcomes inferior to those produced by the other two diets. Although there was limited evidence of better general health indicators for dogs fed raw meat diets, these do confer significant risks of pathogens. Hence, based on this study, the healthiest and least hazardous dietary choices for dogs appear to be nutritionally sound vegan diets.

The evidence from these large-scale studies, pooled with evidence from smaller studies reporting similar outcomes (Wakefield *et al*., 2006; Brown *et al*., 2009; Semp, 2014) indicates that dogs and cats maintained on nutritionally sound vegan diets generally experience health as good as, and in some respects better than, that of those maintained on meat-based diets. This illustrates that neither dogs nor cats have biological requirements for particular ingredients, including meat. Instead, they have biological requirements for specific nutrients. Provided that diets are formulated to be nutritionally complete and balanced, and palatable to companion animals, with sufficient bioavailability so that ingredients are adequately digestible and absorbable, animals should thrive on such diets. This is supported by the studies conducted to date, with respect to nutritionally sound vegan diets. However, such diets must be nutritionally complete and balanced. Hence, a complete commercial diet is normally recommended by experts in the field. (AKn)

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Vegetarian

Vegetarians do not usually eat **meat** or offal from terrestrial or aquatic animals. They do often consume some animal products, notably dairy and **eggs**, but not those from animals that have been killed. Most Hindus consider themselves to be vegetarian and follow a lacto-vegetarian diet, avoiding eggs. Some in south-west India eat **fish**. Those following a **vegan** diet may also refer to themselves as strict vegetarians. (CJCP)

Verbascose

An **oligosaccharide** of five **sugar** residues, three **galactose**s and one **glucose**, all 1→6-linked, and **fructose**, linked to the glucose via 1→2 linkage, molecular weight 828. Verbascose is present in small amounts in the tubers, rhizomes and seeds of certain plants, where its accumulation during maturation and disappearance during **germination** suggests it is a reserve **carbohydrate**. The classic source is mullein (*Verbascum thapsus*) root. (JAM)

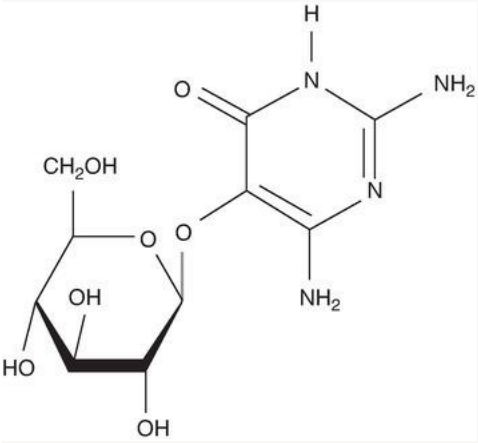
Very low-density lipoprotein (VLDL)

A plasma **triacylglycerol**-rich (> 60%) **lipoprotein** of density <

1.006 synthesized in the liver of non-ruminants. The predominant apoprotein is apoB100. (DLP)

Vicine

A gluco-**alkaloid** ($C_{10}H_{16}N_4O_7$, molecular weight 304) isolated from the seed of *Vicia sativa* and *V. faba*, both **legume** vetches. **Poisoning** in livestock has been reported from these plants as well as *V. villosa* (hairy vetch). Ingestion of hairy vetch seeds caused death in chicken and turkey poults. In a survey of 23 herds of cattle, ingestion of hairy vetch apparently caused dermatitis, conjunctivitis and **diarrhoea**, with 6–8% morbidity and 50% mortality among those affected. **Abortion** was reported occasionally among the herds affected. (KEP)



Villi

Finger-like projections (sing. villus) of the epithelial cell layer of the **small intestine** which increase the surface area for **absorption** tenfold. (SB)

See also: Gastrointestinal tract

Vinasse

The residue from alcoholic **fermentation**s, especially those based

on beet **sugar**. A rich source of **phosphorus**, vinasse is used in livestock feeding and as a fertilizer. (MFF)

Viscosity
The frictional resistance of a fluid, which reduces its ability to flow freely. Certain **non-starch polysaccharide**s (NSPs), such as β-**glucans** from **barley**, often increase the viscosity of **digesta** through the **water-holding capacity** of their large hydrophilic molecules. These NSPs can reduce **nutrient absorption**, increase water consumption and alter the **gastrointestinal microflora**. They also cause wet and sticky excreta and **litter**, which may increase the incidence of ill health, dirty animals and dirty products (such as eggs). (TA)

Vitamin
Complex **organic compound** found in foods and required by animals. Vitamins include the **fat-soluble vitamins**, A, D, E and K, the **water-soluble vitamin C** and the eight **B-complex vitamins**: **thiamine**, **riboflavin**, **pyridoxine**, **niacin**, folic acid, **biotin**, **pantothenic acid** and vitamin B_{12}. In response to sunlight, the skin of many mammals (including humans, pigs, rats and ruminants) and birds (including chickens) can synthesis **vitamin D_3**, but dogs and cats are unable to perform such a cutaneous synthesis of vitamin D_3. In contrast to many animals (including humans, pigs, rats, ruminants and chickens), cats cannot synthesize **niacin** from **tryptophan**. Vitamins are intimately involved as **coenzyme**s or co-**substrates** or they facilitate reactions in cellular **metabolism**. A deficiency of any vitamin over

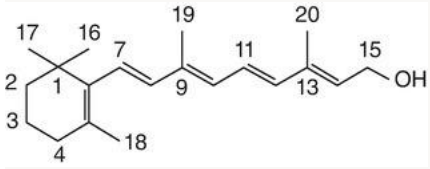
sufficient time results in somewhat repeatable symptoms and may lead to death. Not all foods have all vitamins and not all foods have the same concentration of vitamins in the edible portion of the food. With the exception of vitamin C, all vitamins are required in the diets of non-ruminant animals. Primates, including humans, and guinea pigs and a few other animals require a dietary source of vitamin C. Because of fermentative **digestion**, the microorganisms in the rumen of **ruminant animal**s produce the B vitamins (including vitamin B_{12} in the presence of **cobalt**), and therefore little attention is given to the B vitamin content of their diets. The fat-soluble vitamins, however, must be supplied. Vitamins are also produced commercially and are commonly added to mixed diets for all farm animals. (NJB; GW)

Vitamin A

Descriptor for all compounds (other than **carotenoid**s) that possess the biological activity of all-*trans* retinol. Retinol supports all known functions of the vitamin. The term provitamin A is used to describe carotenoids that give rise to vitamin A activity. Quantitatively, the most important carotenoid is all-*trans*-β-carotene. Most farm animals obtain their vitamin A in the form of carotenoids, unless their diets are supplemented artificially. The Committee on Animal Nutrition of the National Academy of Sciences–National Research Council periodically updates the requirements for provitamin A carotenoids and vitamin A for most domestic animals (available at http://www.nap.edu/index.html).

Retinol consists of a non-aromatic ring structure, an isoprenoid side-chain and an alcohol functional end group (see figure). Retinol

exists predominantly in the all-*trans* configuration. Retinol is sensitive to destruction by **oxidation** and isomerization by ultraviolet light. Vitamin A must be obtained in the diet of all farm mammals and birds and is required for normal **growth** and cellular differentiation, **reproduction** and vision. Retinol exists in animal products almost exclusively in the form of retinyl **ester** (primarily as the palmitate ester), whereas in plants carotenoids serve as the retinol precursor. The major natural sources of provitamin A for livestock are green pasture, **silage** and **hay**. Most other common feeds, except yellow **maize**, contain little provitamin A activity. **Lucerne** meal has been used as a source of supplemental provitamin A activity. In addition, synthetic vitamin A can be fed as a component of a mixed ration or included in vitamin/mineral mixtures. Retinyl esters, often in conjunction with an **antioxidant**, are most commonly used for this purpose.



Retinyl esters are hydrolysed in the intestinal lumen to retinol by the action of a pancreatic retinyl **ester hydrolase** and absorbed as the free alcohol. In contrast, carotenoids are absorbed as such and metabolized to retinol once inside the intestinal **enterocyte**. There, retinol is re-esterified with palmitic or **stearic acid**, incorporated into **chylomicron**s and secreted into the lymphatic system. The majority of retinyl ester is taken up by the liver, with much of that remaining taken up by bone marrow cells. In the

parenchymal cells of the liver the retinyl ester is hydrolysed to retinol, which is then re-esterified and stored in the liver stellate cell or exported for delivery to the peripheral target tissues. Retinol is the primary vitamin A **metabolite** found in the **blood** and it circulates bound to a serum retinol-**binding protein** (RBP), which is also bound to transthyretin (prealbumin).

Vitamin A deficiency can be demonstrated in nearly all farm animals. The signs of vitamin A deficiency in mammals include **night blindness**, abnormal keratinization of mucus-secreting epithelial tissues (for example, trachea and vagina), poor growth, reproductive abnormalities in both the male and female and fetal anomalies. For example, in pregnant cows, deficiency of the vitamin can lead to the birth of dead, uncoordinated or blind calves. In the chicken, hypovitaminosis A leads to poor growth, loss of vision, **ataxia**, epithelial abnormalities, kidney lesions and a fall in **egg production**.

The vitamin A **metabolite**, retinaldehyde, plays an essential role in vision. In the pigmented epithelium of the retina, esterified all-*trans* retinol is hydrolysed and isomerized to 11-*cis* retinol and further oxidized to 11-*cis* retinaldehyde, which is shuttled to the rod outer segment of the eye to combine with opsin to form rhodopsin. It is this form of the vitamin that plays a key role in enabling vision in dim light. 11-*cis* Retinaldehyde also serves as a light-absorbing pigment in the cone cells of the retina which are responsible for vision in daylight.

Retinaldehyde can be further oxidized to another active vitamin A metabolite, retinoic acid. The all-*trans* configuration of retinoic

acid is the most abundant form. All-*trans* retinoic acid acts by binding to nuclear retinoic acid receptors (RARs) to satisfy the growth and differentiative functions of the vitamin. There are three subtypes of RAR (α, β and γ) encoded by three separate genes, and multiple isoforms are produced by alternative splicing or differential promoter use. These receptors serve as ligand-activated transcription factors which regulate the state of activity of **retinoid**-responsive genes. The RARs bind to specific sequences of DNA called retinoic acid response elements. In conjunction with other proteins, including the heterodimeric retinoid-X receptor (RXR) partner and other co-modulator proteins, the ligand-bound RAR regulates transcription by de-repressing higher-order chromatin structure and by facilitating transcriptional initiation (in the case of positively regulated genes). The mechanistic details of transcriptional repression are less well understood. The changes in gene expression elicited by all-*trans* retinoic acid are cell-type specific and result ultimately in changes in cell activity or differentiation. Additional retinoic acid **isomer**s (9-*cis* retinoic acid, 13-*cis* retinoic acid, 9,13-*cis* retinoic acid) and oxidation products (4-hydroxy-all-*trans* retinoic acid, 4-oxo-all-*trans* retinoic acid, 18-hydroxy-all-*trans* retinoic acid and 4-oxo-13-*cis* retinoic acid) have been described but the importance of these metabolites in normal physiology remains to be resolved. The 9-*cis* isomer of retinoic acid has been shown to bind to the RXR which serves as a heterodimeric partner for many nuclear receptor proteins, including the RAR. However, the necessity for RXR ligand in vitamin A signalling has not been proven. Oxidized

metabolites of retinoic acid are believed to represent retinoic acid catabolites, although a number of these have been shown to retain some biological activity. Additional vitamin A metabolites have been described (14-hydroxy-4,14-retro-retinol, 4-hydroxy-retinol and 4-oxo-retinol) but their physiological importance remains to be established.

Animals made deficient in vitamin A and then fed all-*trans* retinoic acid appear normal with the exception of night blindness, thus questioning the biological importance of the aforementioned retinol metabolites. In the chicken 3,4-didehydroretinoic acid is present in addition to all-*trans* RA, and these metabolites appear to be equipotent in RAR binding and gene expression. Both retinol and retinoic acid are subject to glucuronidation. (MC-D)
See also: Retinyl palmitate

Vitamin A excess
Vitamin A and its **metabolite**s given in excess can be toxic. Toxicity can result from acute exposure or chronic administration of retinyl esters or exposure of embryos to vitamin A or its metabolites at critical times in development. In both animals and humans, toxicity can also result from the pharmacological administration of retinoic acids or active **retinoid** analogues. Lesions include mucous cell formation in keratinized membranes, scaly or thickened skin, bone softening and fracture, haemorrhage and fetal **resorption** or congenital abnormalities. An upper limit for safe intake of retinyl **ester** in cattle has been set by the National Academy of Sciences USA at 16–30 times the daily requirement. In contrast, **carotenoid**s do not appear to be toxic, even in large

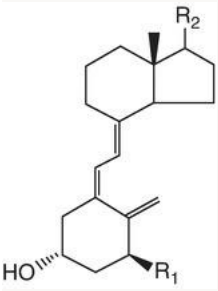
amounts. (MC-D)
See also: Retinyl acetate; Retinyl palmitate; Vitamin A

Vitamin B complex:
see B-complex vitamins

Vitamin C
Also known as ascorbic acid. This **water-soluble vitamin** is in citrus fruits in particular and is taken as a dietary supplement by many humans. Deficiency symptoms are known as scurvy. (CJCP)
See also: Antioxidants, Ascorbic acid; History of Nutritional Sciences; Vitamin deficiencies

Vitamin D
A general term to describe compounds that act in preventing the disease rickets in the young and osteomalacia in the adult. It functions by its conversion first in the liver to 25-hydroxyvitamin D and in the kidney to 1,25-dihydroxyvitamin D. This hormonal form of vitamin D then stimulates the intestine to absorb **calcium** and **phosphorus**, stimulates **osteoblast**s and **osteoclast**s of bone to mobilize calcium from bone, and stimulates renal reabsorption of calcium together with the **parathyroid hormone**. The elevation of these mineral nutrients in **blood** results in the mineralization of the skeleton and the prevention of hypocalcaemic **tetany**, a disease of **convulsion**s resulting from low blood calcium. The vitamin D **hormone**, 1,25-dihydroxyvitamin D, functions by interacting with a nuclear receptor that forms a transcription complex on target genes with specific DNA elements called vitamin

D responsive elements. Vitamin D has the general structure:



where R_1 is H or OH and R_2 is a hydrocarbon side chain. (HFDeL)

Vitamin deficiencies

Vitamin deficiencies may occur due to inadequate concentrations in the diet, to storage or processing losses, or to inadequate **absorption**. The requirements are low in comparison with other nutrients and in some cases the gut microflora can synthesize adequate quantities for their host. For ruminants this usually provides adequate supplies, but for non-ruminants the caecal and **large intestine fermentation** may occur after the site of absorption, leading to low levels of absorption unless the animal is coprophagous. The table gives the most common symptoms of deficiency of all the vitamins and **pseudovitamins**. (CJCP)

Vitamin	Deficiency symptoms	Prevalence	Predisposing factors

Vitamin	Deficiency symptoms	Prevalence	Predisposing factors
A (retinol)	Eye disorders and xerophthalmia in extreme cases, skin disorders, low milk yields and rebreeding difficulties in cattle	Rare except in cattle fed a diet low in β-carotene	Ruminant diet lacking green forage
Biotin	Epidermal tissue disorders, scaly skin, foot lesions, soft keratinized tissues (hoof, beak, horn)	Largely unknown, especially in ruminants	Low availability in wheat and barley

Vitamin	Deficiency symptoms	Prevalence	Predisposing factors
B_1 (thiamine)	Reduced energy availability, muscle weakness and cramps, head bent back (star-gazing), heart defects	Rare due to ubiquitous presence of thiamine in food and synthesis by micro-organisms	Fish products containing thiaminase
B_2 (riboflavin)	Slow growth and various species-specific disorders, e.g. clubbed down and curly toe in chicks, nerve degeneration in pigs	Rare in ruminants	Riboflavin-barring gene in some strains of poultry

Vitamin	Deficiency symptoms	Prevalence	Predisposing factors
B_3 (niacin)	Inappetence, scaly dermatitis, intestinal ulcers, chondrodystrophy in chickens, pellagra in pigs	Rare, but occurs in poultry and pigs	Reduced availability in cereals, high leucine content of diet
B_5 (pantothenic acid)	Ill-thrift, crusted skin around eyes or mouth, goose-stepping in pigs, depigmentation or hair/feather loss	Occurs in pigs and poultry on high cereal diets	Low folic acid and biotin, high cereal diet

Vitamin	Deficiency symptoms	Prevalence	Predisposing factors
B_6 (pyridoxine)	Ill-thrift, hyperkeratosis, diarrhoea	Clinical symptoms rare due to wide distribution of vitamin And synthesis by microbes	None
B_{12} (cyanocobalamin)	Nervous disorders, rough coats, ill-thrift, pine	Occurs in pre-ruminant calves	Inadequate Co in diet
C (ascorbic acid)	Swelling and bleeding gums, weak and aching bones	Rare, but occasionally occurs in very young animals	Stress, infections, overcrowding
Carnitine	None under practical conditions	Non-existent	None

Vitamin	Deficiency symptoms	Prevalence	Predisposing factors
Choline	Reduced growth rate, leg weaknesses (perosis in poultry, possibly splayleg in pigs)	Rare, due to ubiquitous nature in feed and ability to synthesize	Low folic acid, B_{12} or methionine status
D	Rickets in young growing animals, thin-shelled eggs in poultry and (less commonly) osteoporosis in adult animals	Can occur in ruminants at end of winter and in young, growing non-ruminants if not supplemented	Low dietary Ca, lack of exposure to sunlight

Vitamin	Deficiency symptoms	Prevalence	Predisposing factors
E	Myopathy, white muscle disease in calves, heart failure, encephalomalacia and exudative diathesis in chicks, weak immunity	Common in all farm animals	Diet high in polyunsaturated fatty acids, stress, low Se in diet, mycotoxins
Folic acid	Anaemia, low growth rate	Rare	Low vegetable diets, B_{12} or iron deficiency
Inositol	Never observed in farm animals, but rodents develop alopecia	Non-existent	None

Vitamin	Deficiency symptoms	Prevalence	Predisposing factors
K	Poor blood coagulation	Rare (gut synthesis in ruminants, horses and pigs), supplementation required in poultry	Animals that have consumed anticoagulants

Vitamin E

One of the four **fat-soluble vitamins**. All of the compounds with E activity are 6-hydroxychromanes (substituted 6-member heterocyclic double rings) with 16-carbon phytanyl or isoprenoid side chains. The homologue (also called a vitamer) with greatest vitamin E activity is α-**tocopherol** ($C_{29}H_{50}O_2$, molecular weight 430.69). The four naturally occurring **tocopherols**, i.e. α, β, γ and δ, each contain three asymmetric carbons at C-2, C-4′ and C-8′. Each has the potential for the *R* or *S* configuration. All of the natural tocopherols have the *R* configuration at C-2, C-4′ and C-8′, are designated by the prefix '*RRR*' and exist in plants in the active, unesterified form. Chemical synthesis of a tocopherol results in random assembly at each of the asymmetric carbons. Thus, a total of eight stereoisomers (2^3) results when a specific tocopherol is chemically synthesized. The mixture of stereoisomers resulting from chemical synthesis of a tocopherol is designated by the prefix

'all racemic' or 'all-rac'.

Vitamin E is biosynthesized in leaf chloroplasts and found in the **lipid**-rich areas of plant cells, such as membranes and in **oil** droplets. Hence, vegetable oils are good sources of vitamin E, which occurs principally as α, γ and δ tocopherol. Vitamin E activity was first associated with the ability of lettuce leaves to prevent fetal **resorption** in animals fed rancid **lard**. Later, α-tocopherol was isolated from wheatgerm oil. Tocopherols in feeds are released from their *in vivo* locations in plants during **digestion**. Likewise, commercially prepared α-tocopheryl esters are hydrolysed by esterases in intestinal contents to α-tocopherol. **Absorption** of the alcoholic forms is concurrent with and facilitated by other **fats** in the diet, but they must be solubilized by **bile** acids in order to interact with the surface of **enterocyte**s where vitamin E is absorbed by a non-saturable, non-carrier-mediated, passive **diffusion** process. Tocopherols may also gain access to enterocytes as part of micelles. In the enterocyte, they are incorporated into **chylomicron**s, which are transported to the lymphatics, thence to the thoracic duct and into the bloodstream. The efficiency of absorption is relatively low (20–40%). Diseases or conditions that affect lipid absorption are likely to result in diminished absorption of the tocopherols and hence can lead to a deficiency of vitamin E.

The liver discriminates among the various forms that arrive in the chylomicrons. α-Tocopherol is preferred, as are those stereoisomers with the 2*R* configuration. The selectivity is believed to be imposed by the hepatic tocopherol transfer protein which

facilitates α-tocopherol incorporation into VLDL for delivery to tissues. α-Tocopherol is stored in cellular lipophilic locations such as cell membranes and **adipocyte**s. Tissues that accumulate the greatest concentrations of α-tocopherol are **adipose tissue** and **adrenal** gland. The **turnover** of α-tocopherol varies greatly between tissues. In rats fed *RRR*-α-tocopheryl **acetate**, the half-life of α-tocopherol was less than 11 days for plasma, liver and **small intestine**; 11–15 days for erythrocytes, heart and **skeletal muscle**; and 29–77 days for brain, testes, adipose tissue and spinal cord.

The biological effectiveness of the eight stereoisomers of α-tocopherol produced in the chemical synthesis of the vitamin have been evaluated using the rat resorption–gestation assay (Weiser and Vecchi, 1982). The relative values of the four **isomer**s of α-tocopherol with C-2 in the *R* form are (in IU mg^{-1}) 1.49 (4*R*, 8*R*), 1.34 (4*R*, 8*S*), 1.09 (4*S*, 8*S*) and 0.85 (4*S*, 8*R*). Values for the C-2 *S* series of α-tocopherol are roughly one-third of their *R* counterpart. One **international unit** (IU) is equivalent to the activity of 1 mg of all-rac α-tocopheryl **acetate**, the chemically synthesized form of the vitamin with eight potential stereoisomers.

Many of the effects of a vitamin E deficiency are made more striking by a **selenium** deficiency. Selenium is a component of the enzyme **glutathione peroxidase**, which provides a protective role due to destruction of H_2O_2. A deficiency of vitamin E is generally accompanied by an increase in lipid peroxidation as identified by visible tissue damage such as altered tissue architecture and by an increase in measurable **blood** and tissue

malondialdehyde, or exhaled ethane or pentane. These products are the result of **fatty acid oxidation**. Adverse consequences of vitamin E and selenium deficiencies are **mulberry** heart disease in pigs, nutritional muscular dystrophy (also known as 'white muscle disease') in many animals, stiff lamb disease in newborn lambs, **exudative diathesis** in chickens and pigs, testicular degeneration, atrophy of ovaries, and sterility and resorption of fetuses in all farm animals. These symptoms all relate to a loss of cellular integrity.

Placental transfer of vitamin E is inefficient. The latest estimates of requirements for vitamin E for beef cattle (15–60 IU kg^{-1} diet for calves), dairy cattle (calves 15, lactating cows 25 IU kg^{-1} diet), fish (25–100 mg kg^{-1} diet), horses (~80–100 IU kg^{-1} diet), **laboratory animal**s (rat 27, mouse 32 IU kg^{-1} diet), pigs (44 IU kg^{-1} diet), poultry (~5–10 IU kg^{-1} diet) and sheep (lambs 20, adults 15 IU kg^{-1} diet) and can be found in the *Nutrient Requirement* series published by National Academies Press in Washington, DC.

Hypervitaminosis

E has been studied in rats, chicks and humans. Available data indicate maximum tolerable levels to be in the range of 1000–2000 IU kg^{-1} diet. A tentative presumed upper safe use level is suggested to be 75 IU kg^{-1} body weight per day.

The classical approach for assessing dietary vitamin E requirements has been to use **growth** or **reproduction** as response variables. Research has shown that **mammary gland**

health in dairy cows, beef colour and immune system efficacy are also important. **Supplementation** of 1000 IU per day during the dry period and 500 IU per day to lactating cows has reduced the incidence of clinical mastitis. Supplementation of 500 IU per day for the last 100 days of the finishing period results in fresh beef products that have a colour display life that is about 100% longer than products from unsupplemented cattle. Blood neutrophils obtained from cows fed 500 IU per day had greater ability to kill bacterial pathogens than neutrophils from cows fed no supplemental vitamin E. (DMS)

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Vitamin E acetate

α-Tocopheryl acetate, $C_{31}H_{52}O_3$, molecular weight 472.73. All-racemic (all-rac) α-tocopheryl acetate is the commonly used form of supplemental vitamin E for dietary fortification. The **antioxidant** reactivity of α-**tocopherol** is dependent on a functional alcohol group attached to carbon 6 of the chroman ring system. The acetate **ester** at C-6 stabilizes α-tocopherol against

oxidation prior to consumption. Intestinal tract esterases hydrolyse the acetate ester, resulting in all-rac α-tocopherol which is freely available for **absorption** and restored in its vitamin E activity. One **international unit** (1 IU) of vitamin E activity is defined as the activity produced by 1 mg of all-rac α-tocopheryl acetate. (DMS)

Vitamin K

Vitamin K was discovered in 1935 as an essential factor in the prevention of haemorrhagic symptoms in chicks, related to its involvement in the synthesis of prothrombin, a **blood** clotting factor. The discovery was made by a group of Danish scientists, who gave the name 'koagulation factor' to the vitamin, which became shortened to the K factor and eventually to vitamin K.

Vitamin K is a generic term now used to describe a family of **fat**-soluble compounds, which although differing in origin and/or function, share a common 2-methyl-1,4-**naphthoquinone** ring, but differ in the (lipophilic) side-chains linked at the 3-position (Fusaro *et al*., 2020). The three main forms are vitamin K_1, or vitamin PK or **phylloquinone** (PK); vitamin K_2 or **menaquinone** (MKn) (Fig. 1) and vitamin K_3 or **menadione** which is a synthetic, water-soluble analogue of vitamin K that can be converted to K_2 in the intestine. Phylloquinone (K_1) occurs naturally in plants and menaquinone (K_2) can be synthesized in the gut by microbes. The vitamers are relatively stable at ambient temperatures but are rapidly destroyed on exposure to sunlight.

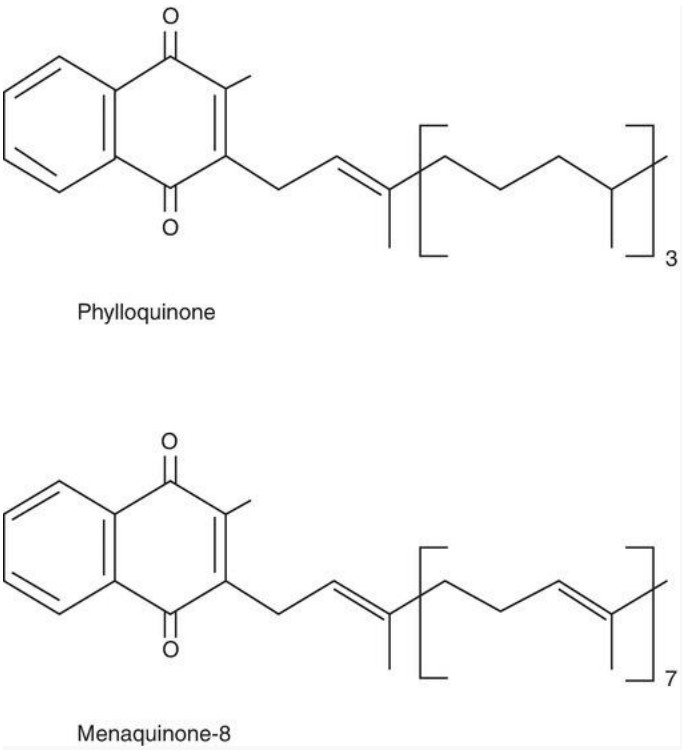


Fig. 1. Structure of phylloquinone and a common menaquinone.

By the mid-1970s it was demonstrated that vitamin K was a **substrate** for a microsomal **enzyme** that converted inactive hepatic precursors of the vitamin K-dependent proteins to their active forms by the α-carboxylation of specific glutamyl residues. Members of this class of gamma-carboxyglutamic acid (Gla) proteins include the vitamin K-dependent blood coagulation factors (prothrombin, factor VII, factor IX and factor X) and co-regulators of blood coagulation (**protein** C, protein S and protein Z); and growth arrest-specific protein 6 (Gas6) which has been characterized as a cell survival factor, a **growth factor**, and a co-factor in the uptake of apoptotic cells by macrophages. A second group of Gla-containing proteins includes osteocalcin and matrix Gla protein (MGP); these proteins being required for regulation of bone growth and extraosseous calcification. Two other Gla-containing proteins, PRGP-1 and PRGP-2, are possibly involved in

signal transduction. Vitamin K-dependent **carboxylase** activity can be demonstrated in most tissues.

In the blood-clotting process, prothrombin is the inactive precursor of thrombin, an enzyme that converts the protein **fibrinogen** in **blood plasma** into **fibrin**, the insoluble fibrous protein that holds blood clots together. Without vitamin K, blood coagulation is seriously impaired and uncontrolled bleeding occurs. Prothrombin normally must bind to **calcium** ions before it can be activated. If the supply of vitamin K is inadequate, then the prothrombin molecule is deficient in γ-carboxyglutamic acid, a specific amino acid responsible for calcium binding. The presence of uncarboxylated proteins in liver or blood indicates a vitamin K deficiency.

The anticoagulant, warfarin (Coumadin^{R}), and other 4-hydroxycoumarins are effective **antagonist**s of vitamin K action *in vivo*. They interfere with the ability of tissues to recycle the co-product of the carboxylase reaction, vitamin K 2,3-epoxide, to the enzymatically active reduced form. This microsomal enzyme, vitamin K epoxide reductase, has the ability to reduce the epoxide to the **quinone**, and the quinone to the hydro-quinone form of the vitamin. Both reduction steps are inhibited by warfarin, resulting in a decrease in the concentration of the hydroquinone form of vitamin K and decreased carboxylase activity. As there are other cellular quinone reductases that are not warfarin-sensitive, administration of vitamin K can overcome a warfarin inhibition of vitamin K action. Chloro-K (2-chloro-3-phytyl-1,4-naphthoquinone) is an effective inhibitor of the carboxylase, and

the reduced form of this analogue has been shown to be competitive vs. the reduced vitamin site. Substitution of a trifluoromethyl group, a hydroxymethyl group or a methoxymethyl group at the 2-position of the naphthoquinone ring also results in inhibitory compounds. Tetrachloropyridinol and other polychlorinated phenols also directly inhibit the carboxylase. A diagram of the main involvement of vitamin K in **metabolism** is shown in Fig. 2.

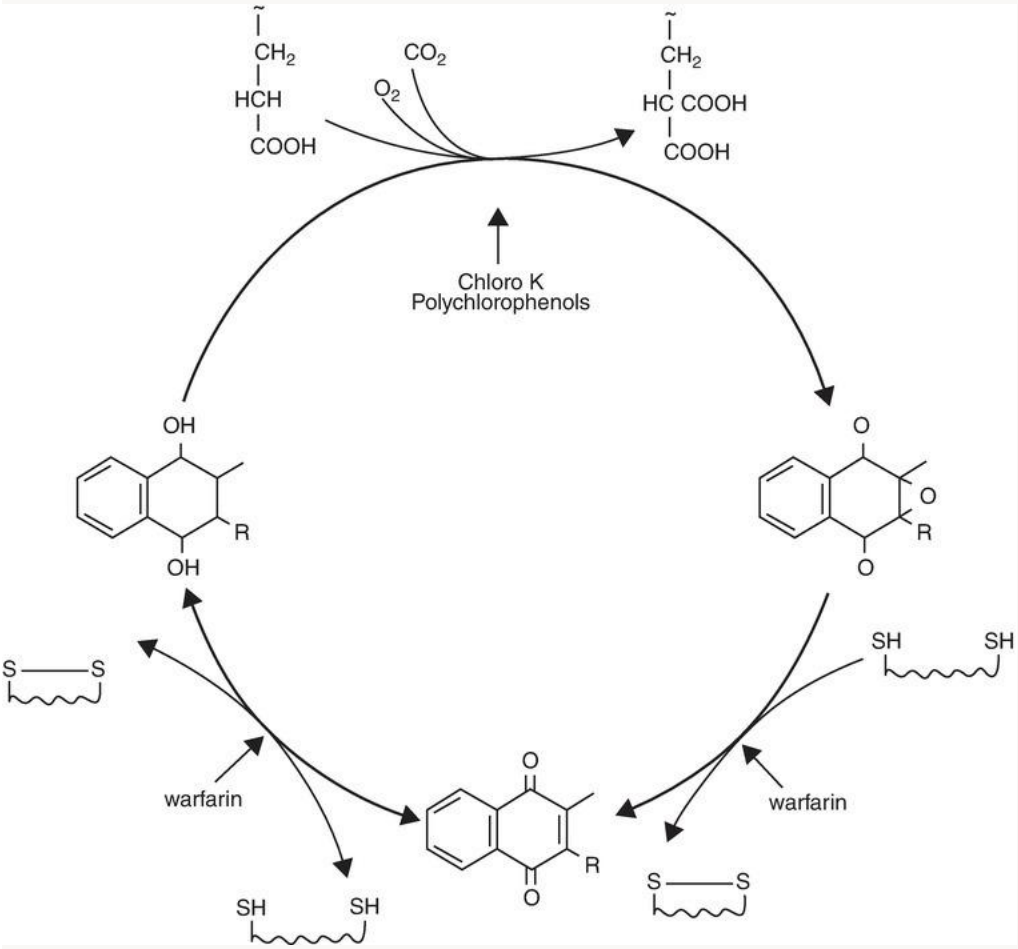


Fig. 2. Metabolism of vitamin K by the vitamin K-dependent carboxylase and the epoxide reductase. Sites of inhibition are indicated.

Proteins containing γ-carboxyglutamic acid, dependent on vitamin K for their formation, are also present in bone, kidney and other tissues. The vitamin is also involved in the binding of calcium

in bones and other tissues, this process involving Gla proteins mediated by the enzyme γ-glutamyl carboxylase that utilizes vitamin K as a co-factor. Carboxylation allows them to bind (**chelate**) calcium ions, which they cannot do otherwise. Research suggests that deficiency of vitamin K may also weaken bones, potentially contributing to osteoporosis, and may promote calcification of arteries and other soft tissues (Fusaro *et al*., 2020).

Although the vitamin is stored in the liver, the supply is limited in humans. Therefore a regular intake from the diet is recommended. The recommended daily intake (RDI) or adequate intake (AI) of vitamin K in humans is based on ensuring normal blood coagulation, the range estimated by several agencies being 55–170 μg per day for adult males and females (Fusaro *et al*., 2020). Since it is now known that vitamin K is involved in the maintenance of healthy bone and possibly in the prevention of **atherosclerosis**, these RDIs may have to be reassessed. Also, as pointed out by Shearer *et al*. (2012), there is still a lack of suitable biomarkers or clinical endpoints that can be used to determine vitamin K requirements of adult humans.

The dietary requirements of vitamin K for pigs and poultry are around 0.5 mg kg^{-1} and 0.4–1.75 mg kg^{-1}, respectively. Although this vitamin can be synthesized by microbes in the **large intestine**, the process is probably too slow in the gut for the vitamin to be absorbed effectively. Commercial diets are routinely supplemented with menadione **sodium** bisulphite, to ensure adequacy. When deficient, haemorrhaging may occur from the navel of piglets at birth and from the **castration** wound. In some

cases, haemorrhaging occurs without causing death.

Supplementation of the sow diet with vitamin K corrects the problem. Chicks or turkey poults fed a diet deficient in this vitamin are likely to develop haemorrhages following a bruise or injury to any part of the body and may bleed to death. Mature fowl are not so easily affected, but when breeding hens are fed diets deficient in vitamin K, the chicks have low reserves of the vitamin and are therefore susceptible to severe bleeding because of greatly prolonged blood-clotting time.

In cattle, when the rumen is fully functional the ruminal microorganisms synthesize all of the necessary B vitamins and vitamin K, at least enough for **growth** and **maintenance**. Therefore ruminating cattle should not require supplementation with B vitamins or vitamin K. (RB)

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Vitamin nomenclature

Nomenclature of vitamins involves two main classes: the **fat-**

soluble vitamins, A, D, E and K; and the **water-soluble vitamins**, **thiamine**, **riboflavin**, **pantothenic acid**, **pyridoxine**, **biotin**, nicotinic acid, folic acid, vitamin B_{12} and **ascorbic acid** (**vitamin C**). Not all vitamins need to be part of the diet for all animals. For example, **vitamin D** may be produced in the skin by exposure to sunlight. The water-soluble vitamins can be produced by intestinal tract microorganisms and be absorbed into the body. In **ruminant animal**s, ruminal contents flow to the **small intestine** and the vitamins can be absorbed there. In non-ruminant animals that practise **coprophagy** (consumption of dung), vitamins produced by microorganisms in the **large intestine** can be absorbed and utilized when night faeces are consumed and digested. (NJB)

Vitamin premix
A mixture of purified fat-soluble and **water-soluble vitamins** usually in a carrier (**glucose**, **sucrose**, **starch** or **lactose**) to dilute the concentration of the vitamins to facilitate a more uniform distribution of them in a mixed diet or **supplement**. The concentration of each vitamin in the premix is adjusted to meet the requirement of the animals consuming the diet, taking into account the vitamin content of the unsupplemented diet. (NJB)

Vitamin supplement:
see Mineral and vitamin supplements

Volatile fatty acids (VFAs)
Weak **organic acid**s with short chain lengths, most commonly

acetic, propionic and butyric acids. These are monocarboxylic, alkanoic acids with the characteristics shown in the table.

	Molecular weight	Boiling point (°C)	pKa
Acetic	60	118	4.76
Propionic	74	141	4.87
Butyric	88	163.5	4.83

These acids produce readily detectable odours that range from pungent to rancid. In the 1940s steam distillation was used to extract them from the **digesta** and **blood** of ruminants in order to gain insight into their metabolic importance. In ruminants, the VFAs account for 50–85% of the **metabolizable energy**; in non-ruminants, their contribution ranges from negligible to substantial depending upon the intake of forages or other fermentable constituents, and upon the **adaptation** of the animal.

VFAs are produced by microbial **fermentations** in a wide variety of anoxic habitats in addition to the digestive tracts of the animals. In livestock operations, these habitats include high-moisture **forage** and **grain** stored in air-tight structures, manure storage containers and manure lagoons. A wide variety of fermentative organisms degrade **carbohydrates**, proteins, **lipids** and other classes of degradable **organic compound**s to the VFAs and possibly **lactic acid**. Where residence times of the **organic matter** are relatively long, i.e. 5 days or longer, and there are no inhibitory factors, such as acidic pH, the VFAs are completely

metabolized to CO_2 and CH_4. This complete decomposition of organic matter is possible because of the syntrophic association of VFA-catabolizing and **methane**-producing bacteria. The VFA-catabolizing bacteria have slow **growth** rates, hence the requirement for long residence time. These organisms would be present in lagoon sediment and in manure digestion systems designed to convert manure-carbon to methane. Feed particles in livestock digestive tracts have residence times of typically 2 days or less and so the VFA-catabolizing bacteria are not able to proliferate; VFAs accumulate in the digestive tract and are available for **absorption**.

Silage fermentations are unique because bacterial fermentation is inhibited by low pH. Following ensilage of feedstuffs that have readily degradable carbohydrate fractions, aerobic **metabolism** depletes available **oxygen** to make the environment anaerobic. The most water-soluble carbohydrate fraction is rapidly fermented to lactic acid and acetic acid. The pH of the fermenting feeds falls to 3.5, causing microbial fermentation to cease. Consequently, lactic acid is not converted to VFAs, nor are VFA-catabolizing bacteria able to grow. Hence, the silage is stabilized against spoilage and further fermentation.



Removal of air from corn silage is important to prevent aerobic fermentation, allowing anaerobic fermentation to produce the acids necessary for preservation of the feed. Photo courtesy of Jess Johnson. Licensed under CC BY-SA 2.0.

In the digestive tract, bacteria, **protozoa** and anaerobic **fungi** accomplish the conversion of carbohydrates (and **amino acid**s) to VFAs. The microbes use **glycolysis** to catabolize carbohydrates to **pyruvate** and then certain enzymes of the **citric acid** cycle to yield the VFAs. The profile of the VFAs produced is a function of microbial enzymatic abilities, growth rate, pattern of acids that allows the organism to maximize its ATP yield, substrate-product carbon balance, and substrate-product **oxidation**–reduction balance. VFAs are readily absorbed from the digestive tract via a pH- and concentration-dependent VFA/**bicarbonate** anti-portal mechanism. Absorption rate is increased at lower pH. The absorption rate depends on chain length, ranked as **butyrate** > **propionate** > **acetate**. VFA absorption is associated with bicarbonate appearance in the gut lumen. In the gut lumen, VFAs

are metabolized as **energy source**s by the mucosal epithelium, and butyrate is most stimulatory for mucosal cell growth. Butyric acid is oxidized to β-hydroxy butyric acid and released into the portal circulation by the rumen epithelium. VFAs are carried by the portal vein to the liver, where absorbed propionate is quantitatively cleared. In ruminants, propionate is the primary precursor for **glucose** synthesis (providing 40–60% of the total glucose synthesized). Little acetate is taken up by the liver, but it is used extensively as an energy source (25–30% of total CO_2 output) and is the primary carbon source for *de novo* **fatty acid synthesis**. Acetate **turnover** in ruminants is rapid, with a half-time of 3–13 min; utilization by most tissues is **insulin** dependent, but uptake of both glucose and acetate by the **mammary gland** is independent of insulin. Oxidation of propionate, both directly and indirectly (via glucose), totals about 20% of the total CO_2 output. β-**Hydroxybutyrate** is a primer of fatty acid synthesis and is incorporated as an intact 4-carbon unit into the methyl-terminal end of fatty acids synthesized *de novo*, and otherwise is quantitatively oxidized. (DMS)

Voluntary food intake

The food intake of animals allowed continuous unrestricted access to feed (*ad libitum* feeding). It is usually expressed as the weight of food eaten per 24 h.

Control by food and animal factors

The voluntary food intake of individual animals tends to be consistent from day to day as long as diet, physiological

requirements and environment (including day length) remain unchanged. In the long term, voluntary food intake is dependent on both food and animal factors. An important food factor determining intake is the rate at which it is digested. Slowly digested feeds remain longer in the **rumen**, or the non-ruminant **stomach**, than rapidly digested materials, allowing an increased intake. If the nutrient supply is in excess of the animal's requirements, an increase in **digestibility**, and in particular the **energy value** of the food, may decrease voluntary food intake as the animal consumes only sufficient food to supply the amount of energy it requires. For ruminants, this control becomes important when the **diet** concentrate content reaches 60–70%. Voluntary food intake may be stimulated by psychological factors, such as providing a mixture of feeds and the physical presentation of the food. More natural presentation methods (for example, from the floor rather than a raised rack or bunk) may promote greater intakes.

The most important animal factor influencing voluntary food intake is an animal's physiological state. Increased requirements, such as the energy demands of peak **lactation**, are associated with increased intake. **Body composition** is also important: fat livestock tend to have reduced intakes. However, despite increased requirements, animals in late pregnancy have reduced intakes, due to the presence of the fetus. After periods of forced feeding or food deprivation, animals adjust their intake in such a way as to return to their original body weight, or their original rate of weight change. There are also social factors, with isolated livestock or

those that are bullied in a small confined space having low intake, particularly in the case of social animal species, such as sheep.

It is often said that animals 'eat for **calorie**s' and, indeed, that is frequently observed. For example, when the energy concentration of food is increased, voluntary intake is reduced in order, apparently, to maintain a constant intake of energy. Equally, increased energy demands, as during lactation or exposure to cold, are compensated for by increased food intake. However, the concept of caloric control is not sufficient to explain many observed changes in food intake in response to changes in the animal's demand for nutrients, changes in the environment and in the composition of the food.

Hunger and satiety

Motivation to eat is initiated by **hunger** and terminated by **satiety**. Hunger may be either for a specific nutrient, e.g. **sodium**, in which case it is termed euphagia, or may be generalized to evoke a variety of satiety responses. In the short term, voluntary food intake is dependent on the perception of food, as determined by the senses (**taste**, smell, vision and tactile), as well as feedback on distension of digestive organs and post-digestion chemosensory feedback. The different aspects of perception of food combine to provide feedback on the acceptability of different foods, sometimes referred to as **palatability**.



Spices aim to influence our sensory perception of food, which may affect our voluntary food intake. Photo courtesy of Michael Day. Licensed under CC BY 2.0.

The principal taste sensations influencing intake are sweet, sour, **salt** and bitter, which provide information on the **carbohydrate** content, **ion balance**, sodium content and the presence of toxins, respectively. Flavours (*see* Flavour compounds) interact and aversive flavours, such as bitterness, can be masked by pleasurable flavours, such as sweeteners. Most flavours are aversive at high concentrations and pleasurable or neutral at low concentrations, but experience is important in modifying an animal's response to taste stimuli. Some flavours interact, or modify the perceived intensity of another flavour, for example thaumatin and bitter flavours. Food perception is also influenced by tactile senses, hence the physical form of the food can be important – particularly in the case of sheep and goats, whose mouthparts are more sensitive than those of cattle. For example, **forage** leaves that are excessively hairy or waxy can reduce intake, and the presence of thorns can damage sensitive mouthparts. **Cereal**s that are excessively comminuted, such as by grinding, are

often dusty and unpalatable.

Such evidence implies homeostatic control of voluntary food intake and body weight, and various theories (energo-, lipo-, gluco-, amino-, thermo- and ponderostatic) have been proposed to account for this control but no single theory can account for observed levels of intake in all situations. Voluntary control of food intake in any animal depends on integration of feedback from a wide variety of neural and chemical signals, involving brain, eyes, mouth, alimentary tract, liver, and circulating **metabolite**s and **hormone**s. Control mechanisms may operate in the short or longer term and these are considered here in the categories of alimentary, metabolic and central controls.

Alimentary control

Some physical limitations to intake include a very slow rate of eating (for example, due to very sparse food availability, preventing the animal from reaching its potential intake in the time available) or limited capacity of the stomach(s), especially where the food must remain in the stomach for a long time in order to be digested (this is especially true in **ruminant animal**s, which have developed blind stomachs in order to sequester food for long periods to be digested by symbiotic microorganisms and which can only be emptied when a certain degree of digestion has taken place). In cattle and sheep, the capacity to store food in the rumen and to re-masticate the food later during **rumination** is a valuable means of concentrating **grazing** into periods when the environment is favourable.

As an animal eats, its stomach wall becomes stretched, and this

is sensed by mechanoreceptors and transmitted to the central nervous system (CNS), where it contributes to satiation. Digestion proper commences rapidly: breakdown of food constituents into molecules to be absorbed begins, and the bulk of the food begins to be reduced by **absorption** and passage along the digestive tract; these factors reduce the volume of material in the stomach. An early theory of food intake control was based on the simple concept of stomach fill and this is still particularly relevant for ruminants. However, most animals take many meals each day and the size of any one meal is not large, in relation to stomach capacity, suggesting that stomach fill is not the only factor controlling voluntary food intake.

Evidence of an association between meal initiation (hunger) and gut emptying in simple-stomached animals comes from experiments in which differences in rate of food passage, attributable to manipulation of diet nutrient density, ambient **temperature** or the vagus nerve, were reflected in differences in the ratio of mean meal size to mean meal length plus mean interval length. In ruminants, the intake of fibrous foods increases when the foods are ground into small particles before feeding, due to their faster exit from the rumen. An association between meal termination (satiety) and gut filling is seen in experiments in which differences in meal length, attributable to variation in **particle size**, reflected the time taken to consume the same weight of food, but not to absorb the same amount of nutrients.

Several peptides are released in the alimentary tract in response to passage of **digesta**, and some of these also occur in nervous

tissue. Two that have been proposed as satiety agents are bombesin and **cholecystokinin** and it is likely that the combined effects of several peptides, together with other factors, might be sufficient to explain normal satiety.

The wall of the digestive tract is sensitive to chemicals as well as physical stimulation. The rumen wall receptors are sensitive to pH and specifically to the **volatile fatty acid**s, especially **acetate**.

Metabolic control

There are short-term fluctuations in the supply of nutrients from the digestive tract which are involved in the control of **meal frequency** and size. Although the early glucostatic theory of intake control is no longer thought to be valid on its own, there is nevertheless a sensing of the supply of oxidizable substances to the liver which is transmitted to the CNS to play a part in the overall control of intake. In many animals on starchy diets, **glucose** is likely to be the main contributor to this route of satiation. In ruminants, where little glucose is absorbed, the satiating agent at the level of the liver is its precursor, **propionate**, produced by the microbial population of the rumen.

In the longer term, **blood** levels and receptor sensitivities for **metabolite**s, such as **long-chain fatty acid**s, and **hormone**s, such as **insulin** and **leptin**, are involved in the control of food intake. Leptin has the properties of a negative feedback mechanism for maintaining the stability of **body fat** content. It is produced by fat cells in proportion to their fat content, circulates in the blood and influences feeding via CNS receptors.

Central control

Although blood composition is monitored in both brain and liver, and effects of vagal denervation on feeding responses to intraportal infusions of nutrients indicate that the liver does have a part to play, ultimately all components of **feeding behaviour** are coordinated in the brain. The 'dual control' system, based on a hunger centre in the lateral **hypothalamus** and a satiety centre in the ventromedial hypothalamus, is no longer considered valid.

Central neuropeptides and monoamine transmitters that have been implicated in feeding control in **laboratory animal**s have also been shown to be active in farm mammals and, to some extent, in birds. Neuropeptide Y in the brain is probably the most potent known stimulator of food intake in mammals and birds and leptin exerts its intake-moderating activity via this **peptide**. Finally, feeding, drinking and other behaviours are implicated with central release of opioid peptides, and it seems likely that they may be at least partly responsible for positive reinforcement of any activity of a repetitive nature.

Integrated control

As indicated above, no single alimentary or metabolic signal to the CNS can explain how food intake is controlled. It is proposed that numerous factors are involved and that animals learn to minimize the imbalance between the various factors causing hunger and those causing satiety. In different situations, even in the same animal, the relative importance of the various factors is different, making it very difficult to propose a simple hypothesis of the control of voluntary food intake. Nevertheless, the prediction of voluntary food intake is an important aspect of designing diets and

feeding strategies for all classes of livestock(JMF; CJCP; JSav)

Further reading

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Vomiting

Vomiting (emesis) is a complex reflex activity coordinated in the brain stem. Vomiting is associated with a number of actions, including the contraction of the abdominal musculature, which increases intra-abdominal pressure, an expansion of the chest cavity and opening of the upper oesophageal sphincter. Vomiting is a protective mechanism to help to prevent absorption of noxious substances. Pigs vomit easily. In ruminants, vomiting occurs as an injection of abomasal contents into the forestomach.

The stimulation of the vomiting reflex comes from a large number of receptors, such as mechanoreceptors in the pharynx, and tension and chemoreceptors in the gastric and duodenal **mucosa**e. Offending stimuli from the gastrointestinal mucosa can result in vomiting. Vomiting is not always an indication of a primary gastrointestinal problem. Similar stimuli can arise from numerous other organs and a chemoreceptor trigger zone, which is sensitive to the presence of toxins and drugs in the blood, can also cause vomiting. (SB)



Cat's vomit containing a bezoar (tightly packed mass of undigested or partially digested material in the digestive tract), with a serious roundworm infection (*Toxocara cati*) and a tapeworm (*Dipylidium caninum*) at the bottom of the photo. Photo courtesy of Kalumet. Licensed under CC BY-SA 3.0.

Vomitoxin
A **trichothecene mycotoxin**, produced by *Fusarium* fungi. Vomitoxin (**deoxynivalenol** or DON) causes feed refusal and **vomiting** in pigs. Pigs, dogs, cats and ducklings are the most sensitive animals. As little as 5% infected **grain** kernels or 10 ppm DON in feed causes feed refusal in pigs. Chickens may tolerate as much as 100 ppm in the feed. Emetic effects may involve effects on brain **neurotransmitter**s. (PC)

W

Wafering

Common name for pressing or the formation of pellets by compressing meal through a die, with or without heat. (MG)

See also: Pelleting

Water

A colourless, odourless, tasteless liquid, H_2O, required by all organic life forms. Together with CO_2, water is a major end-product of cellular oxidative **metabolism**; for example, for **carbohydrates**, $C_6H_{12}O_6 + 6O_2 \rightarrow 6H_2O + 6CO_2$. Water is taken up in biosynthetic reactions such as the conversion of carbohydrate to **fat** and is thus a required **substrate** for cellular metabolism. Finally, much of the **oxygen** consumed is recovered in cellular water as a result of cellular **oxidation** of foodstuffs. (NJB)

Water buffalo (*Bubalus bubalis*)

There are 169 million water buffalo in the world, compared with a cattle population of 1350 million. There are two main types. The swamp buffalo has large curved horns and is used primarily as a **working animal**; it is found in the Philippines (where it is often called the carabao), in India and in other countries of South-East Asia. The river buffalo is found in India, Egypt, Europe, the Caribbean and South America; it has lightly coiled or drooping straight horns. River buffalo supply both draught power and **milk**; 35% of India's milk animals, other than goats, are river buffalo and they produce almost 70% of India's milk.

Buffalo have been used in India for 5000 years and in China for 4000 years but for only 1000 years in Europe. Most buffalo are

located in Asia but there are 3 million in Egypt, > 1.5 million in Brazil (imported during the past 80 years) and small numbers in Trinidad and other countries of the Caribbean and South America. Water buffalo have a quiet temperament, unlike the wild African buffalo *Syncerus caffer*, which has a reputation for being very dangerous and unreliable.



Indian water buffalo supply both draught power and milk. Photo courtesy of Dr Raju Kasambe. Licensed under CC BY-SA 4.0.

Water buffalo can live in temperate climates but can overheat in hot climates, especially when used for work, because they have a limited ability to lose heat by sweating compared with cattle. Buffalo produce good lean **meat** and provide rich milk. The **butterfat** from buffalo milk is the major source of cooking **oil** (ghee) in India. Buffalo milk contains twice as much butterfat as that produced by dairy cows. Mozzarella cheese is made from buffalo milk. In Hindu countries such as India and Nepal, where cows cannot be killed, the slaughter of buffalo is permitted and their meat can be eaten.

There are no distinct breeds of swamp buffalo but they do vary in size from area to area. For example, swamp buffalo in Thailand average 450–500 kg, whereas in Burma they average 300 kg. There are 18 breeds of river buffalo in India and Pakistan, classified by area of origin: Murrah, Gujarat, Uttar Pradesh, Central India and South India breeds. The swamp buffalo is reported to have $2n$=48 chromosomes and the river buffalo $2n$=50 (Harisah *et al.*, 1989). Crossbreeds have between 48 and 50 chromosomes and may be fertile. Cattle have $2n$=60 chromosomes and will mate with buffalo but offspring are infertile.

When adequately fed, both males and females reach **puberty** at 18 months of age. Oestrus lasts for 24 h (range 11–72 h) with a 21-day cycle. Buffalo show few outward signs of heat and often mate at night. Conception may be as high as 80%. The semen can be frozen. The **gestation period** (310 days) is longer than that of cattle (*c.* 280 days). The first calf is normally born before the dam is 3 years of age. Buffalo will return to heat 40 days after calving, but normally produce only two calves every 3 years.

Buffalo are lean animals with killing-out (dressing) percentages ranging from 53% to 56%. They tend to be highly muscular, because they have been developed for draught purposes. Buffalo meat and **beef** are similar but the meat of buffalo is darker and the **fat** is always white. There is no evidence to indicate that the meat is tougher than that of cattle of a similar age.

Five per cent of the world's milk is produced from buffalo. In countries such as Egypt, the milk yield of buffalo is generally higher (680–800 kg) than that of local cattle (360–500 kg). The

highest yield comes from Murrah buffalo (1800 kg per **lactation**). Calves of some types of buffalo are about the same size as a Holstein calf. They grow very quickly, because of the quality of buffalo milk, and can weigh 360 kg at 1 year old. However, many calves die in India and Egypt because the milk is used for human consumption and not enough is left for the calf. Buffalo udders are very variable in shape, making machine milking difficult. The presence of the calf is not normally needed to stimulate milk let-down, as is the case of many zebu cattle.

Buffalo milk contains 16% total solids compared with 12–14% for cows. Butterfat percentage is 6–8%, compared with 3–5% in cows. Buffalo milk lacks the yellow pigment, carotene, and is therefore white. It can be processed in a similar way to cows' milk. To produce 1 kg cheese requires 8 kg cows' milk but only 5 kg buffalo milk; 1 kg of butter requires 14 kg cows' milk but only 10 kg buffalo milk.

Buffalo are reputed to provide 20–30% of the farm power in South-East Asia. They are said to move easily through mud, because they have large boxy **hooves**, but are no better at working under paddy field conditions than cattle. Because of their limited ability to **sweat**, buffalo are not suitable for working under dry land conditions. They need to wallow after 2 h work to get rid of excess heat produced during work. They can walk 3 km h^{-1}, and can work for 5 h day^{-1}. At this rate of work they may take 6–10 days to plough, harrow and prepare 1 ha of rice paddy.

The domestic buffalo is a ruminant and the general structure of its **rumen**, **reticulum** and **omasum** is very similar to that of

cattle. Therefore the nutrition of the buffalo is broadly similar to that of *Bos taurus* and *Bos indicus* animals. In most trials, buffalo have grown faster than native cattle (range 0.25–1.25 kg per day). This is probably because they have a larger mature body size. Some experiments have shown that buffalo digest **cellulose** more efficiently than cattle (e.g. **straw** fibre 80% vs. 65%). They may have different microorganisms, or proportions of them, in the rumen. However, other experiments show that cattle are more efficient than buffalo. They are often fed mainly on **rice straw**, **maize stover** or other similarly low-quality feeds. Lack of adequate nutrition, in both quality and quantity, is the main reason why buffalo are unproductive. For all practical purposes, knowledge of the nutrition of cattle can be applied to water buffalo, provided that differences in body weight and in the composition of the milk are taken into account. (AJS)

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Water buffalo, feeding strategies to improve milk production and composition

The nutritional composition and properties of buffalo **milk** vary with feeding systems, influenced by on-farm factors and seasonal changes (Abesinghe *et al*., 2020). Buffalo have the inherent ability to produce milk with high **fat** contents ranging from 6% to 8.5% and convert carotene to **vitamin A**, resulting in whiter milk than cows' milk. They are more capable of converting poor-quality fibrous feeds into milk and **meat** compared with cattle. Thus, the predominant feed source in traditional buffalo farming is **straw**-based rations, due to the irregular and inadequate availability of quality, nutritionally balanced feedstuffs in tropical regions. Frequently available feedstuffs include straws from various sources (e.g. **wheat**, paddy, gram, masoor, **soybean**), uncultivated local **grass**, chari, **maize** fodder, **cottonseed** cake and **wheat bran**, which are often fed in a combination of several materials (Yadav *et al*., 2020). Often, rations for buffalo in gestation are mostly straw with very little concentrates, fresh forages, and no **mineral supplementation**. However, diets with a **protein** content of less than 6% and a too-high ratio of straw reduce the voluntary intake of buffalo, resulting in lower milk production. Therefore, it is necessary to fulfil their **nutrient requirement** to improve performance and maximize milk production. The nutrient requirement of buffalo according to the fat percentage of milk is shown in the table.

Milk production – buffalo (nutrients required per kg of milk)

Milk fat %	DCP (g)	TDN (kg)	ME (MCal)	Ca (g)
5	51	0.37	1.28	2.9
6	57	0.41	1.36	3.1
7	63	0.46	1.54	3.3
8	69	0.51	1.80	3.5
9	75	0.56	2.06	3.7
10	81	0.60	2.16	3.9
11	85	0.65	2.34	4.1

DCP, digestible crude protein; ME, metabolizable energy; TDN, total digestible nitrogen
Source: Ranjhan and Pathak, 1979

The recent efforts on buffalo feeding have been focused on improving the nutrient supply and utilization of nutrients, with varying degrees of success. Improving the **digestibility** and **nutrient availability** of **cereal** straws, fodders, industrial and agricultural **by-product**s, addition of **fermentation** modifiers, vitamins and use of rumen bypass protein and fat sources have shown significant potential to improve both **liveweight** gain and milk yield in buffalo. (HP; JKV; HTMH; ENP)

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Water content:

see Dry matter

Water deprivation

When the intake of water, either as liquid or as part of the food before or after **metabolism**, is insufficient to maintain the insensible losses of water through the skin, lungs and obligatory **urine** production by the kidneys, there is a decrease in circulatory volume which in turn leads to a fall in **blood** pressure, a rise in heart rate, circulatory collapse, renal failure and death. Thirst is the main regulator of water balance, reinforced by angiotensin II. Observation of skin turgor in some species provides a useful guide to the necessity for fluid replacement therapy.

If more water than **sodium** is lost, as in pigs (which lack **sweat** glands) when exposed to a high **environmental temperature** and lack of adequate water, a condition of **salt poisoning** develops. This is associated with raised plasma sodium concentration and marked cellular **dehydration**, which may have fatal consequences. Diets fed to pigs should not contain more than 1% salt. (ADC)

See also: Dehydration, body

Water excretion

Water is lost from the body in two forms: as a liquid, mainly in **sweat** and **urine**; and as a gas, by evaporation. Loss of water from the body in liquid form is required because water is the major solvent of the cellular and extracellular environment and the medium in which excretory products are carried to the site of excretion, whether urine, skin or lung. These include not only end-products of **metabolism** but also toxic or detoxified substances made water-soluble by metabolic modification. Water loss from an animal occurs via evaporation (sweat and respiratory) and as liquid water in **milk**, **eggs**, **saliva**, urine and **faeces**. Evaporative water loss is increased (~50%) as the **environmental temperature** increases through the thermoneutral zone. Evaporation is increased with higher air speed but reduced by high humidity. Because of the high heat of vaporization of water (~2.4 MJ g^{-1} at 30°C), evaporative cooling is critical to the regulation of body **temperature** in homeothermic animals (those that maintain body temperature). At high environmental temperatures evaporative cooling, whether by sweating, panting or wallowing, becomes the major route of heat loss. (NJB)

Water-holding capacity

The ability to absorb and retain free water. The water-holding capacity of a feedstuff is primarily governed by the types of non-structural **carbohydrate** (often described as fibre) in the feedstuff. Feedstuffs with high water-holding capacities are

sugarbeet pulp, **linseed** meal, **lupin** seeds and other pulses as well as certain varieties of **barley**, **wheat** and other **cereal**s. Increased intake of **non-starch polysaccharide**s (with a consequent increase in water-holding capacity) often increases the **transit time** of feed in the **gastrointestinal tract**. Although this gives a longer time for digestive **enzymes** and microorganisms to function, increased **viscosity** of the **digesta** tends to reduce nutrient mobility and thus reduce digestibility. In pigs and poultry, feedstuffs with high water-holding capacity tend to increase endogenous losses of nutrients from the gut. **Nutrient availability** in poultry is negatively correlated with the water-holding capacity of the feed. Increased water intake and digesta **viscosity** lead to wet and sticky **faeces**, increasing the risk of health problems and encouraging the colonization of the gastrointestinal tract by pathogens. Finally, the gastrointestinal tract of animals is larger (and proportionately heavier) when they are fed diets with a high water-holding capacity. (TA)

Water intake requirements

Water is essential for life. Water intake should be exactly matched by water loss from the body plus water accumulation in tissue growth. The drinking of water, the consumption of water-containing food, and the endogenous provision of water through **macronutrient metabolism** meet the daily water requirements of animals. The complete **oxidation** of 100 g of **protein**, **carbohydrate** or **fat** to CO_2 generates 41 g, 60 g or 109 g of metabolic water, respectively. The daily water intake of animals is usually 1.5 to 3 times their dry matter (DM) intake, but increases in

response to a plethora of factors, including the high protein and **salt** content of the diet, **environmental temperature**, **lactation**, gestation, **egg production**, disease and exercise. Average requirements of animals for water in a temperate **climate** are summarized in Table 1.

Table 1. Average daily requirements of animals for water at a temperate climate.

Species	Daily water requirements	
	Litres	Litres kg^{-1} body weight
Beef cow (lactating, 500 kg)	60	0.12
Beef cattle (450 kg)	40	0.09
Cat (4 kg)	0.2	0.05
Dairy cow (lactating, 500 kg)	90	0.18
Dairy cow (maintenance, 500 kg)	60	0.12
Dog (30 kg)	1.65	0.055
Horse (medium work, 450 kg)	40	0.09
Horse (lactating, 450 kg)	50	0.11
Human (70 kg)	3	0.043

Species	Daily water requirements	
	Litres	Litres kg^{-1} body weight
Pigs (growing, 30 kg)	6	0.20
Pigs (growing, 60–100 kg)	8	0.10
Pigs (lactating sow, 150 kg)	18	0.12
Poultry, hen (2 kg)	0.5	0.25
Rat (0.3 kg)	0.075	0.25
Sheep (lactating ewe, 50 kg)	6	0.12
Sheep (fattening lamb, 50 kg)	4	0.08

In order to maintain water balance, water intake must exactly counterbalance the water lost from the body as well as water stored in new growth. Water intake is achieved by direct consumption of water or as part of food consumed, or it is produced by **metabolism**. Water produced by metabolism is called metabolic water. Specific estimates of water consumption can be found for pigs and dairy cattle in US National Research Council reports. For pigs, water intake (l per day) = 0.149 + (3.053 × kg daily dry feed intake). For dairy cattle, water intake (kg per day) = 15.99 + ((1.58 ± 0.271) × (kg DM intake per day)) + ((0.90 ± 0.157) × (kg milk

production per day)) + ((0.05 ± 0.023) × (g sodium intake per day)) + ((1.20 ± 0.106) × (minimum daily temperature, °C)). For beef cattle and sheep on **rangeland**s, water deficiencies are more common, as there may be total reliance on natural water sources or bore water, but requirements are harder to define because of the greater extremes of **climate** to which the animals be exposed.

Fattening lambs may imbibe 6.5 l per head per day in hot weather but less than half of this amount normally. Cattle may drink 40 l per head per day, but up to 75 l per head per day in hot weather. The type and intensity of animal performance increases water needs. Water consumption increases with **environmental temperature**, **milk** production and the intensity and duration of exercise.

In **feedlot**s, water has to be provided not only for water intake of the animals, but also for cleaning the pens and equipment, dust control and washing the animals. Emergency provision of several days must be catered for in the case of water extraction from rivers. The estimations of water consumption are most important for feedlot cattle that are often exposed to high temperatures with little shade in parts of the world where drinking water is in short supply, such as Queensland (Australia) and Texas and the Great Plains of the USA.



In feedlots, drinking water requirements are often increased by hot weather, water spillage and wildlife use of water in troughs. Additional water is needed to spray the substrate to prevent dust and to clean the cattle. Photo courtesy of USDA Government. Licensed under CC BY 2.0.

NRC (2001) estimates of water consumption by livestock do not take into account water required for cattle washing, evaporative losses from open water sources (troughs and dams), cleaning water troughs, dampening the yards to reduce dust, cleaning of hospital receival/dispatch areas, feed processing areas and weighbridge, vehicle and machinery washing bays, dust control in pens and on roads, and water for personnel on site. According to Davis and Watts, drinking water accounts for between 75% of total, when cattle are washed, to 90%, when they are not. Therefore, water requirements for feedlots should be calculated as cattle water intake + 10–25%. Cattle washing is necessary if cattle are dirty before they are sent to slaughter, in order to preserve the value of the hide, and also for their **welfare**. Stained leather costs the **beef** industry significant amounts and animals are more likely to be devalued if their coats are dirty. Hence a conservative estimate is that drinking water accounts for 75% of total requirements.

Estimating drinking water consumption by cattle and sheep is difficult because of the multiple factors affecting it, including ambient temperature and humidity, cattle **genotype**, dry matter content of the **diet**, dry matter intake and **water quality**. Typically models of water consumption by cattle have only accounted for 30–40% of the variation in intake (Machado *et al.*, 2021), hence a conservative estimate is necessary in any feedlot design. As Arias and Mader (2007) stated, 'the response of cattle to adverse environmental conditions is markedly individual and highly variable, which can obstruct the accuracy of predictive models'.

In the event of water not being available to cattle, the welfare consequences are rapid and dire (Parish, undated):

> Cattle cannot adapt to water restriction very well. Providing less water than cattle need results in decreased feed intake and reduced performance. Water deprivation for extended periods can result in death. Thirst is a result of water need, and cattle drink to fill this need. Thirsty cattle may indicate water needs are not being met. Cattle should be given all the water they can drink to avoid stress, production losses, and possible dehydration.

Models of water intake have been developed for nearly 70 years, beginning with Winchester and Morris (1956). Early models are likely to be inaccurate for feedlot development today, because cattle used to be slaughtered at much lighter weights, being generally early maturing British breeds, maturing at 500 kg, whereas a modern feedlot will fatten cattle to 750–775 kg. However, it is generally recognized that ambient temperature has the greatest effect on water intake and this is included in NRC estimated daily water intakes (Table 2).

Table 2. Estimated daily water intake (gallons per head per day) for beef cows based on temperature and level of production.

	Growing cattle		Finishing cattle		Pregnant cows		Lactating cows		Mature bulls	
Temp, °F	400 lb	600 lb	800 lb	600 lb	800 lb	1000 lb	900 lb	1110 lb	900 lb	1400 lb	1600 lb
40	4	5.3	6.3	6	7.3	8.7	6.7	6	11.4	8	8.7
50	4.3	5.8	6.8	6.5	7.9	9.4	7.2	6.5	12.6	8.6	9.4
60	5	6.6	7.9	7.4	9.1	10.8	8.3	7.4	14.5	9.9	10.8
70	5.8	7.8	9.2	8.7	10.7	12.6	9.7	8.7	16.9	11.7	12.6
80	6.7	8.9	10.6	10	12.3	14.5			17.9	13.4	14.5
90	9.5	12.7	15	14.3	17.4	**20.6**			16.2	19.0	20.6

Source: NRC *Nutrient Requirements of Beef Cattle*, 8th revised edition: Updated 2016

The NRC Requirements only go up to finishing cattle weighing 453 kg (1000 lb) and 90°F (32.2°C). These cattle are estimated to imbibe 20.6 gallons per day (78 l per day). Adding 25% for other

uses, as described above, the maximum daily requirement if all the cattle are in the finishing stage is 78 +19 = 97 l per day. This will be exceeded on days when the temperature exceeds 32.2°C.

MLA recommendations (Davis and Watts, 2016) state: 'Daily water consumption patterns in lot-fed cattle vary with the season and can range from about 14 L/head/day to 75 L/head/day.' The upper limit may represent an underestimate of maximum water intake. Sexson *et al*. (2012) summarized three studies modelling cattle water intake increases with temperature, which estimated that water consumption increased by 0.22, 1.2 and 1.9 l per °C, but noting that it was not a linear response; rather, it increased curvilinearly with the highest rates of increase at high temperatures. Sexson *et al*. (2012) noted an increase in water consumption of steers (weighing 468 kg) of + 15 l per day for 40°C, compared with 0–10°C. One of the most commonly cited models of water consumption of feedlot steers is that of Hicks *et al*. (1988), who estimated that water intake (litres per day) = 18.67 + 0.3937 maximum temperature (°F) + 0.2432 DMI (kg per day) – 3.870 precipitation (cm per day) – 4.437 (% dietary salt).

Although Arias and Mader (2007) considered the Hicks *et al*. model to be the best, it appears to be an artefact of the experimental design that a negative term is introduced for **salt** intake. Water intake increases positively with salt content of the diet. Thus, their recorded daily water intakes for feedlot cattle of 35.9 l per day may be considered underestimates,

Newer models based on meta regression can predict free water intake more accurately. That of Appuhamy *et al*. (2016) for dairy

cows explained 76% of the variability in water intake, including in the model dry matter intake and content, mean ambient temperature as both linear and squared functions, milk yield (for lactating cows) and dietary sodium and potassium content. However, models for beef cattle have not yet reached that level of accuracy. The latest model by Machado *et al*. (2021) for Brangus cattle in the subtropics explained only 32% of variability in intake by incorporating the following factors: dry matter intake, maximum temperature and daily precipitation. The uncertainty in modelling the water intake of beef cattle in feedlots means that additional capacity must be included in feedlot design to account for potentially high levels of consumption during very hot conditions. (GW; NJB; RB; CJCP)

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Water melon:

see Melon

Water quality

Drinking water for humans is usually treated to improve its safety. Possible treatments include coagulation, sedimentation, granular media filtration, adsorption, ion exchange, membrane filtration and slow sand filtration. In regions with water shortages highly saline

waters, such as sea water, are treated to make them potable. Water contributes to humans' intake of **magnesium** and possibly **calcium**. Hard water is associated with a reduced incidence of ischaemic cardiovascular disease, probably due to the Mg. **Fluorine** is sometimes added to reduce dental caries. For farm animals, water intake may be restricted by excess total dissolved solids, especially when caused by salinity, sulphur, sulphate, **iron**, **manganese** and **nitrate**. It may also be polluted with potentially toxic compounds such as **heavy metals** and **pesticide**s. Beef cattle and sheep on **rangeland** are most likely to be offered water of low quality (Wright, 2007), with the most common problems for surface water being: blue-green **algae** (cyanobacteria); bacteria, viruses and parasites; **sulphates**; and dissolves solids (TDS); and for groundwater: sulphates; dissolved solids (TDS); nitrates; and **iron** and **manganese**. Other parameters that may be of concern include water **taste** and odour, **temperature** and pH/alkalinity. (RB; CJCP)

Reference

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Water requirements:

see Water intake requirements

Water-soluble vitamins

A term embracing the **B-complex vitamins** and **vitamin C**. It thus includes **thiamine**, **riboflavin**, **pyridoxine**, **niacin**, folic

acid, **biotin**, **pantothenic acid**, **vitamin** B_{12} and **ascorbic acid** (**vitamin C**). (NJB)

Water temperature
Most aquatic animals are poikilotherms (body **temperature** conforms to water temperature) and their **metabolic rate** increases with water temperature. **Growth** is usually faster at higher temperatures but water temperatures outside the optimal range of a species will negatively affect its physiology, leading to reduced growth and feed consumption. At higher temperatures, increased production of metabolic wastes (**ammonia** and **carbon dioxide**) combined with lower dissolved **oxygen** levels may reduce **water quality**. Water temperature tolerance varies significantly among **fish** species and other aquatic animals. (DAN)
See also: Freezing; Fresh water; Sea water

Waxes
Fatty acid esters of long-chain primary alcohols. Alcohol chains of 8 to > 40 carbons have been identified in both plants and animals. Some secondary alcohols occur and monoenoic alcohols are found in cetaceans. The **ester** linkage of waxes is hydrolysed with great difficulty. (DLP)

Weaning
The prevention of access of **suckling** mammals to either their mother's **mammary gland**s or an artificial source of **milk**. In the natural process young mammals gradually replace their mother's

milk with other sources of nutrients. In some production systems weaning has become an abrupt event. Examples are the weaning of piglets at 3 weeks and of lambs at 4 or 5 weeks, both done to reduce the interval to rebreeding. The ability of young animals to survive and grow on solid food alone is more closely linked to their age than their weight. Young fast-growing animals receiving copious amounts of their mother's milk are usually slower in developing their **enzyme** systems for the **digestion** of solid food than their slower-growing contemporaries that have been forced to augment their mother's milk with solid food.

As well as depriving the suckling mammal of milk, it also may deprive it of physical or emotional contact. The natural time of weaning is primarily determined by the requirements of the offspring for milk, and occurs gradually after some months, but in mammals used for milk production for human consumption, especially dairy cows, offspring are typically abruptly deprived of access to their mother's mammary glands just a few hours after birth, with the mother's milk replaced by an artificial source. Similarly, meat animals may be abruptly weaned from their mother so that the mother can conceive again. This shortening of the reproductive cycle allows the maximum number of offspring to be raised in the shortest time. After weaning, livestock may have either no contact with their mother, or they may have contact over a fence, which reduces the stress of separation. This stress, coupled with the change in diet, may result in increased susceptibility of the animals involved to diseases. (CJCP; JJR)



When to wean a lamb? The ability of young animals to survive and grow on solid food alone is more closely linked to their age than their weight. Photo courtesy of Peter O'Connor. Licensed under CC BY-SA 2.0.

Weed dispersal by animals

Weeds are frequently spread by herbivores by ingestion and dispersal in **faeces**. The faeces offer a good source of nutrients and moisture, depending on animal species. Pasture management plays a critical role in minimizing weed seed dispersal. Late harvesting for **hay** encourages consumption of weeds that have flowered and whose seeds are eaten, compared with cutting less mature herbage for **silage**. Herbivores, such as horses, that deposit faeces in a latrine disperse weed seeds into concentrated areas, compared with cattle and sheep that deposit faeces more randomly. Weed seeds may be potentiated by the **gastrointestinal tract** of herbivores, depending on the hardness of the seed. Soft seeds have higher viability than hard seeds. (CJCP)

Weende analysis
Analysis of **carbohydrates** was, for many decades, accomplished by **proximate analysis** procedures developed at the Weende Experiment Station in Germany over 100 years ago and hence frequently referred to as Weende analysis. The procedure divided carbohydrates into soluble (**nitrogen-free extract**) and insoluble (**crude fibre**) fractions, the former being the digestible portion and the latter the less digestible portion. Crude fibre was determined by boiling the sample in weak acid and then in weak alkali. The residue so obtained was dried and the loss from it, upon ignition, was the crude fibre. Nitrogen-free extract was determined by difference, being the weight of material remaining after subtracting from the weight of starting material the values previously obtained for crude fibre, **crude protein**, **ether extract** and **ash**. Consequently, Weende analysis entailed a **proximate analysis** of the sample under test. Weende analysis served nutritionists well for over a century in that it enabled feeds to be separated into broad categories such as **roughages** with high crude fibre and concentrates with low crude fibre. However, the **digestibility** of crude fibre may sometimes be higher than that of nitrogen-free extract. Consequently, crude fibre does not separate carbohydrates into readily digestible and less readily digestible portions. A more recent method uses detergent extraction to separate carbohydrate fractions. (CBC)
See also: Acid detergent fibre; Neutral detergent fibre

Weir formula
A formula for calculating **heat production** from respiratory

exchange data, mainly used in human studies:

Heat output (kcal) = 3.9% l O_2 produced + 1.1% l CO_2 consumed

For farm animals the **Brouwer formula** is more appropriate. (JAMcL)

See also: Indirect calorimetry

Welfare

A concept of harmonious living by animals, which includes nutrition. The fundamental importance of good nutrition to animal survival means that nutrition has the potential to impact on welfare to a major extent. Farmers, who are directly responsible for managing their livestock, believe that nutrition has a greater impact on welfare than other perceived welfare concerns, such as bodily mutilations, transport or stocking density in housing. Although it is evident that good nutrition is essential for the high levels of productivity expected of modern husbandry systems, there are several nutritional problems that regularly afflict livestock. These include a failure to provide a diet with adequate fibre and that requires animals to forage for a substantial part of the day, nutritional inadequacy of diets provided to the highest-producing animals, in particular dairy cows in peak yield, inadequate diets fed to parent stock and insufficient feed for livestock in extensive grazing systems during drought. (CJCP)

Key reference

Phillips, C.J.C. (ed.) (2016) *Nutrition and the Welfare of Farm Animals*. Springer, Cham, Switzerland, 247 pp

Wet feeding:
see Liquid diets

Wet season
In many parts of the world, especially in the tropics and subtropics, defined wet and **dry season**s are normal. In most regions wet seasons occur in the warmer months, resulting in optimum conditions for plant growth. In equatorial regions two **rainy season**s per year are not uncommon.

In the wet season, where **grazing** is available livestock generally have sufficient natural vegetation, which is high in protein and low in fibre, for their current needs and recovery from dry-season underfeeding. Where grazing is not available, animals are often stall-fed or tethered during the rains, to protect cropping areas. Because demands for labour are high at this time, cut-and-carry is often inadequate. For animals in these conditions, wet-season feeding stress is possible. The start of the rains is followed by ploughing and planting. Where land pressure is high and rainfall adequate, two arable crops are needed every year (e.g. **wheat**, **rice**). In the arid and semi-arid regions rainfall tends to be variable, in both amount and pattern of distribution, often threatening production of stable foods. When available, irrigation expands the growing season. (TS)

Wheat (*Triticum* spp.)
The whole seed of the wheat plant. Wheat is a very important food **grain** and third in terms of global production after **maize** and

rice. It is the most important staple crop in temperate zones, several types being grown in Europe, Australia and North America. These include soft white winter, hard red winter, hard red spring and soft red winter wheat, the colour describing the seed colour. Hard wheats contain more **crude protein** (CP) than soft wheats. The most important types are: *Triticum aestivum*, used in bread-making and animal feeding; *T. durum*, used in making pasta; and *T. compactum*, a softer type used for cake baking, crackers, biscuits, pastries and **flour**s.



Heads of wheat (*Triticum aestivum*) ready for harvesting. Photo courtesy of Dag Endresen. Licensed under CC BY 2.0.

During threshing the wheat husk – unlike that of **barley** and **oats** – detaches from the grain, leaving a less fibrous product. As a result, wheat is only slightly lower than maize in **metabolizable energy** (ME) value but contains more crude protein, **lysine** and **tryptophan**. The CP concentration ranges from 60 to 220 g kg^{-1} dry matter (DM) but is normally between 100 and 170 g kg^{-1}. The

amount and quality of the proteins present in wheat are very important since they determine the suitability of the flour for bread making. The mixture of proteins present in the **endosperm**, collectively referred to as **gluten**, have elastic properties and comprise two main proteins: prolamin (gliadin) and glutelin (**glutenin**). The main **amino acid**s present in wheat gluten are glutamic acid (330 g kg^{-1}) and **proline** (120 g kg^{-1}), and the proportion of essential amino acids is similar to that of other **cereal**s, with lysine being the first limiting amino acid for pigs and poultry. The grains also contain (per kg DM) 256–636 g **starch**, 5–40 g **ether extract** and 133–366 g neutral detergent fibre (NDF).

The main components of the wheat grain are a starchy endosperm, **bran** and germ, representing 80–85%, 12–18% and 2–3% of the grain, respectively. The **endosperm** is mostly composed of starch and proteins, while most of the fibre, vitamins, minerals and phytochemicals are concentrated in the outer and germ layers (Pomeranz, 1988).

Wheat is used mainly as an **energy source** in the human diet but it also contains significant amounts of other important nutrients, including proteins, fibre and minor components, such as **fats**, vitamins, minerals and phytochemicals. Table 1 illustrates an assessment of the importance of wheat and other cereals in the British diet. Cereals and breads were found to be the main source of energy for all age groups, contributing 31% for adults, and of **non-starch polysaccharide**s (**dietary fibre**), with bread alone contributing about one-fifth of the average daily intake. In addition, the cereals, including wheat, contributed significantly to the daily

intake of protein, B vitamins and **iron**.

Table 1. Percentage contributions of cereals and cereal products to average daily intake of some essential nutrients and food components of adults (aged 19–64) in the UK (from Shewry and Hey, 2015)

	Total		Breads	
	Men	Women	Men	Women
Energy	31	31	12	10
Protein	23	23	11	11
Carbohydrates	45	45	21	18
NSP	40	37	21	18
Thiamin	36	35	16	15
Riboflavin	22	22	5	4
Niacin[a]	25	26	11	10
Pyridoxine	16	18	5	4
Folates	27	27	12	12
Iron	40	38	16	15
Calcium	32	30	19	15
Magnesium	28	28	13	13
Sodium	31	31	19	18
Zinc	25	25	12	12
Copper	34	32	15	14
Selenium	28	27	13	12

[a] Only partly available. NSP, non-starch polysaccharides (dietary fibre).

The presence of wheat gluten in the diet can trigger adverse inflammatory, immunological and autoimmune reactions (coeliac disease) in some people, which has led to their avoiding wheat and to a widespread introduction of gluten-free foods. Related reactions may occur in poultry and can be alleviated by dietary **supplementation** with β-**glucanase** enzyme. Similar therapy is being used with some success in affected humans.

By-products of flour **milling** are also used as human food products, namely wheat germ meal and wheat bran. After cleaning (screening), sifting and separating, wheat is passed through corrugated rollers, which crush and shear the kernels, separating the bran and germ from the **endosperm**. Clean endosperm is then sifted and ground to flour. The remaining product can be separated into middlings, bran, germ and mill run. Mill run includes cleanings (screenings) and all leftover fines and is often used for animal feeding. Wheat bran is an excellent source of **dietary fibre** (300–600 g kg^{-1}), with low levels of energy and other nutrients. Wheat germ meal is high in CP, fat and energy at around 370 g kg^{-1}, 103 g kg^{-1} and 4300 kcal kg^{-1}, respectively, and in addition contains high levels of vitamins and minerals, since most of these nutrients are concentrated in the germ fraction.
Wheat is commonly used for feeding to farm livestock when it is surplus to human requirements or is considered not suitable for the human food market. Otherwise it may be too expensive. Milling-quality wheat generally results in better performance than

feed-grade wheat, because it contains fewer impurities such as small stones, weed seeds and broken kernels. Some wheat is grown for feed purposes. It can be used as a replacement for maize as a high-energy ingredient and it requires less protein supplementation than maize. Enzyme supplementation of wheat, barley or **rye** diets with a fungal β-**glucanase**/**xylanase** enzyme complex has been shown with **laying hen**s to result in improved **nutrient digestibility**, reduced intestinal **viscosity** and a reduction in the incidence of dirty **eggs**.

Wheat is very palatable if not ground too finely and can be utilized efficiently by all classes of poultry and pigs. Good results are obtained when wheat is coarsely ground (hammer mill screen size of 4.5–6.4 mm) for inclusion in **mash** diets. Finely ground wheat is not desirable, because it is too powdery, causing discomfort to all livestock in eating it unless the diet is pelleted. Finely ground wheat readily absorbs moisture from the air and **saliva** in the feeder, which can result in feed spoilage and reduced **feed intake**. Also, feed containing finely ground wheat can bridge and block feed lines in feeding equipment. The whole grains can be fed to poultry and sheep and can be crushed prior for feeding to cattle, pigs and horses. One benefit of wheat as a feed ingredient is that it improves pellet quality, due to its gluten content, so that the use of a pellet binder may be unnecessary.

As noted above, the presence of wheat in diets for poultry (and to some extent pigs) can be deleterious because of high **viscosity** found in the digestive tract, reducing **nutrient digestibility** and destabilizing the resident microbiota. Supplementation of

commercial feeds with the β-glucanase enzyme helps to mitigate this effect.

By-products of the flour milling industry are very desirable ingredients for poultry and pig diets. In general the by-products with lower levels of **crude fibre** are of higher **nutritive value** for poultry and pig diets. Table 2 shows the typical composition of wheat and two by-products – wheat middlings and wheat shorts – commonly used in poultry and livestock feeding. Nutrient composition can be quite variable, depending on differences in crop variety, fertilizer practices and growing, harvesting and storage conditions. Therefore periodic analysis of batches of wheat and by-products for nutrient content is recommended.

Table 2. Typical composition of wheat and wheat by-products for poultry feeding (Blair, 2018)

	Wheat	Wheat middlings	Wheat shorts
Dry matter (g kg^{-1})	880	890	880
ME (kcal kg^{-1})	3180	2200	2750
ME (MJ kg^{-1})	13.26	9	11.3
Crude fibre (g kg^{-1})	26	73	69
Crude fat (g kg^{-1})	20	42	46

	Wheat	Wheat middlings	Wheat shorts
Linoleic acid (g kg^{-1})	9.3	17.4	19
Crude protein (g kg^{-1})	135	159	165
Amino acids (g kg^{-1})			
Arginine	6	9.7	10.7
Glycine + serine	10.6	13.8	17.3
Histidine	3.2	4.4	4.3
Isoleucine	4.1	5.3	5.8
Leucine	8.6	10.6	10.2
Lysine	3.4	5.7	7
Methionine (Met)	2	2.6	2.5
Met + cystine	4.9	5.8	5.3
Phenylalanine (Phe)	6	7	7
Phe + tyrosine	9.8	9.9	12.1
Threonine	3.7	5.1	5.7
Tryptophan	1.5	2	2.2
Valine	5.4	7.5	8.7

	Wheat	Wheat middlings	Wheat shorts
Major minerals (g kg^{-1})			
Calcium	0.6	1.2	1
Phosphorus (total)	3.7	9.3	8.6
Phosphorus (non-phytate)	1.8	3.8	1.7
Chloride	0.6	0.4	0.4
Magnesium	1.3	4.1	2.5
Potassium	4.9	10.6	10.6
Sodium	0.1	0.5	0.2
Trace minerals (mg kg^{-1})			
Copper	6	10	12
Iodine	0.04	NA	NA
Iron	39	84	100
Manganese	34	100	89
Selenium	0.33	0.72	0.75
Zinc	40	92	100

	Wheat	Wheat middlings	Wheat shorts
Vitamins (IU kg^{-1})			
Vitamin A	667	5000	NA
Vitamin E	15	20.1	54
Vitamins (mg kg^{-1})			
Biotin	0.11	0.33	0.24
Choline	778	1187	1170
Folacin	0.22	0.76	1.4
Niacin	48	72	107
Pantothenic acid	9.9	15.6	22.3
Pyridoxine	3.4	9	7.2
Riboflavin	1.4	1.8	3.3
Thiamin	4.5	16.5	18.1

Wheat middlings consists of fine particles of wheat bran, wheat shorts, wheat germ, wheat flour and some of the offal from the 'tail of the mill'. This mixture of shorts and germ is the most common by-product of flour mills. In conventional feed manufacturing this by-product is regarded as a combination of bran and shorts and tends to be intermediate between the two in composition. It is commonly included in commercial feeds as a source of nutrients and because of its beneficial influence on pellet quality. When

middlings (or whole wheat) is included in **pelleted feed**s, the pellets are more cohesive and there is less breakage and fewer fines. The name 'middlings' derives from the fact that this by-product is somewhere in the middle between flour on one hand and bran on the other. This by-product is known as pollards in Europe and Australia. The composition and quality of middlings vary greatly, due to the proportions of fractions included, and also the amount of screenings added and the fineness of grind. The North American feed regulations require that the product must not contain more than 95 g crude fibre kg^{-1}.

Steam **pelleting** of wheat middlings has been shown to increase the ME and CP utilization in poultry diets by rupturing the **aleurone** cells and exposing the content of the cells to attack by digestive enzymes. (RB)

References

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Wheatfeed:

see Milling by-products

Whey

A **by-product** of cheese manufacture after the curds have been removed from **milk**. Whey contains approximately 93% water, 5% **lactose**, 1% **protein**, 0.6% **ash** and 0.4% **fat**. Whey can be fed in liquid form to pigs, or dried for manufacture of **milk substitute**s. (PCG)
See also: Dried whey

Whey protein
Proteins consisting of the **albumin**s and globulins found in **milk**, but not the **casein**, which is removed during cheese manufacture. Whey proteins may be concentrated by ultrafiltration to produce whey concentrate (12% protein), or the **lactose**, **minerals** or both may be removed to produce demineralized, delactosed whey (30% protein). (PCG)

Whole-crop silage
Silage made from **cereal**s in which the seeds have begun to form but are not yet ripe. The entire plant is ensiled. Crops used for this purpose are **barley**, **wheat**, **triticale**, **oats**, **sorghum**, **rye**, **rice** and **maize**. Worldwide, maize is the most popular cereal crop for conservation as silage (see table). The advantage of whole-crop over **grass silage** is that **grain** formation in whole-crop gives the silage a high **starch** content and thus provides more rapidly available energy, but conversely whole-crop has a lower **crude protein** content than grass silage. However, **urea** treatment or mixing with **forage legumes** can alleviate this problem. Typical chemical analyses are outlined in the table.



Wholecrop maize silage being loaded and rolled in a clamp. Photo courtesy of Werktuigendagen. Licensed under CC BY-SA 2.0.

Nutrient composition of whole-crop silage

	Whole-crop wheat silage	Whole-crop maize silage	Grass silage
Dry matter (g kg^{-1})	350–500	300	200–250
Metabolizable energy (MJ kg^{-1} DM)	9.5–11.5	11–12	10.5–12
Digestibility (g kg^{-1} DM)	60–70	70–75	65–75
Crude protein (g kg^{-1} DM)	90–110	80–100	120–180
pH	3.8–4.8	3.5–4.5	3.7–4.2

	Whole-crop wheat silage	Whole-crop maize silage	Grass silage
Starch (g kg^{-1} DM)	150–300	250–350	0
Ammonia (g kg^{-1} TN)	30–70	40–70	10–100

Like grasses, whole-crop cereals contain soluble **sugars** as the main non-structural **carbohydrate**, but unlike grasses their **digestibility** does not fall during maturation, as formation of starch in the seed offsets decreased digestibility of other plant parts. In areas where maize will not grow, barley and wheat (in temperate regions) and sorghum (in arid and semi-arid areas) are used. The optimal **harvesting** stage for whole-crop silage is between the milky and late mealy-ripe stages. Corn crackers are fitted to forage harvesters for maize to crack the grain, so reducing the passage of undigested grain through the ruminant gut without **digestion**. Whole-crop is easy to ensile because it has a high **dry matter**, low buffering capacity and ample sugar for a good **fermentation**. However, at feed-out these silages are more prone to aerobic spoilage, partly due to the high dry matter content, which makes compaction more difficult and can allow the survival of larger **yeast** populations during the fermentation phase. (DD)

Willow (*Salix* spp.)

More than 300 species of a tree or shrub that grows in temperate

regions. Willow has simple leaves, as well as male and female flowers on one or two stems. They have no flower cover, but bracts covered with fur can be seen at the base of their flowers. Its male flowers have two to 30 stamens. Female flowers have two stamens and an ovary.



Weeping willow tree (*Salyx babylonica*). Photo courtesy of Moonjazz. Licensed under Public Domain Mark 1.0.

Useful and medicinal species include *Salix alba*, *S. pentanda*, *S. viminalis*, *S. fragilis*, *S. triandra*, *S. purpurea*, *S. caprea* and *S. daphnoides* (Zargari, 1997). The bark of the willow tree contains a **glycoside** called salicoside or salicin, with the formula $C_{13}H_{18}O_7$, which is abundantly found in the leaves and female flowers and the bark of old trees, and is considered a precursor of important drugs containing salicylic acid (Zargari, 1997; Tawfeek *et al.*, 2021). From the **oxidation** of salicin in the presence of dilute nitric acid, a

compound called helicin ($C_{13}H_{16}O_7$) is obtained. Another active compound is spireine ($C_{22}H_{27}O_4N$). If the two compounds of helicin and spireine are hydrolysed, salicylic aldehyde and D-**glucoside** are produced, which are used in the perfumery industry (Zargari, 1997). In addition to these glucosides, the bark of willow trees contains substances such as wax, **gum**, resin, calcium **oxalate** and **tannin** and 322 compounds and secondary **metabolite**s (Tawfeek *et al*., 2021). Bioactive compounds extracted from the bark of willow trees are claimed to have anti-convulsant, anti-inflammatory, high antioxidant, anti-cancer, anti-diabetic, antimicrobial and anti-**obesity** characteristics, as well as being protective of the nervous system and the liver and a strong pain killer for humans and domestic animals (Tawfeek *et al*., 2021). The use of willow extracts in the feeding of domestic animals (poultry and ruminants) is believed to reduce tension and **heat stress**, and potentially improves the performance and health of the host (Saracila *et al*., 2021). Willow trees may be used in phytoremediation, reducing harmful elements, particularly heavy and toxic **metals** in the earth (Zhao and Yang, 2017). (AS; BH-G; CJCP)

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Wilting

A method of reducing the moisture content of crops in the field, using natural resources of wind and solar energy. Wilting of herbage crops for **silage** requires the herbage to be cut with a mower and left in the field for varying periods prior to lifting and ensiling. In poor weather conditions, dry matter (DM) content of crops will increase only slightly and in extended wilting periods soluble **sugars** and **protein** content will be reduced. In contrast, during good weather conditions wilting will be rapid with minimum losses of soluble sugars and protein content. Under these conditions the DM content of the crop may exceed 350 g kg^{-1}. Ensiling of wilted herbage can result in the **fermentation** process being inhibited with high pH (> 4.5) and high residual sugar content of > 50 g kg^{-1} DM. Wilting may also reduce undesirable microorganism activity, such as clostridia, and result in silage free of butyric acid. Wilting of crops to > 300 g kg^{-1} will almost eliminate **silage effluent** production. Rapid wilting of **grass** crops has been shown to give improved nutritive quality with higher DM intakes and animal production responses. (RJ)



Wilting a grass crop by turning it helps to increase the dry matter content before storage. This is important to improve the fermentation quality. Photo courtesy of Jack Berry. Licensed under CC BY 2.0.

Wind sucking:
see Sucking

Winemaking residues
Winemaking residues, or winery pomace, are **by-product**s of **grape** juice production. Winery waste pressed with the stalks consists of 30% stalks, 30% seeds and 40% skin and pulp. Its nutritional value is similar to that of **straw** (see table). Pomace without stalks may be fed to dairy cattle (up to 6.5 kg per day), providing a good **feed** when supplemented with concentrates and **hay**. Grape seed may be separated from the pomace and pressed for its **oil**. The **energy** required to digest the residual grape seed meal, due to its high fibre and tannic acid contents, is so great that realistically it is only usable as a carrier for feed ingredients such as

molasses. Grape marc, the deseeded pomace, has a lower fibre content than pomace and can be fed to horses at < 10% of total diet. Pulp and seeds are good sources of **calcium** but poor sources of **phosphorus**, **magnesium** and **sodium** and have a **copper** level capable of causing hypercupraemia in some species. Winery by-products are generally only usable in diets for ruminants and horses. (JKM)

The nutrient composition of winemaking residues

	Nutrient composition (g kg^{-1} DM)					
	Dry matter (g kg^{-1})	Crude protein	Crude fibre	Ash	Ether extract	NFE
Fresh leaves	300	158	92	86	134	530
Seeds	930	96	457	42	152	256
Oil cake (hydraulic press)	885	136	440	52	85	287

	Nutrient composition (g kg^{-1} DM)					
	Dry matter (g kg^{-1})	Crude protein	Crude fibre	Ash	Ether extract	NFE
Pomace (stalk, skin, seed)	406	117	255	77	99	452
Pomace (stalk and skin)	465–881	137–149	236–358	89–128	50–70	429
Pomace (skin)	889	140–190	220–320	63–80	66–80	350–387

NFE, nitrogen-free extract.
Amended from FAO (2002) Feed resources information service. Available at http://www.fao.org/ag/AGA/AGAP/FRG/AFRIS/Data/19.HTM

Withdrawal feed

A feed given in the final period before slaughter, used when the diets of animals destined for meat include antibiotics or other drugs that cannot be allowed into human food. These substances

are omitted from the withdrawal feed, allowing time for their residues to be cleared from the animal's body. (MFF)

Withholding period

The minimum period that needs to elapse between the last use of a medication on an animal and the shearing or slaughtering of the animal, or the collection of **milk** or **eggs** from the animal for human consumption, in order to ensure that the product's residues fall to or below the maximum permitted limit. Withholding periods can also apply to insecticides, defoliants and other chemicals applied to pasture or crops that are intended to be fed to animals. The time required to eliminate drug residues varies. For example, the withholding period for a particular moxidectin anthelmintic is nil for **milk** and **beef**, and 7 days for **deer meat**. Imidocarb used to treat cattle with tick fever requires a withholding period of 28 days. An export slaughter interval is a similar concept; in this case it is a period which is determined by the importing country.

In some countries all food except water is withdrawn prior to slaughter to reduce digestive tract contents. This is known as a 'wet curfew'. (MFF; GMcLD)

See also: Withdrawal feed

Further reading

Australian Pesticides and Veterinary Medicines Authority (2022) Withholding periods (residues). Available at https://apvma.gov.au/node/1020 (accessed 4 September, 2022).

Wood chewing

Performed by a number of species, but particularly **herbivore**s

such as deer and sheep, as part of their diet. It may indicate a deficiency in the diet, particularly supplementing fibre intake. It often involves destruction of a wooden object followed by **chewing** and ingestion of the wood fibres. These may cause splinters of wood to lodge in the buccal cavity or oesophagus, which can be dangerous, in particular in dogs that chew sticks thrown for them to fetch. In the case of horses, wood chewing can be a sign of a deficient environment and diet, as in individually stabled horses. In horses it should be distinguished from crib-**biting**, which does not necessarily involve consumption of wood fibres. (CJCP)



Wood chewing in dogs fulfils a behavioural need but may cause splinters in the mouth. Photo courtesy of Greg Walters. Licensed under CC BY 2.0.

See also: Stone and stick chewing

Wood residues

Wood contains a high percentage of potentially digestible **carbohydrates** but is largely indigestible when fed in the form of untreated sawdust or chips. Wood **by-product**s include treated

and untreated wood, **cellulose** and paper. Exposing the cellulose from the protecting **lignin**, rendering it more accessible to cellulose-splitting enzymes, can increase **digestibility**. The most promising treatments are chemical, ball **milling**, steam, muka (heating at 210°C followed by milling) and solid **fermentation** using fungi. Lignocellulose can be released from lignin and **hemicellulose** by chemical treatment to produce cellulose, which has a high **energy value** for ruminants, and it is also digestible by horses and adult pigs. In adult pigs the digestibility of the **organic matter** in average cellulose is 53%. Ground cellulose is 90% digestible by sheep but cellulose in the form of torn sheets is only 79% digestible. (JKM)

Wool

The wool fibre consists of a column of dead, keratinized cells surrounded by a cuticle, grown in the wool follicle from cells in the dermal papilla (Fig. 1). The follicle bulb is supplied by **blood** vessels and the primary follicles have associated sebaceous and **sweat** glands, and an arrector **muscle**; the secondary follicles have a sebaceous gland. As the fibre elongates, these cells become keratinized, i.e. the protein **keratin** is synthesized (Fig. 2). Wool follicles are grouped in a follicle group with three primary (P) follicles producing large-diameter fibres and several secondary (S) follicles producing thinner fibres (Fig. 3). The S:P ratio determines the inherent overall fibre diameter of that breed or individual.

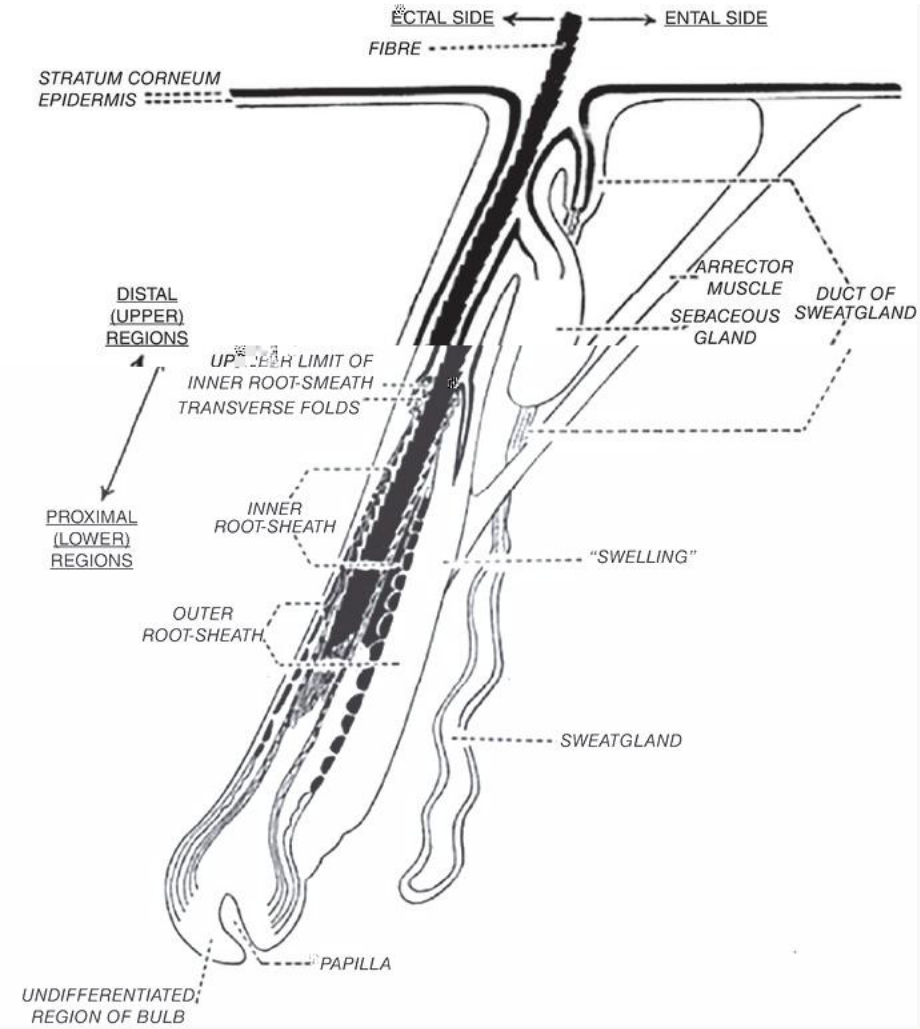


Fig. 1. The structure of a primary wool follicle (from Roberts, 2006).

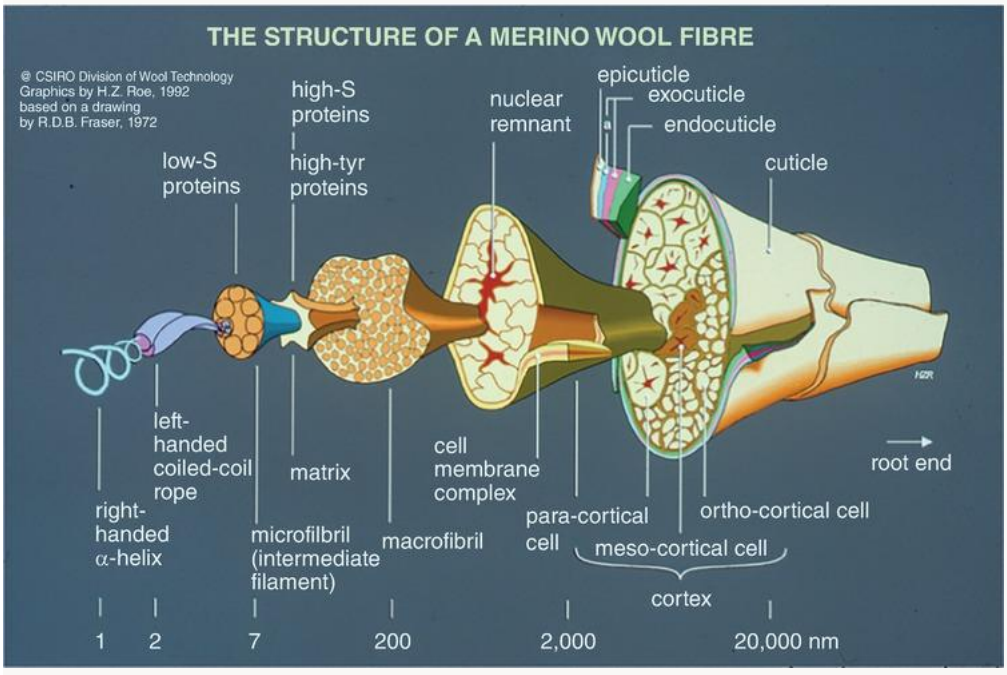


Fig. 2. Diagram of a wool fibre showing cells, cuticle and the biochemistry of the fibre. (CSIRO, undated). Licensed under CC BY 3.0.

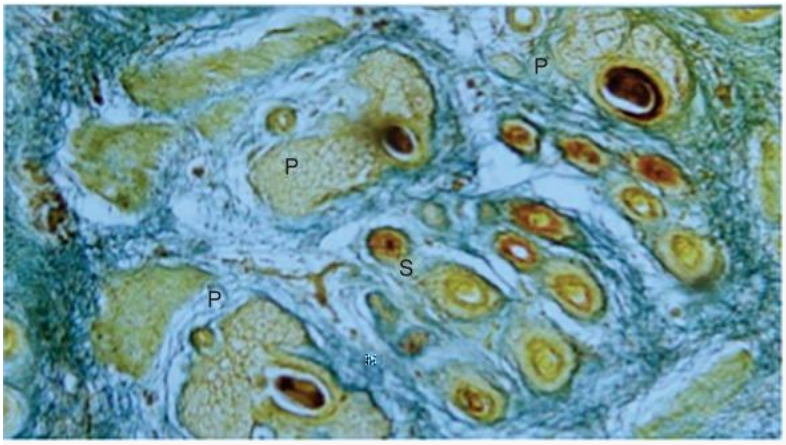


Fig. 3. The follicle group (Ansari-Renani *et al.*, 2011) showing the three primary follicles and several secondary follicles, with their sebaceous glands.

Wool terminology

The fleece is the whole of the animal's fibre covering; a staple is a group of many thousands of fibres (Fig. 4); and crimp is the regular wave in a fibre. Wool can be described as 'fine' or 'strong'. These terms refer to the fibre diameter: fine wool has a small diameter (12–25 μm), strong wool is thicker (25 μm or more). Wool that is fine because it has been grown by nutritionally stressed sheep is called 'hunger fine'. This wool may have 'breaks' – places in the fibre where the diameter is reduced due to underfeeding (the fibre will break here during spinning). 'Tender' wool is wool in which the fibres have a low tensile strength. Some fibres have a medulla (an empty space in the middle of the fibre) and these are called kemp fibres.



Fig. 4. A wool staple, showing pronounced crimp (selected part of a

photo by C. Goodwin, published under a CC BY-SA 4.0 licence)

Wool growth

Wool growth is determined principally by the sheep's **genotype**. Within any breed or strain, however, the annual weight of wool produced and the quality of that wool are both influenced to a large extent by feeding. Seasonal changes in wool growth, which can be very large (more than fourfold in some breeds), are due in part to circa-annual changes in **photoperiod** and in part to quantitative and qualitative changes in the nutrition available to the grazing animal in the course of the year, as well as to changes in physiological state (e.g. pregnancy and **lactation**), which tend to be associated with season.

Energy intake can affect wool production, particularly at high levels of **protein** intake. The major nutrient determining wool production is protein, or more specifically the **sulphur**-containing amino acids, **methionine** and **cysteine**, since 13% of the wool protein, **keratin**, is **cystine**, which is derived from them. **Rumen microorganisms** can synthesize methionine in the rumen, by a pathway that is dependent on adequate **sulphate** in the diet. Methionine undergoes conversion to cysteine, most probably in the **liver**, and it is the rate at which cystine is synthesized from cysteine in the wool follicle that determines the rate of fibre growth.

The length of the wool fibre and the fibre diameter (D), which are the main determinants of fleece weight (W), are both affected by nutrition. The ratio $W:D^3$ is relatively insensitive to nutritional

influence and can be regarded for most purposes as remaining constant for individual animals. This affords a means of assessing the wool production potential of sheep subjected to different nutritional regimes. (AJFR; GMcLD)

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Wool biting

A stereotyped oral behaviour in sheep and goats, believed to be due to inadequate **roughage** supplies, particularly in the housed animals. (CJCP)

See also: Coat licking

Wool growth and quality, effects of nutrition

Animal nutrition plays a key role in the productivity and economic impact of animal production systems. Its interactions with genetics, health and animal management are crucial to understanding the complexity of the factors involved and the potential responses to be obtained. The production of natural fibres is not an exception to this complex phenomenon that occurs in different regions of the world, particularly in those mainly oriented towards wool production.

The effect of **sheep nutrition** on wool growth and quality (Fig.

1) has been extensively studied and the focus of this entry is centred on the analysis of the scientific evidence principally generated during the past 20 years about the effect of nutrition to produce fine and superfine wool in pastoral systems, including its potential effects on fibre quality, and further practical application.



Fig. 1. Wool growth and quality, such as the crimp, are affected by the nutrition of the sheep. Photo courtesy of Brian. Licensed under CC BY 2.0.

Wool growth: feed intake and nutritive value of the diet

Feed intake

There is no agreement in the literature about the exact form of the relationship between wool growth and **feed intake**, where both positive linear and curvilinear relationships have been found. Controlled feeding experiments have established the importance of large effects of feed intake on the rate of wool growth; three- to fourfold changes in the rate of wool growth may be induced in an individual animal. However, there is a maximum wool growth rate, depending on sheep genetics (breeds and strains). At this maximum, food increases do not determine changes in the wool growth rate and it has been suggested that this is primarily

influenced by the extent and direction of body weight change. Normally, under grazing conditions, feeding levels are insufficient to achieve the highest growth rates. High wool-producing animals are often those that have responded to a greater extent to increased feed intake, explained mainly by a higher proportion of active follicles and/or a higher efficiency of feed utilization.

Variations in wool growth rate are observed 3–12 weeks after **sheep feeding** changes occur (Fig. 2). The principal effects of **undernutrition** are mainly observed on reductions in fibre production, but, in extreme situations, follicles also stop their growth.

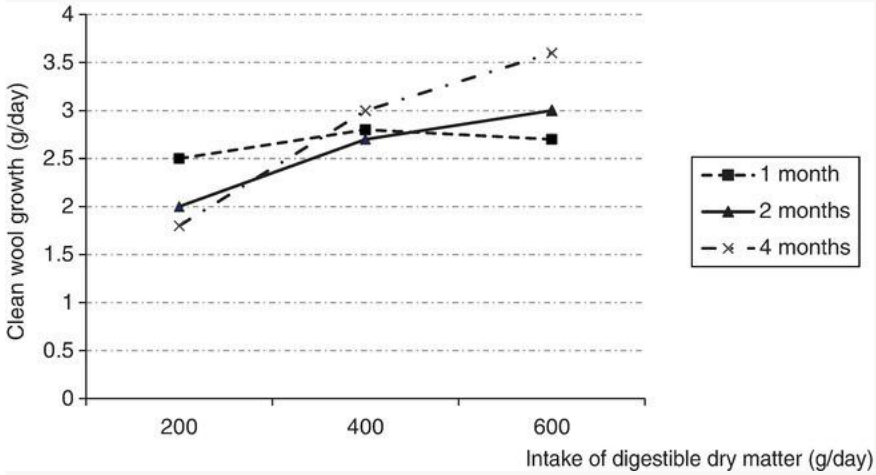


Fig. 2. Relationship of wool growth rate for fine-wool Merino sheep during the first, second and fourth months after the establishment of a dietary change (Adapted from Langlands and Donald, 1977).

However, the efficiency of conversion of feed to wool can be greater on low intakes than on high intake of the same diet. When the diet is changed to an unrestricted quantity, changes in conversion efficiency from 0.81 to 0.46 g wool per 100 g of dry matter (DM) consumed are observed (Saville and Robards, 1972; Robards *et al.*,1974, 1976). Usually, high **digestibility** of the diet

increases consumption and **efficiency of feed conversion** (FCE). An average of 2 g of wool is produced for every 100 g of digestible DM, and this value is affected by **net energy** efficiency and **maintenance** costs. In summary, the level and direction of sheep feeding will influence wool growth efficiency, being greater at low feed intakes and when the changes occur from low to high intakes. Thus, in these circumstances, carryover effects always temporarily reduce the efficiency of the high-intake relative to the low-intake diets.

Protein and energy

Energy is the most common nutritional deficiency in sheep productivity under grazing conditions. With restricted energy consumption, wool growth slows, fibre diameter is reduced, and there is development of weak positions (breaks) along the wool fibre profile. An increase in **energy intake**, except at very low levels of protein content in the diet, usually produces a positive effect on wool growth. Protein is usually the most expensive component of the diet of sheep and protein requirements are highest for growing lambs and lactating ewes that are producing **milk** proteins.

Microbial protein intake available for **digestion** and **absorption** in the intestines is closely related to the intake of **digestible energy** by the animal, rather than to the protein content of the diet. The major nutritional limitation to wool growth is the amount and composition of **amino acid**s available to wool follicles. Maximum rates of wool growth can be attained on

maintenance intakes of energy with about 150 g of **ideal protein** available for intestinal digestion. There are significant interactions between the effects of protein and energy supply on fibre diameter, length and volume of wool, but it is normally a small interactive effect in comparison with the main effect of protein. Very high rates of wool growth are obtainable with moderate energy intakes when **casein** is administered through the **abomasum**. The amount of protein available for digestion and absorption in the **small intestine** is positively related to **digestible energy** intake, and energy supply frequently appears to be the main dietary factor correlated with wool growth.

The net efficiency of dietary **protein utilization** for wool growth is very low (0.20–0.25 g kg^{-1}), and the gross efficiency even lower (0.10–0.15 g kg^{-1}). When **liveweight** loss occurs, wool growth continues, at the expense of body protein. The individual net dietary protein efficiency for wool production varies hugely according to the differences between amino acids and procedures of measurement, highlighting the Cys, Met and Ser efficiencies of 0.45, 0.21 and 0.36, respectively (Reis, 1979).

The amino acid composition of protein and the ratio of protein and energy are critical for wool growth. **Sulphur**-containing amino acids (**cysteine** and **methionine**) play a major role in wool growth. An important function of methionine is the provision of cysteine via the transulphuration pathway; it can also be catabolized via the **transamination** pathway. At normal levels of methionine absorbed by sheep, about three-quarters of the methionine-S is converted to cysteine-S. Both length growth (L)

and diameter (D) of wool fibres respond to changes in protein supply. Generally, the ratio of L:D remains approximately constant.

Presumably the necessity to continue to produce wool fibre despite fluctuations in the supply of **oxygen** and nutrients, due to transportation of O_2 from red **blood** cells to the mitochondria during periods of increased metabolic activity and nutrient demand, has resulted in some of these unique features (L and D), while others reflect the high level of DNA and **protein synthesis** occurring in the follicle. The major role of amino acid supply in controlling wool growth is evident, but scientific evidence indicates that small interactions with energy supply can occur (Reis *et al*., 1992). The concentration of **urea**, **cystine**, methionine and other essential amino acids in plasma increases with protein level. Increasing energy supply reduces the concentration of urea and essential amino acids in plasma but not that of cystine or methionine.

Minerals and vitamins

Many vitamins and **trace element**s are necessary for wool growth. The macro mineral, sulphur, plays an important role in wool production, as it is necessary for the synthesis of high-sulphur amino acids (SAA) by rumen microorganisms.

Copper deficiency causes **depigmentation** of wool in black sheep and the steely wool syndrome. Wool growth rate is reduced by this deficiency, but a reduction in feed intake may be involved. Copper has direct effects on the activity of an unidentified enzyme on **oxidation** of thiol groups to form disulphide linkages (keratinization). Copper is also necessary for the activity of

tyrosinase and the tyrosinase-related proteins involved in melanin synthesis and is also involved in **zinc** effects, being specifically required by rapidly proliferating tissues. There is some evidence that copper **supplementation** stimulates wool growth. Zinc deficiency causes brittle wool and loss of crimp; extreme deficiency causes cessation of fibre growth and fleece shedding. Various abnormalities, such as fractured basal ends of fibres and loss of cuticle scale, will appear in wool fibres after 2 weeks of zinc deficiency.

Selenium also plays a role in wool growth. Its deficiency reduces wool growth, even without a reduction in feed intake; selenoproteins have key metabolic roles as **antioxidant**s and affect the redox status of cells. Oxidative stress causes gene repression through modulation of transcription factors. Such changes may induce temporary growth arrest and lengthening of the cell cycle in the follicle.

Increasing **sodium** in the diet (to 80 g kg^{-1} DM) significantly decreases feed intake, digestibility, liveweight gain and wool growth, either as a main effect or through an interaction with **potassium** (Thomas *et al*., 2007). Wool growth is depressed at high sodium and potassium levels in the diet. Nonetheless, in one study the efficiency of wool growth increased from 10.0 to 15.4 g kg^{-1} **organic matter** intake when the lowest and highest levels of the sodium and potassium were incorporated in the diet, respectively (Masters *et al*., 2005).

Fat-soluble vitamins, namely **vitamin A** and **vitamin D**, are

required for sheep wool production. **Cholecalciferol** (vitamin D_3) receptors are in the outer root sheath, bulb and dermal papilla of the follicle, and alopecia occurs with defects in the vitamin D receptor, retinol (vitamin A), appearing to influence follicle function by altering keratinocyte proliferation and differentiation too, with direct effects on the expression of **keratin** genes. At present there is little evidence implicating α-**tocopherol** (**vitamin E**) or phytylmenaquinone (**vitamin K**) in follicular growth events.

In lambs and **hogget**s, B vitamins (folic acid, **thiamine**, vitamins B_6 and B_{12}) are important for maintaining high rates of fibre growth because of their roles as co-factors for enzymes involved in the **metabolism** of **methionine** and **cystine**. However, in adult sheep there is no experimental evidence for an effect of the supply of individual vitamins on wool growth. It is generally assumed that the rumen microorganisms synthesize sufficient B vitamins for the animal's needs, but proof is currently lacking for high rates of wool growth. The only direct demonstration of a **vitamin deficiency** negatively affecting wool growth occurs in pre-ruminant lambs supplied with diets deficient in folic acid.

Wool quality

Feed intake

The changes in feed intake on wool growth include changes in fibre diameter, fibre length and staple length. Indeed, considering the same body surface, changes in wool production can be influenced by the supply of nutrients available to wool follicles during the process of fibre growth.

Nutrition and environment

Exposure of areas of skin to heat or cold induces localized changes in skin **temperature**, indicating that wool growth, especially in length, is specifically retarded by low temperatures. The effects are presumably related to reductions in **blood flow** and hence to nutrient supply. Localized high temperatures do not influence wool growth until unphysiologically high values are reached (> 32°C). Using the same diet, the main factors affecting the growth rate of wool are **climate** season and **genotype**. The existence of a uniform seasonal rhythm of wool growth, on a constant diet, provides indirect evidence which suggests that this rhythm, with maximum growth in summer and minimum in winter, is induced mainly by seasonal changes rather than temperature. The seasonal change in fibre diameter is significantly greater than change in fibre length (71.4% and 41.4%, respectively) (Schlink *et al*., 1999).

The wool growth of Merino sheep will respond to changes in nutrition throughout the year, but breeds with a large inherent rhythm in wool growth rate (e.g. Cheviot or Scottish Blackface) show little or no response to changes in nutritive status during winter. Shearing date affects the quantity of wool produced, reflecting an interaction between nutrition and temperature (early spring *vs*. later spring) in Merino and Polwarth breeds (Table 1).

Table 1. Effect of shearing date in Uruguay (43° 39′ S and 54°40′ W) on fleece weight, fibre diameter, wool growth and body weight (mean) in Merino and Polwarth breeds (adapted from Fernandez Abella *et al*., 1991, 2020).

	Shearing date				
	15 August	15 September	15 October	15 November	Breed
Fleece weight (kg)	3.86 + 0.31^{b}	4.01 + 0.36^{ab}	4.29 + 0.41^{b}	4.29 + 0.44^{a}	Polwarth
	4.95 + 0.41^{a}	5.50 + 0.41^{b}	5.60 + 0.46^{a}		Merino
Fibre diameter (μ)	23.52+ 0.92^{a}	23.8 + 1.13^{a}	24.1 + 0.98^{a}	23.7 + 1.22^{a}	Polwarth
	20.2 + 0.85^{a}	20.4 + 1.08^{a}	20.5 + 1.13^{a}		Merino
Body weight (kg) (at shearing)	45.5 + 1.15^{b}	46.3 + 2.00^{b}	51.0 + 2.23^{s}	51.5 + 2.78^{s}	Polwarth
	63.15 + 1.87^{b}	66.48 + 3.42^{a}	67.33 + 2.51		Merino

	Shearing date				
	15 August	15 September	15 October	15 November	Breed
Wool growth (annual average; mg cm^{-2} per day)	1.15 + 0.28[b]	1.49 + 0.32[ab]	1.71 + 0.41[a]	1.66 + 0.39[a]	Polwarth
	1.38 + 0.33[b]	1.70 + 0.38[a]	1.73 + 0.27[a]		Merino

Note: Means for wool traits between columns for each breed at each shearing date with different superscripts differ significantly ($P < 0.05$).

The manipulation of the diet for reducing **methane** emissions and increasing wool production has been studied by different research groups, where they have evaluated different nutritional components in the diet, mainly **nitrate** and **urea**. The results show a potential approach to improve wool productivity and reduce the wool carbon footprint, by changing the ruminal concentration and composition of **volatile fatty acid**s (de Raphelis-Sissan *et al*., 2014). However, more research is needed to improve the understanding of the metabolic and physiology processes involved and the practical issues to implement this approach in commercial situations.

Influences of ewes' nutrition during pregnancy and lactation on the wool production and quality of their progeny

The ewe's maternal nutrition during pregnancy and lactation can have permanent effects on the progeny's wool production and quality, particularly on fleece weight and to a lesser extent fibre diameter. Further, underfeeding of ewes during mid and late pregnancy promotes lighter fleece weights and broader fibre diameters in their progeny, with an extra positive effect of improving lamb survival and lamb **weaning** weights. In addition, adequate ewe nutrition in late pregnancy can improve progeny lifetime wool production and reduce fibre diameter in both single and multiple-born and reared lambs, and even overcome the detrimental effects on those traits because of poor nutrition during early and mid-pregnancy. Management and nutritional practices that improve wool and **meat production** efficiency reduce carbon footprints (Wiedemann *et al*., 2016).

The interaction between nutrition, genetics, reproduction and wool traits

Wool production can be increased by selecting sheep that are more efficient in transforming feed to wool, particularly through increases in efficiency of absorbed nutrients rather than improving the digestibility of the energy or protein in the food eaten by sheep. There is no re-ranking between animals selected or not selected for better wool production across different environments. However, the differences increase in favour of high-wool-producing animals when the supply of nutrients exceeds animal requirements. Ruminal microbiota communities can be altered by animal

genetics, affecting **digesta** flow from the **rumen** and **protein metabolism** in sheep. Sheep selected for increased clean fleece weight showed differences in rumen bacterial population across different nutrition regimens. These findings suggest the possibility in the future of improving wool and other productive traits by animal selection and management of gut species.

Productive implications of enhancing nutrition of ewes and their progeny (lifetime) on wool production and quality

Most of the world's high-quality wool is produced in pastoral systems, in marginal areas for other more intensive production, and which are subject to the effects of climatic variability and the fluctuations of pasture growth and nutritive value. In this context, Table 2 shows a summary of the effects of improving nutrition at different moments of the ewe's productive cycle, and also of lamb rearing after weaning, and its impact on wool production and quality, and further effects on other productive traits of economic relevance. The impact of improving ewe nutrition during late pregnancy and lactation on the productive life of the progeny is also shown, with particular emphasis on wool growth and quality.

The wool production and quality of Merino ewes can be predicted by their liveweight and liveweight change during the reproductive cycle, particularly at joining, and their liveweight change during pregnancy and lactation. Wool characteristics are influenced more by changes in liveweight during late pregnancy than during early pregnancy or lactation (Table 2). In addition, adequate ewe nutrition during late pregnancy can overcome the negative effects on wool production of restrictive feeding during

early pregnancy. Along the productive cycle of the ewe, in general, an increment in the level of nutrition above maintenance has a positive effect on wool production and quality as well, as increasing reproduction performance, health status and animal **welfare**. In addition, adequate feeding of lambs after weaning increases liveweight gain and wool growth and quality. In relation to lifetime effects of improving nutrition of the ewe during pregnancy and lactation, the scientific evidence suggests that wool quantity and quality of the progeny can be substantially and permanently enhanced. These potential effects on the progeny can be predicted from the ewe´s liveweight profile.

Supplementation with Met, Cys, Lys and Ser and other amino acids in the diet of growing animals improves wool production in most of the experiments performed. However, the responses are not consistent when ewes are supplemented with key amino acids during late pregnancy and lactation. In addition, the efficiency and utilization of using amino acid supplements to enhance wool production is very low, even when rumen bypass **protein supplement**s are implemented. Under grazing conditions, the use of amino acid supplements in sheep is not cost effective.

Table 2. The productive and reproductive effects of enhancing nutrition during different stages of the ewe productive cycle and its progeny and lamb rearing after weaning.

Ewe productive cycle	Ewe/lamb nutrition status (above maintenance)	Ewe/lamb wool production and quality	Progeny wool production and quality	Ewe or progeny other traits
Before and after joining	↑ LW and CS	↑ GFW & CFW ↑ SL & FD	–	Ewe ↑ F & FEC
Mid and late pregnancy and lactation	↑ LW and CS	↑ GFW & CFW ↑ SL & FD & SS	↑ GFW & CFW ↑ SL & FD	Progeny ↑ BW & WW ↑ LS
Lamb rearing after weaning	↑ LW, CS, REA, and FT	↑ GFW & CFW ↑ SL & FD & SS	–	–

BW, birth weight; CFW, clean fleece weight; CS, condition score; F, fertility; FD, fibre diameter; FEC, fecundity; FT, fat thickness at REA; GFW, greasy fleece weight; LS, lamb survival; LW, liveweight; REA, rib eye area; SL, staple length; SS, staple strength; WW, weaning weight. Adapted from Thompson *et al.*, 2011; Ramos *et al.*, 2019.

In future nutrition wool research, more attention must be paid to: (i) wool quality traits and interactive effects, particularly in fibre diameter and staple strength – given their economic importance in

wool price; (ii) nutrition and genetic manipulation of rumen microbiota, precision nutrition to reduce the wool carbon footprint and improve animal health and welfare; and (iii) interactive effects between nutrition and genetic selection for fitting the breeds and their strains to different environments, particularly when sheep wool production has been moved to marginal environments or is part of more complex productive systems (silvopastoral and cropping/pastoral). (FM; DFA)

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Working animals

Draught animals are normally fed only on low-quality **roughage**, such as **maize stover** and standing **hay**, because that is the only feed available. Better-quality feeds are used for other farm animals such as dairy cows, pigs or poultry. When fed on such low-protein feeds, cattle are not able to consume more energy than 1.4 times their daily **maintenance** requirement. Cattle undertaking a day's medium to heavy work could easily use up energy at a rate of 1.8 times their maintenance requirement. Under such conditions these animals will lose weight. In some parts of the tropics, especially where the rains fall for only 3 months in the year, the quality of the available grass is so low during the **dry season** that the animals may lose weight even when they are not working. They may then reach the ploughing and planting season in an underfed condition. When they are worked they will lose more condition and may

eventually be unable to complete a full day's work.

Because females breed their own replacements, the total herd size needed to maintain a working animal population can be reduced by two-thirds if female animals are the main source of power. This reduction in herd size is desirable when the land available for animal feeding is limited. However, if the cows are required both to work and to produce **milk**, their **energy requirement**s are considerably increased. A cow working for 6 h per day, and producing 5 l of milk at the same time, has to consume 2.0–2.2 times its maintenance requirement if body weight and milk production are to be maintained. Such levels of intake require the feeding of **grain** in addition to fibrous feeds such as dry savannah grass. An alternative strategy could be to organize the breeding programme so that the cows produce milk at times when they are not required to work.



Working animals play a substantial role in many developing countries. Photo courtesy of Rod Waddington. Licensed under CC BY-SA 2.0.

Work does not significantly increase the **protein requirement** and any extra that is needed can easily be supplied by the food given to provide the extra energy for work. This is true

even when the quality of the feed is low. Therefore, when calculating the feed requirements for work, the energy requirement is much the most important consideration.

To maintain **energy balance**, working animals must consume energy equivalent to the sum of their maintenance energy needs and the energy expended doing work. Much of the energy used by a draught animal is used simply in walking. This can vary from 1.5 to 8.0 J m^{-1} kg^{-1} liveweight, according to ground surface. The former figure would relate to an animal walking on a smooth road, the latter to an animal walking through a muddy paddy field. The **net energy** (NE) required from the feed for work is 3.3 times the work accomplished, to allow for the mechanical inefficiency of work. Thus, an animal achieving 3 MJ of work a day in pulling a plough would need to use 9.9 MJ NE. Assuming that the efficiency of converting **metabolizable energy** (ME) into NE for work is 66%, this means that the animal would need an extra 9.9/0.66 MJ (15 MJ) ME each day to accomplish this amount of work without losing weight.

Work does not seem to increase the food intake of working cattle, though it may for horses. Large working horses have a greater capacity for work than cattle and may have an energy requirement up to 2.5 times maintenance. The amount of food that working cattle will consume depends on their size and the quality of the food offered. It can range from 4.0 kg dry matter (DM) per day for an ox of 250 kg on a low-quality diet to > 13 kg per day for one of 700 kg on a high-quality diet. (AJS)

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Wuchang bream (Megalobrama amblycephala): *see* Blunt snout bream

X

Xanthine oxidase

A **molybdenum**-containing enzyme widely distributed in **milk**, **small intestine**, liver and kidney. Xanthine is produced in the breakdown of the **purine** bases, adenosine and guanosine. Xanthine oxidase utilizes molecular **oxygen** (O_2) in the conversion of xanthine to uric acid and **hydrogen peroxide** (H_2O_2). (NJB)

Xanthophyll

A yellow **carotenoid**, also called **lutein**, $C_{40}H_{56}O_2$, molecular weight 569. Produced by polymerization of isoprenoid units, it is one of the accessory pigments in plants that absorb light. It has no

vitamin A activity. (JAM)

Xerophthalmia

A condition in which the cornea dries and thickens. It is caused by severe **vitamin A** deficiency in calves deprived for a long period of green forages or other sources of vitamin A. Other species deprived of vitamin A show corneal keratinization. (WRW)

See also: Eye diseases; Night blindness; Vitamin deficiencies

Xylan

A homopolysaccharide of **xylose**, having (1→4)-linked β-D-xylopyranosyl residues. It is classified as a **hemicellulose**. The homoglycan is uncommon and the term xylan refers to branched polymers in which the backbone consists of xylose residues and the branches of other **sugars**. D-Xylans are the most common of the hemicelluloses, occurring in all parts of land plants, primarily as structural components. They may account for up to 30% of the dry weight of woody tissue in angiosperms. The most common side-chains are **arabinose**, the **disaccharide** of arabinose or a methylated **glucuronic acid** (*O*-acetyl-L-arabino)-(4-*O*-methyl-D-glucurono)-D-xylan; a substantial portion of xylans are acidic due to this side-chain. Arabinose side-chains are common in the **endosperm** of **barley**, **wheat** and **rye**. D-Xylans are also major structural components of **maize** cobs, **cereal** hulls, **bran**s and **straws** and fruit skins. **Cottonseed** bran and **groundnut** shells are industrial sources of xylose. Xylans are major **substrates** for ruminant **fermentation**. Some angiosperms secrete **gum** exudates and the side-chains of the **polysaccharide**s contain

galactose and xylose, as well as arabinose and **uronic acid**s. Xylans are also skeletal glycans in some **algae**, e.g. *Chlorophyta* or green algae. (JAM)
See also: Arabinoxylans; Carbohydrates; Dietary fibre; Structural polysaccharides; Xylanases; Xyloglucans

Xylanases
Enzymes that hydrolyse chains of **xylose** residues. For example, 1,4-β-D-xylanase acts on the (1→4)-β-D chains of **xylan**s, **arabinoxylans**, glucuronosylans and related polymers. These microbial enzymes work in concert with **glycosidase**s and, in the case of D-xylans, β-D-xylosidases attack the non-reducing terminal **sugar**. They are usually isolated from bacteria (e.g. *Aureobasidium pullulans*, *Aspergillus niger* and *Trichoderma viride*). (JAM)
See also: Carbohydrates; Dietary fibre; Xyloglucans

Xylitol
Sugar alcohol, $C_5H_{12}O_5$, molecular weight 152, produced by reduction of the **aldehyde** group of **xylose**. (JAM)
See also: Carbohydrates

Xyloglucans
Heteropolysaccharides consisting of a (1→4)-linked β-D-glucan core to which single (1→6)-α-D-**xylose** units are attached. The term is actually a misnomer, as L-**fucose** and D-**galactose** may also be linked to the xylose residues. Xyloglucans are the major hemicellulosic component of the cell wall of dicotyledonous plants. Their ability to **hydrogen**-bond with **cellulose** and thus connect

cellulose fibres to **pectic substance**s is due to the structural similarity between xyloglucans and cellulose. Despite the presence of side-chains, the primary enzyme that attacks cellulose, endo-1,4-β-D-**glucanase**, also hydrolyses xyloglucans. Several xyloglucans can be extracted from seeds and are important industrially because they form gels. These seed components stain blue with **iodine** and are collectively known by the archaic term amyloid. (JAM)
See also: Carbohydrates; Dietary fibre; Hemicelluloses; Structural polysaccharides

Xylose
A **pentose** monosaccharide, $C_5H_{10}O_5$, molecular weight 150, widely distributed in plants, almost exclusively as a component of **polysaccharide**s. Xylose is the major constituent of the **hemicellulose**s in wood, **straw**, **maize** cobs, **groundnut** shells, **grain** brans and hulls. Small **intestinal absorption** is by passive **diffusion**. (JAM)
See also: Arabinoxylans; Carbohydrates; Dietary fibre; Monosaccharides; Xylan; Xyloglucans

Y

Yam

Starchy tubers including taro or cocoyam (*Colocasia esculenta* (L.) Schott), winged yam or water yam (*Dioscorea alata* L.), yellow yam (*Dioscorea cayenensis* Lam.), Chinese yam (*Dioscorea esculenta* (Lour.) Burk.) and white yam (*Dioscorea rotundata* Poir). They are grown primarily as human food. The aerial parts can be used for ruminant feed and the peel from tubers for pig feed. Tubers are more palatable cooked than raw, as cooking destroys the **alkaloid** diocorene. Considerable variation is found in the growth habit amongst the varieties listed. Climbing varieties are found with small leaves, while non-climbing varieties have large leaves.



Field of taro yams in the Punjab, Pakistan. Photo courtesy of Sunni Person. Licensed under CC BY-SA 3.0.

Cocoyam is a tuberous plant with large leaves, similar in shape to elephant ears. Cattle and sheep find the leaves very palatable. In feeding trials with poultry, cocoyam meal has been shown to be a poor substitute for **maize** meal, depressing growth and food conversion efficiency. Cocoyam contains up to 0.4% of **oxalates** but their effects can be reduced by cooking or the addition of

calcium carbonate to the ration. Cooked cocoyam is often fed to pigs.

Typical composition of yam products (% dry matter (DM)).

	DM (%)	**CP**	**CF**	**Ash**	**EE**	**NFE**	**Ca**	**P**
Cocoyam leaf, fresh	8.2	25.0	12.1	12.4	10.7	39.8	1.74	0.58
Cocoyam leaf meal	–	23.2	13.2	9.9	5.9	57.4		
Cocoyam tubers, fresh	26.2	8.7	1.7	4.0	0.4	85.2		
Cocoyam meal	95.2	2.9	0.7	4.9	3.4	87.9		

	DM (%)	CP	CF	Ash	EE	NFE	Ca	P
Winged yam leaf, fresh	24.1	12.0	25.3	7.9	2.3	52.5	0.95	0.16
Winged yam tuber peel, fresh	25.9	11.7	6.6	9.5	1.0	71.2		
Yellow yam tuber peel, fresh	21.7	7.4	7.6	7.5	0.7	76.8		
Yellow yam meal	98.9	5.34	5.39	3.93	0.80	84.5		

	DM (%)	CP	CF	Ash	EE	NFE	Ca	P
Chinese yam tuber peel, fresh	7.0	10.0	7.6	6.3	0.9	75.2		
White yam tuber peel, fresh	17.7	11.2	9.5	9.8	1.2	68.3		

CF, crude fibre; CP, crude protein; DM, dry matter; EE, ether extract; NFE, nitrogen-free extract

Winged yam is the main cultivated variety, with very large tubers and a climbing growth habit. Leaves are smaller than those found on cocoyam. Tubers are grown for human food but the peel is a valuable feed for livestock. Yellow yam tubers do not store well. Peelings are used for pig feed. Chinese yam is a climbing variety that produces small oval tubers that are sweet in **taste** and have thin peel. The peel can be used for pig feed. White yams are grown widely in West Africa and have tubers that store well. As with other

varieties, the peel can be fed to pigs. (LR)

Yarrow (*Achillea millefolium*)

A perennial plant from the Asteraceae family, with a height of 20–90 cm, that grows naturally in a wide region of the northern hemisphere (Zargari, 1997; Ali *et al*., 2017). The leaves are without petioles, and are long and covered with **hairs**, whereas the flowers are compound and capitulum shaped.



Yarrow (*Achillea millefolium*). Photo courtesy of Dvortygirl. Licensed under CC BY-SA 4.0.

The floral branches of yarrow contain essential **oil** and a glucoalkaloid called achilleine; they also contain **inulin**, phytosterol, **tannin**, aconitic (acrylic acid), volatile oil, **polyphenol**s, betaine lactone, acetylene compounds, resin, phosphate, **nitrate** and **potassium salts** and **organic acid**s

(Zargari, 1997; Dalili *et al*., 2022). The plant contains essential oil at 0.13–0.25% by weight, which includes cineol, thuyon, borneol, **formic acid** and **valeric acid**. The blue color of the essential oil is related to the presence of azeulen following distillation (Zargari, 1997).

The claimed therapeutic properties of yarrow include curing bleeding, treating menstrual disorders, curing insomnia and vision problems, being anti-epileptic and anti-convulsant, alleviating haemorrhoids, having anti-inflammatory, anti-wound, and anti-cancer effects, and providing pain relief (Zargari, 1997; Ali *et al*., 2017; Dalili *et al*., 2022). In veterinary medicine, it can be used to treat haematuria (i.e. the presence of blood in urine) and scabies in sheep (Zargari, 1997). As a natural and phytogenic additive, it can potentially play an important role in improving intestinal microbiota, reducing serum **lipid** levels and modulating **immunity** (Norouzi *et al*., 2015; Pliego *et al*., 2022). (AS; BH-G; CJCP)

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Yeast

Single-celled, eukaryotic organism. Yeasts have been used since antiquity in baking and brewing. An important species is *Saccharomyces cerevisiae*, used extensively in the winemaking, brewing and baking industries. In animal feeding, yeasts are used as both a **probiotic** and a nutrient source. The yeasts commonly used in probiotics are ***Candida*** *pintolopesii*, *C. saitoana*, *Torula utilis*, *Saccharomyces cerevisiae* and *S. boulardii*. Live yeasts have been reported to increase beneficial bacterial populations in the **rumen**, leading to increased **feed intake**, weight gain, milk yield and **feed conversion** efficiency, and protect against acidosis. *S. cerevisiae* is the yeast most frequently used as an animal feed. It is used in diets, particularly for non-ruminants, as a source of **protein** and B **vitamins**. **Ribonucleic acid** may account for 30% of the total **nitrogen** in yeasts. When this is digested by **monogastric** animals the **purine metabolite**s include uric acid; this can result in elevated blood uric acid levels with adverse effects on **fat** and **carbohydrate metabolism** (Heuzé, *et al*., 2018).

Fodder yeast can be grown on various **by-product**s, including

citrus press liquor, **potato** pulp, apple pomace, **molasses**, sulphite waste liquor from the paper industry, wood and fruit wastes. Brewers' dried yeast is commonly used as a nutrient source. The dry matter (DM) content of dried brewers' yeast is usually about 936 g kg^{-1} and the typical nutrient composition (g kg^{-1} DM) is **crude protein** 489, **neutral detergent fibre** 88, **acid detergent fibre** 25, **ash** 70, **ether extract** 24, **starch** 109, **calcium** 2.9 and **phosphorus** 13.1. **Cattle** can be fed 1–2 kg per day, and lambs at 1.25% and steers at 1.85% of the total diet. Calves can be fed 3–5% or 2 g kg^{-1} of starter diet. Pigs can be fed 5% (sows 100–400 g per day) and poultry at 9% for male chicks and 2–3% of total diet for female chicks. (JKM; GMcLD)



Yeast cells under the microscope. Photo courtesy of Blueshift 12. Licensed under CC BY 2.0.

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Yeasts as probiotics:
see Probiotics

Yeasts in gastrointestinal tract:
see Gastrointestinal microflora

Yellow catfish (*Pelteobagrus fulvidraco*):
see Catfish

Yellowtail (*Seriola quinqueradiata*)
A member of the tuna family, farmed in sea cages in Japan and some Far East countries at a **water temperature** range of 12–30°C. Those with a market size of 5 kg or less and those over 5 kg are called hamachi and buri, respectively. Larvae are fed live food organisms (e.g. **rotifers** and artemia), enriched with n-3 **fatty acid**s. Grower diets consist of either trash fish supplemented with vitamins or soft extruded feeds. Wild juveniles are also used for farming and they are gradually weaned on prepared feeds. (SPL)



Yellowtail amberjack (*Seriola Ialandi*). Photo courtesy of Brian Gratwicke. Licensed under CC BY 2.0.

See also: Marine fish

Yolk pigments

Yolk colour is determined naturally by the presence of **carotenoid**s in the feed, since poultry cannot synthesize these compounds. Therefore for markets that demand **eggs** with a rich yellow-coloured yolk it is necessary to include ingredients such as yellow **maize** or **lucerne** meal in the diet as a source of carotenoids. Other good natural sources are concentrated extracts from certain plants such as marigold or paprika. Providing **laying hen**s with access to good **forage** is another method of increasing yolk colour.

Carotenoids are a fat-soluble group of yellow, red and orange pigments and can be divided into two large groups: carotenes and xanthophylls. The presence of **fat** in the diet assists their absorption. Xanthophylls are more important in egg yolk coloration than carotenes. Maize **gluten** meal is a particularly potent source, containing up to 300 mg **xanthophyll** pigments kg^{-1}. The most important xanthophylls for egg yolk coloration are zeaxanthin and

lutein. The former results in yolks being more orange-red in colour, while lutein results in a more yellow hue.

Synthetic additives can be used at a concentration of 2–20 mg/kg^{-1} to increase yolk colour, in situations where the diet is lacking in carotenoids. Some provide a yellow colour and others a more orange-red colour. They include **astaxanthin**, β-apo-8′-carotenoic acid-ethylester, canthaxanthin, citranaxanthin, lutein, xanthophyll and zeaxanthin. Combinations of these carotenoids can be used to provide the particular yolk colour required. Supply companies usually provide a yolk colour fan to assist egg producers in selecting the correct combination. (RB)

Yolk sac

The yolk sac is one of the first extra-embryonic membranes to form during embryogenesis. This membrane enables the embryo to access the nutrients, primarily **lipids**, contained within the yolk. It is a bi-layered structure: the inner membrane (endoderm) takes up nutrients by non-specific phagocytosis and transports them to the vascularized outer membrane (mesoderm), from which they are transported to the developing embryo. Prior to exporting the lipids, **hydrolysis**, re-**esterification** and the synthesis of **lipoprotein**s takes place within the membrane. In the domestic chicken the membrane begins to form on day 1 of **incubation** and by day 5 the membrane encapsulates the yolk. The membrane is attached to the embryo at the midgut by the so-called yolk stalk but there is little evidence for nutrients being taken up directly during embryogenesis via the stalk. The rapid uptake of lipids by the yolk

sac membrane in the last week of incubation is mirrored by the accumulation of the fat-soluble **antioxidant**, **vitamin E** (the concentration in the embryo's liver increases by up to fivefold during the last week of **incubation**). While its prime function is to provide a surface for the uptake of nutrients, the yolk sac membrane also, in the first week of incubation, provides a surface for the exchange of respiratory gases, a function performed in the latter stages of incubation by the chorio-allantoic membrane. (NS)

Ytterbium (Yb)
A rare-earth **metal** with an atomic mass of 173.04. There is no known nutritional value of Yb for animals. Because of its low rate of absorption in the gut, it is often used as a **marker** to measure **digesta** flow. (PGR)

Yttria (Y_2O_3)
Yttrium oxide, molecular weight 225.8. It is mainly used as an exogenous **indicator** in the **digestibility** measurement in aquatic animals, since it is more sensitive and it has a lower rate of absorption in the gut than Cr_2O_3 which is absorbed to some extent in digestive tracts. (QS)

Yuca:
see Cassava

Z

Zein

The major storage protein in the **endosperm** of **maize**. It contains very little **lysine** or **tryptophan** and in consequence has a very low **biological value**. (MFF)

Zeolites

Microporous crystalline solids with well-defined structures. They generally contain the elements **silicon**, **aluminium** and **oxygen** in their framework and cations, water or other molecules within their pores. Many occur naturally as **minerals**, being widely distributed in oceanic sediments and volcanic regions. Others are manufactured commercially for specific uses.

Zeolites are often referred to as molecular sieves, because they are porous. They are used in a variety of applications with a global market of several million tonnes per annum. Major uses include petrochemical cracking, water purification and softening and in the separation and removal of gases and solvents.

The unique microporous nature of zeolites makes them excellent catalysts and they are often referred to as shape-selective catalysts. These shape-selective properties are also the basis for their use in molecular adsorption. (MG)

Zinc (Zn)

A mineral element with a molecular mass of 65.39. Zinc is an essential dietary component for all farm animals. It is one of the most biologically active **mineral** elements; it is an indispensable

part of over 200 **enzymes** in mammalian systems. All known classes of enzymes have at least one representative that contains Zn. In addition, Zn helps to regulate gene expression by virtue of its ability to associate with histidyl and sulphydryl groups in proteins to maintain structural integrity and facilitate receptor binding to specific DNA sequences. These protein structures are called Zn fingers; two examples in mammalian systems are the androgen and **glucocorticoid** receptors. Although Zn has no redox potential, it can influence oxidative processes, especially those involving **iron** and possibly **copper**, by protecting sulphydryl groups from **oxidation**.

Ingested Zn is absorbed primarily from the upper **small intestine**. The specific mechanisms of **absorption** have not been completely defined but probably involve specific divalent cation transport proteins that are located in the plasma membranes of the **enterocyte**s. These include DCT1 for Zn influx and ZnT-1 and -2 for Zn efflux.

After Zn is absorbed into the **blood**, it is transported to the liver and other organs bound mostly to serum **albumin**. Transport proteins similar to those found in the intestine probably influence uptake into the liver and other tissues. Zinc concentration in the serum or plasma is approximately 1.0 mg l^{-1}. During low dietary intakes of Zn, plasma Zn concentration can decrease to one-third of the normal value within a very short time. Plasma Zn is often used to assess the Zn status of an animal, but other factors such as stress and infection can affect plasma Zn as well and lead to false indications of Zn status. Excess Zn in the diet will increase plasma Zn concentrations above normal; however, most animals are able to adapt to reasonably high intakes by reducing the rate of absorption, which may return plasma Zn to near normal. Zinc itself is not highly toxic but if relatively high amounts are ingested over a long period, copper and iron absorption can be depressed and lead to deficiencies of these minerals.

Zinc deficiency in mammals manifests itself in numerous and varied physiological abnormalities. For example, the initial response, after a few days of consuming a low Zn diet, can be low

plasma Zn. This is soon followed by a reduction in food intake and a slowing of body weight gain in young animals, or weight loss in mature animals. Extended intakes of low Zn diets can result in skin lesions usually referred to as **parakeratosis**. Pigs are especially sensitive to Zn deficiency and readily develop these lesions. Even a marginal Zn deficiency can cause reproductive failure, especially in males. Sperm maturation is dependent on Zn and if the deficiency becomes severe the defects are not reversible. Supplementing the diet with adequate Zn can reverse most other signs of the deficiency.

Zinc is present in many forages and plant seeds at concentrations ranging from 20 to 50 mg kg^{-1} and these will often supply the required amount of Zn. However, because of the amount of fibre in forages and phytic acid in seeds, the bioavailability of Zn can be limited by impaired absorption. The US National Research Council sets the requirement of Zn for most farm species, including dairy and beef cattle, horses, goats and poultry, at 30–40 mg kg^{-1} diet; and for sheep, between 20 and 33 mg kg^{-1} diet. The requirement for pigs is set somewhat higher, at 100 mg Zn kg^{-1} diet for young animals of 3–5 kg body weight, but then it drops to 50 mg kg^{-1} diet for those weighing 50–120 kg. The Zn requirement of commercially reared fingerling channel **catfish** was found to be 20 mg kg^{-1} dry diet. (PGR)

See also: Absorption; Availability; Metallothionein

Further reading

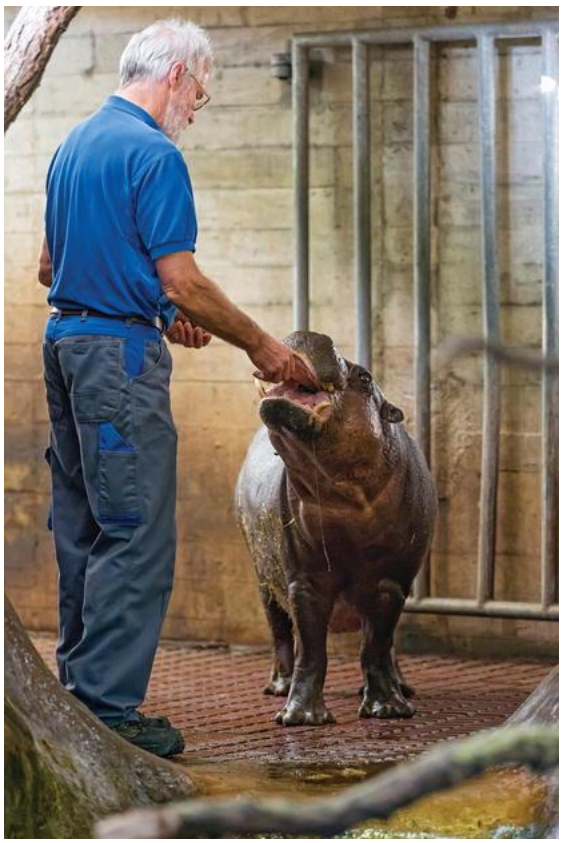
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Zoo animals, nutrition

Zoo animal nutrition has a history dating back to 1918 with Dr Corsen-White, a pathologist with University of Pennsylvania Medical School. She recognized **bone disease** in primates at Philadelphia Zoological Garden and created a 'zoo cake' to nutritionally **supplement** the produce that was being fed. Nowadays, there are approximately 23 nutritionists employed by 18 zoos and aquariums in the USA and Canada. Additional comparative nutritionists consult for zoos or are employed by universities. Qualifications for being a zoo or comparative nutritionist typically include having a Master's or Doctorate in animal or human nutrition.



Feeding a female pigmy hippo at Zoo Zurich. Photo courtesy of Tambako. Licensed under CC BY-ND 2.0.

The American Zoo and Aquarium Association (AZA) Nutrition Advisory Group (NAG) was created (1994) to share information on both nutritional research and practical applications to zoo animals. Shortly afterwards, the Comparative Nutrition Society (CNS) formed (1996) to enhance relationships between field scientists and zoo nutritionists.

Diet formulation software is a tremendous help with determining the most appropriate feed items and their amounts for zoo animals. Formulation programmes can be purchased or individually created to balance diets more quickly and more easily. When formulating diets for exotic animals, considerations are given to the **gastrointestinal tract** anatomy, general feeding ecology, nutrient contents of wild foods (if known), feeding behaviours, hypothesized nutrient and **energy requirement**s, feeds readily available, financial budgets and behavioural **enrichment**. Within the gastrointestinal tract anatomy, simple or pre-gastric **stomach** structure, length of the **small intestine**s, and lengths and volumes of the caecum and large intestines help to identify diet type. Classifying the animals as carnivores, omnivores, herbivores, insectivores, piscivores, granivores, frugivores, etc. determines the basis of their nutritional needs. Occasionally, there is published information about nutrient composition of foods consumed by the animals in the wild, but it is only a snapshot of the consumed diet. **Nutrient requirement**s of these animals are largely unknown. The National Research Council has published several nutrient requirement books written for domestic animals, which are heavily relied upon in the zoo nutrition field to help approximate nutritional needs of similar species. Some easy examples include using a horse as a model for a zebra, a domestic cat model for a tiger, and a dog model for the omnivorous bear species. A horse model is also used for an elephant because both are considered large, **monogastric** herbivores. A cow or goat is typically used as a model for ruminant hoofstock. However, exotic ruminants are now being further classified as browsers (i.e. consuming leaves, buds and bark), grazers (i.e. consuming grasses) or intermediates (i.e. switching between **browsing** and **grazing** depending on food availability) and different feed sources are being evaluated to meet this identified need.

A variety of items are available for feeding these animals; it is important to remember that they require nutrients, not specific food items. Acquiring items consumed by their wild counterparts would be economically impossible for most zoos and would likely

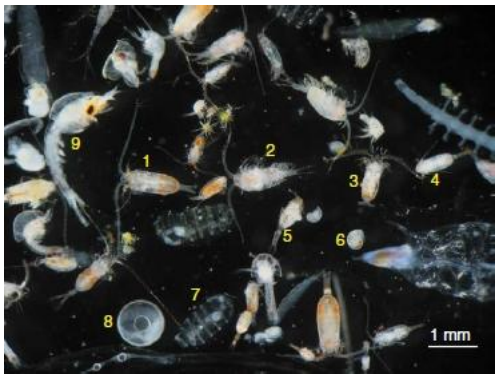
be difficult to import. Nutritionally complete feeds for zoo animals, similar to dog and cat foods, are manufactured by several companies. The feeds are in the form of extruded kibbles, pellets, dry gel mixes, or canned feeds. Raw **meat** diets are also manufactured as nutritionally complete feeds by a few manufacturers in North America and are based on **beef** or horse meat with added vitamins, minerals and fibre. Zoos feed various prey items such as insects, fish, poultry, lizards, rabbits, rodents and livestock. There is a wide array of commercially available insects such as mealworms, wax worms, crickets, earthworms, fruit flies and various others. Insects have an inverse **calcium**:**phosphorus** ratio (< 1.0) which can lead to problems with bone development when they are relied upon solely as a food source. Insects can be fed a high-**calcium** diet and/or be dusted with a mineral/vitamin mix to increase the calcium concentration and minimize the inverse ratio. **Fish** are heavily relied upon as a prey item for some of the animals in zoos. There are many species available to zoos, including capelin, herring, mackerel, silversides and smelt. When a diet contains a significant amount of fish, the fish need to be supplemented with vitamins, especially thiamin and **vitamin E**. Other prey items can include poultry, mice, rats, rabbits, guinea pigs, pigs, goats or calves of various ages and sizes. These items can be purchased frozen from a variety of vendors. Produce can also comprise part of the diet and can be obtained from local sources. **Hay** is considered a staple food item for most zoos, too. It is fed in large quantities to perissodactyls and artiodactyls along with pellets and/or a **mineral supplement**. As mentioned earlier, many animals have a significant reliance on browse (i.e. leafy tree branches). Obtaining significant quantities of browse is challenging, especially in temperate locations. Some zoos in the USA grow their own supplies, others partner with local utility companies that trim trees, while some ship it in from western or southern states. It is important to establish a list of safe browse species to feed, as some species of browse that are safe for one species can be toxic to another. This makes proper plant identification important.

While it is necessary to meet the animals' nutritional needs, it is also important to meet their psychological needs. Depending on the species, some ideas include offering their food in puzzle feeders, split it into multiple feedings, seasoning it with spices, cooking, **freezing**, or scattering it throughout the habitat for **foraging**. Browse also provides mental and physical stimulation in the stripping of leaves and bark for consumption.

Some nutritional diseases seen in zoo settings include **obesity** in many different species, cardiovascular disease in great apes, suspected rumenitis and **mineral deficiencies** in various hoofstock species, and **diabetes** in primates. **Vitamin D** deficiency and subsequent metabolic **bone disease** are problems with herbivorous reptiles, birds and primates. There are still many unknown nutritional needs of zoo animals, but progress is being made to provide the best possible diets for them. (DAS)

Zooplankton

Tiny aquatic animals that drift freely in the water. They are the main consumers of the primary producers, **phytoplankton**. Several groups of these microscopic animals make up zooplankton, from the larvae of large fish and invertebrates, to fully grown worms and crustaceans. Zooplankton are often classified by their size: categories include macrozooplankton (visible range), mesozooplankton, microzooplankton (20–200 μm) and nanozooplankton (2–20 μm). Their guts produce countless faecal pellets contributing greatly to the marine 'snow' and thereby accelerating the flow of nutrients and **minerals** from surface waters to the bottom of the seas. Most **marine fish** hatcheries culture zooplankton such as **rotifers**, artemia and copepods to feed small larvae before they are ready for formulated diets. (SPL)



Just a small sample of the many different zooplankton that live in the ocean. Photo courtesy of Adriana Zingone, Domenico D'Alelio, Maria Grazia Mazzocchi, Marina Montresor, Diana Sarno. The LTER-MC team is licensed under CC BY-SA 4.0.

See also: Aquatic organisms; Fish larvae; Live fish food

Zymogens

Enzymatically inactive precursors of proteolytic enzymes. Zymogens are typically synthesized by cells in an inactive precursor form and are then later activated in response to a physiological event. For example, pancreatic zymogens (**trypsinogen**, **chymotrypsinogen**, procarboxypeptidase and proelastase) are digestive **enzymes**, released from the **pancreas** in an inactive proenzyme form, that are converted to activated forms in the **small intestine** through a series of reactions initiated by the enzyme enteropeptidase (also known as **enterokinase**). This group of zymogens is also called pancreozymin. The zymogens are delivered to the small intestine by the pancreatic duct, where they are activated by specific proteolysis. (GG)

Unnumbered Image

The Australian dried abalones are depicted being displayed in racks. The abalones resemble circular egg-like muscular shells encrusted with small clams.

Unnumbered Image

The coastal net pens off the coast of Maine are featured in the image which is spread out like a tent across the steel poles and chains amid the ocean.

Unnumbered Image

A photo features the Artemesia tridentata plant, a dwarf shrub with brownish seed stalks.

Unnumbered Image

An image depicts a giant perch with an elongated body, and large mouth with protruding jaw.

Unnumbered Image

A diagram depicts a row of circular shaped globular actin molecules aligned across the thin filament of tropomyosin with elliptical shaped troponin having striped pattern amid the actin

molecules.

Unnumbered Image

A photo depicts a field covered in aloe vera plants, their tubular-shaped flowers blooming in a bright yellow color.

Unnumbered Image

A photo features a row of Amaranth opopopeo plants with bright red flowers blooming from the base to the top of the shoot.

Unnumbered Image

An image depicts a herd of brownish-white thick-coated Angora goats with their horns pointed to the back.

Fig. 1.

The reactions are as follows: Folate is converted to dihydrofolate by the conversion of N A D H plus H superscript positive to N A D P superscript positive. Dihydrofolate is converted to H 4 folate by the

conversion of N A D H plus H superscript positive to N A D P superscript positive. H 4 folate forms N-10 formyl H 4 folate by the conversion of A T P to A D P plus P i and by releasing formate. H 4 folate is reversibly converted into N-5 N-10 methylene H 4 folate by reversible conversion of serine to glycine in the presence of vitamin B 6. N-5 N-10 methylene H 4 folate is converted to N-5 methyl H 4 folate by the conversion of N A D H plus H superscript positive to N A D plus. N-5 N-10 methylene H 4 folate is converted to dihydrofolate in the presence of d U M P to d T M P which is take up for D N A synthesis. N-5 methyl H 4 folate is converted to H 4 folate in the presence of vitamin B 12, coupled with the conversion of homocysteine to methionine. Methionine is converted to S A M. S A M is converted to S A H, coupled with the conversion of protein to C H 3 protein, D N A to C H 3 D N A, and guanidinoacetate to creatine. S A H is converted to homocysteine y the conversion of H 2 O to adenosine. Homocysteine is converted to methionine, coupled with the conversion of choline to betaine and dimethylglycine to glycine. Homocysteine is utilized during oxidative stress. N-10 formyl H 4 folate is converted to H 4 folate, couple with conversion of H 2 O to formate and N A D P superscript positive to N A D P H plus H superscript positive plus C O 2. N-10 formyl H 4 folate is converted to purine synthesis during the formation of D N A. N-10 formyl H 4 folate is converted to N-5 N-10 methenyl H 4 folate by releasing H 2 O. N-5 N-10 methenyl H 4 folate is converted to N-5 formyl H 4 folate or folinic acid y the addition of H 2 O. N-5 formyl H 4 folate is converted back to N-5 N-10 methenyl H 4 folate by the conversion of A T P to A D P plus

P i. N-5 N-10 methenyl H 4 folate is reversibly converted to N-5 N-10 methylene H 4 folate by the reversible conversion of N A D P H plus H superscript positive to N A D P superscript positive. N-5 N-10 methenyl H 4 folate is reversibly converted to N-5 formimino H 4 folate by the release of N H 4 superscript positive. L-histidine is converted to N-formimioglutamate which is in turn converted to N-5 formimino H 4 folate, coupled with the conversion of H 4 folate to L-glutamate.

Fig. 2.

In mitochondria, serine is reversibly converted to glycine, when T H F is reversibly converted to N-5 N-10 methylene T H F in the presence of S H M T 2. Glycine is converted to N-5 N-10 methylene T H F, in the presence of G C S by releasing N H 3 and by the conversion of T H F plus N A D superscript positive to C O 2 plus N A D H plus H superscript positive. N-5 N-10 methylene T H F is reversibly converted into N-10 formyl T H F by bifunctional enzyme M T H F D 2 and M T H F D 2 L present in adult tissues. N-10 formyl T H F is converted to T H F in the presence of A L D H 1 L 2 and M T H F D 1 L by releasing C O 2 and formate. This formate moves from mitochondria to cytosol. In cytosol, formate and T H F are converted to N-10 formyl T H F in the presence of M T H F D 1. N-10 formyl T H F is converted to T H F in the presence of A L D H 1 L 1 by releasing C O 2. N-10 formyl T H F is reversibly converted to N-5 N-10 methylene T H F in the presence of M T H F

D 1. N-5 N-10 methylene T H F undergoes H cys methylation or gets converted to dihydrofolate in the presence of thymidylate synthase and by the conversion of d U M P to d T M P. This dihydrofolate is utilized in the formation of D N A. T H F is reversibly converted to N-5 N-10 methylene T H F in the presence of S H M T 1 and by the reversible conversion of serine to glycine.

Fig. 1.

The reactions are as follows: Dietary glycerol undergoes ruminal fermentation in a cow's stomach, which produces acetate, propionate, and butyrate. Propionate is converted into succinyl Co A which undergoes Krebs cycle in the liver. Phosphoenol pyruvate obtained from Krebs cycle is converted into glyceraldehyde-3-phosphate which is further converted into triacylglycerol and fructose-6-phosphate. Fructose-6-phosphate is converted into glucose-6-phosphate and then to glucose. Dietary glycerol and glycerol from adipose tissue enter the bloodstream and form alpha-glycerol phosphate and glyceraldehyde-3-phosphate. Non-esterified fatty acids from adipose tissue and alpha-glycerol phosphate from blood stream form triacylglycerol.

Fig. 2.

The pathways are as follows: Food nitrogen intake is broken down into proteins and N P N compounds. The proteins are classified into rumen undegradable intake proteins R U I P and rumen degradable intake proteins R D I P. R U I Ps are directly broken down into amino acids in abomasum. R D I Ps are broken down into peptides and then to amino acids in rumen. These amino acids form microbial proteins. N P N compounds are converted into N H 4 and then to microbial proteins. Salivary glands release N P N compounds. Liver recycles urea and N H 4. Urea in liver moves to salivary glands and kidney, and excreted in urine.

Fig. 3.

The flowchart presents that milk fatty acids are formed from blood plasma lipids 50 percent and de-novo synthesis in the mammary gland 50 percent. Blood plasma lipids are formed from lipids from adipose tissue 20 percent and lipids from the dietary origin 80 percent.

Unnumbered Image

An image depicts the rounded bales of straw grouped one above the other.

Unnumbered Image

A diagram depicts the lateral view of the bull's reproductive tract. The bladder, seminal vesicles, and ampullae extend down from the prostate. The urethra extends down from the Cowper's glands on the other side just below the rectum and terminates at penis. The ampullae extend down to the testis enclosed within scrotum and empididymis.

Unnumbered Image

An image depicts the bamboo forest with lined up bamboo trees having ringed stems with equally spaced nodes.

Unnumbered Image

An image depicts a banana tree with a thick truck, elongated leaves and a bunch of bananas.

Unnumbered Image

An image depicts a closer view of Barley which is green in color and spindle shaped having pointed auricles.

Unnumbered Image

The graph plots the basal metabolism in calories day inverse and B T U day inverse corresponding to the body weight in k g and l b s. A trend ascends from the basal metabolism point of 0 calories to over 10,000 calories through the body weight of 0.01 to 5000 k g. The basal metabolism of mice, dove, and sparrows ranges between 1 and 10 calories and between body weight of 0.01 and 0.1 k g. The basal metabolism of canaries, rats, pigeons, guinea pigs, and ducks ranges between 10 and 100 calories between body weight of 0.1 and 1.0 kilogram. The basal metabolism of rabbits, cat, goose, domestic fowl, 20 percent deviation lines, dogs, sheep and humans ranges between 100 and 1000 calories between body weight of 1.0 and 100 kilograms. The basal metabolism of swine, ponies, beef steers, dairy cows, beef steers, beef cows, dairy bulls, horses, and elephants ranges between 1000 and over 10,000 calories between body weight of 100 and 5000 kilograms.

Unnumbered Image

An image depicts a Great blue heron in bluish gray color with an elongated neck, daggerlike bill and long legs ingesting Ballyhoo alongside the shore.

Unnumbered Image

An image depicts the shattered dried beans with a measuring cup. The beans include red kidney bean, pinto, and cannellini.

Fig. 1.

The elements in the structure of vitamin K 1 are as follows: A condensed chain of two fused six-member rings, first ring is a benzene ring, second ring has two carbons double-bonded to O and one carbon single-bonded to C H 3, C H 2, C H, C, C H 2, C H 2, C H 2, single bond, C H single-bonded to C H 3 above and below. The last six carbons are within square brackets. The elements in the structure of vitamin K 2 are as follows: A condensed chain of two fused six-member rings, first ring is a benzene ring, second ring has two carbons double-bonded to O and one carbon single-bonded to C H 3, C H 2, C H, C, C H 2, C H 2, C H 2, double bond, C H single-bonded to C H 3 above and below. The last six carbons are within square brackets.

Fig. 2.

In the chart, chloro K and polychlorophenols do the addition of C O O H by utilising C O 2 and O 2. Warfarin generates a disulfide bond

as well as disrupts a disulfide bond in order to switch between hydroxyl and carbonyl groups.

Fig. 1.

The parts of the primary wool follicle in distal or upper regions, proximal or lower regions, ectal side, and ental side are as follows: papilla, undifferentiated region of bulb, outer root sheath, inner root sheath, transverse folds, upper limit of inner root sheath, swelling, fibre, epidermis, stratum corneum, arrector muscle, sebaceous gland, sweatgland, and duct of sweatgland.

Fig. 2.

The morphological components from outer to inner, from root end to root tip, on a scale of 1 to 20,000 nanometres are as follows: cuticle, epicuticle, exocuticle, endocuticle, cortex made of ortho-cortical cell, meso-cortical cell, and para-cortical cell, cell membrane complex, nuclear remnant, macrofibril, matrix made of high tyrosine proteins and high sulphur proteins, microfibril or intermediate filament made of low sulphur proteins, left-handed coiled-coil rope, and right-handed alpha helix.

Fig. 2.

The graph plots clean wool growth in grams per day versus intake of digestible dry matter in grams per day. The line for one month starts at (200, 2.5), goes to (400, 2.8), and ends at (600, 2.7). The line for two months starts at (200, 2), goes to (400, 2.7), and ends at (600, 3). The line for four months starts at (200, 1.8), goes to (400, 3), and ends at (600, 3.6). All data are approximate.

Unnumbered Image

The structure of Calbindin depicts a six-membered ring with bottom-left edge linked to O H, and top edge linked to a six-membered ring attached with a five-membered ring, wherein the top edge of the five-membered ring is linked to a trigonal chain.
The structure of Calciferol depicts a six-membered ring with bottom-left edge linked to O H, and top edge linked to a six-membered ring attached with a five-membered ring, wherein the top edge of the five-membered ring is linked to a trigonal chain with a double bond.

Unnumbered Image

The structure of Carnosine depicts a five-membered ring with two N atoms coupled with a six-membered ring with one O atom and

one N atom, wherein the O and N atom is linked to a chain terminating with N atom and the other edge of the six-membered ring is linked to single bond O and double bond O.

Unnumbered Image

The structure of Calcitriol depicts a six-membered ring with bottom-left and bottom-right edges linked to O H, and top edge linked to a six-membered ring attached with a five-membered ring, wherein the top edge of the five-membered ring is linked to a trigonal chain terminating with an O H group.

Unnumbered Image

A diagram depicts the flow as follows: Water - oven drying at 100 degrees Celsius; Dry matter is classified as ash and organic matter. Ash - furnace at 500 degrees Celsius, H C I digestion, minerals N a, K, C a, M g, P, etcetera, Trace elements, C u, M n, Z n, F e, etcetera; Organic matter is further classified as lipid, carbohydrate, and protein. Lipid - ether extract, solvent extraction; carbohydrate - reducing sugars, enzymatic methods, C F, A D F, N D F, M A D F, and N S P; Protein - C P equals 6.25 N, Kjeldahl-N and Dumas-N.

Unnumbered Image

The structure of Cholecalciferol depicts a six-membered ring with O H group on bottom-left, a double bond on top-right, coupled with a chain on top linked to a six-membered ring and a five-membered ring, wherein the top edge of the five-membered ring is followed by two trigonal patterns.

Unnumbered Image

The structure of Cholesterol depicts two six-membered rings, one with H and O H at position 3, double bond between 5 and 6 positions, H atom at position 9 from wherein the six-membered ring is coupled with a five-membered ring with position 17 linked to trigonal patterns.

Unnumbered Image

The structure of Cholic acid depicts the two six-membered rings at the base with O atoms on left edge of one ring and on right edge of the other ring. The top edge of the right six-membered ring is linked to a six-membered ring with O atom and a five-membered ring is coupled with a chain terminating with a single bond O and double bond O.

Unnumbered Image

The structure of Calcium formate depicts C single bond H, wherein C is double bonded to O on one end and single bonded to O on the other, this O atom is single bonded to C a followed by O single bond C single bond H double bond O.

Unnumbered Image

The structure of Cinnamic acid depicts a six-membered ring connected to a double bond followed by single bond O H and double bond O.

Unnumbered Image

The structure of Cobalamin depicts the corrin ring positioned in the center by four coordinated nitrogen bonds from four pyrrole groups.

Unnumbered Image

The map marks United States of America, Canada, Mexico, Brazil,

Argentina, Russia, China, Iran, Turkey, Indonesia, and Australia for the 82 percent of the World's cereal production in 2008. The countries such as India, china, regions to the West of Russia, parts of Canada, United States of America, and Brazil are marked for World's population.

Unnumbered Image

The data inferred in percent from the pie chart is as follows: Sweet potatoes - 70, Rice - 12, Grains and Wheat - 7, Soy and legumes - 6, Additional vegetables - 4, Fruit - 3, Oils - 2, Nuts, Other potatoes, Seaweed, Sugars, Fish, Dairy, Eggs, Pork-meat, and Flavorings and alcohol - 1. The food consumed includes 85 percent of carbs, 09 percent of protein, 06 percent of fats, 96 percent of vegan diet, 98 percent of vegetarian, 99 percent of pesca veg, greater than 4 percent of animal prod, greater than 1 percent of fish, and greater than 1 percent of meat-pork.

Unnumbered Image

The structure of Creatine depicts N single bonded to N and double bonded to N on the left end and linked to a single bond O double bond O on the right end.

Unnumbered Image

An illustration depicts the life cycle of a typical marine shrimp species. The fertilized eggs turn out to Nauplius followed by Protozoea, Mysis, Megalopa, Juvenile, Subadult and Adult. The Juvenile is alongside the estuary, megalopa and subadult on the coastal side, Mysis, Protozoea, Naupilus, fertilized eggs, and adult on the offshore.

Unnumbered Image

The equation of Sterculic acid is as follows: C H 3 (C H 2)7 C double bond C (C H 2)7 C O O H, here C double bond C is bonded to C H 2. The equation of Malvalic acid is as follows: C H 3 (C H 2)7 C double bond C (C H 2)6 C O O H, here C double bond C is bonded to C H 2.

Unnumbered Image

The structure of Cysteine depicts two trigonal patterns with N H 2 at the center, H S on the left end, and O H on the right end, having double bond O in between N H 2 and O H.

Unnumbered Image

The structure of Cystine depicts the four edges of the right sided six-membered ring with O on top edge and N on bottom edge. On the other side, a six-membered ring with five edges is depicted with S on top-left and bottom-left, and a double bond at the bottom-right side, connected to N and O on top-right and bottom right.

Unnumbered Image

The structure of Cytosine depicts a six-membered ring with N atoms at top-right and bottom positions, wherein top edge is bonded to N H 2 and bottom-right edge is double bonded to O.

Fig. 1.

Part a plots the G of intramuscular fat per 100 grams of fresh meat. The data inferred is as follows: Pasture - 0.55; Concentrate - 0.7. Part b plots the g of intramuscular fat per 100 grams of fresh meat. The data inferred for the concentrate feed level is as follows: 1.5 percent - 0.9; 1.8 percent - 0.7; ad libitum - 1.1. All the above-mentioned values are approximate.

Fig. 2.

Part a plots the W B S F expressed in N. The data inferred is as follows: Pasture - 43; Concentrate - 45. Part b plots W B S F expressed in N. The data inferred for the concentrate feed level is as follows: 1.5 percent - 63; 1.8 percent - 63; ad libitum - 77. All the above-mentioned values are approximate.

Unnumbered Image

An illustration depicts the duodenum with first part on top which connects to Pylorus of the stomach labeled as the superior duodenal flexure. The minor duddenal papilla and major duodenal papilla are labeled as the second part which is a descending part. The horizontal part at the bottom is the third part. The inferior duodenal flexure is between the second and third part of the duodenum. The ascending part at the bottom is labeled as the fourth part followed by the duodenojejunal flexure which continues as jejunum of the small intestine.

Fig 2.

Part a plots the W B S F expressed in N. The data inferred is as follows: Pasture - 43; Concentrate - 45. Part b plots W B S F expressed in N. The data inferred for the concentrate feed level is

as follows: 1.5 percent - 63; 1.8 percent - 63; ad libitum - 77. All the above-mentioned values are approximate.

Fig. 3.

Part a plots the percent of total fatty acids. The data inferred for pasture versus concentrate are as follows: S F A - 30 and 38; M U F A - 10 and 15; P U F A - 55 and 50. Part b plots the percent of total fatty acids for concentrate feed level. The data inferred for 1.5 percent, 1.8 percent, and ad libitum is as follows: S F A - 62, 61, and 61; M U F A - 30, 28, and 32; P U F A - 5, 8, and 7. Part c plots the percent of total fatty acids for forage or concentrate ratio. The data inferred for 75 over 25, 50 over 50, and 25 over 25 is as follows: S F A - 62, 64, and 60; M U F A - 30, 29, and 35; P U F A - 5, 5, and 4. All the above-mentioned values are approximate.

Unnumbered Image

The structure of dioxin depicts three interconnected six-membered rings. The second and third position of the left-most ring is bound to C l atoms. The fifth and tenth position of the mid ring has O atoms. The seventh and eighth position of the right-most ring is bound to C l atoms.

Fig. 1.

Part a plots the G of intramuscular fat per 100 grams of fresh meat. The data inferred is as follows: Pasture - 0.55; Concentrate - 0.7. Part b plots the g of intramuscular fat per 100 grams of fresh meat. The data inferred for the concentrate feed level is as follows: 1.5 percent - 0.9; 1.8 percent - 0.7; ad libitum - 1.1. All the above-mentioned values are approximate.

Unnumbered Image

The graph plots the energy balance, wherein a trend representing k subscript m ascends from the y value of F H P to the point M E subscript m on the horizontal line representing metabolizable energy intake. A trend representing k subscript production ascends from the point M E subscript m. A dotted ascending line extends from a point above F H P towards the point M E subscript m.

Unnumbered Image

The graph plots heat exchange versus environmental temperature. The region between T subscript minimum and T subscript C is marked as chemical regulation, region between T subscript C, T subscript B, and T subscript max is split as comfort zone and physical regulation. A horizontal trend representing evaporation

loss stretches constant from T subscript min to T subscript C and rises through T subscript B and T max with the ascending portion highlighted with dotted line. A trend representing non-evaporation loss descends from the T min to T subscript C and remains constant through T subscript C, T subscript B and T max with the constant portion highlighted with dotted line.

Unnumbered Image

The structure of Epinephrine depicts a six-membered ring with position 2 and 3 single bonded to O atoms, fifth position linked to a trigonal chain pattern with O and N atoms.

Unnumbered Image

The structure of Ergocalciferol depicts a six membered ring with third position bound to O H group, sixth position with a single bond, first position linked to an interconnected six-membered and five-membered rings, wherein the top edge of the five-membered ring is linked to a trigonal chain pattern.

Unnumbered Image

The structure of Ergosterol depicts two interconnected six-membered rings with third position bound to O H group and the right six-membered ring coupled to an interconnected six-membered ring and five-membered ring, wherein the top edge of the five-membered ring is linked to a chain of trigonal patterns.

Unnumbered Image

The structure of Ergocalciferol depicts a six membered ring with third position bound to O H group, sixth position with a single bond, first position linked to an interconnected six-membered and five-membered rings, wherein the top edge of the five-membered ring is linked to a trigonal chain pattern.

Unnumbered Image

The graph plots the energy balance, wherein a trend ascends from the y value of F H P to the point M E subscript m on the horizontal line representing metabolizable energy intake. A trend representing k subscript production ascends from the point M E subscript m.

Unnumbered Image

A diagram depicts an oval-shaped egg with a circular yolk at the center having yolk blastoderm at the top alongside the inner edge and the yolk outlined by the yolk vitelline membrane. The oval-shaped inner layer is the inner shell membrane which is outlined by the outer shell membrane followed by the shell covered with cuticle. The bulge at the right end includes the air cell and the fiber-like element stretching across the left end between the inner shell membrane and yolk vitelline membrane is labeled chalazae.

Unnumbered Image

A diagram depicts the different segments of the oviduct. The ovary surrounded by clustered elements is labeled ova. The magnum is a tubular-like structure forming zig-zag pattern from the infundibulum, which extends down to isthmus, uterus, vagina and rectum with cloaca.

Unnumbered Image

An illustration depicts the following phases of the gross energy of food. The gross energy of food turns to apparently digested energy and energy of faeces. The digested food turns to metabolizable energy and energy of urine and methane. The metabolizable energy turns to retained energy that is growth, milk, eggs, wool, fetus, etcetera, Heat that is basal energy plus energy of activity plus heat

increment of feeding and retrievable work.

Unnumbered Image

The flow of the illustration is as follows: The gross energy including faecal energy points to digestible energy with urinary energy plus C H 4 which further points to metabolizable energy with heat increment followed by net energy which is classified as retained energy and net energy for maintenance pointing to heat.

Unnumbered Image

The flounder, a fish with a flat diamond shaped body in grey spots on a white tinted body. The dab, a fish with irregular shaped greyish brown body having small head and pointed face. The turbot, a fish with its left side of the body flat and scale less with numerous knobs. The megrim, a fish with translucent light brown tinted body with dorsal and anal fins edges in black. The common sole, a flat fish with eyes on the right side of the head and fringes on the other side.

Unnumbered Image

The structure of Flavonoids depicts two interconnected six-membered rings, one marked as A including the positions 5, 6, 7, and 8 on the left end and the ring marked as C includes the positions 2 prime, 3, and 4 on the right end, wherein position 2 prime is bound to a six-membered ring marked as B with positions 2 prime, 3 prime, 4 prime, 5 prime, and 6 prime.

Unnumbered Image

The structure of Flavonols depicts two interconnected six-membered rings, one on the left is single bonded to two O H groups, and the other on the right with O atom is single bonded to O H at position 3 and double bonded to O at position 4, wherein position 2 is linked to a six-membered ring labeled B bound to R, R prime, and O H groups.

Unnumbered Image

The structure of Folate depicts a six-membered ring with two N atoms, and single bonded to N on left end and O H on the right end, the ring linked to another six-membered ring with two N atoms, linked to a N atom followed by a six-membered ring coupled with double bond O single bond N single bond H, wherein N H is linked to single bond O double bond O on top and at the base.

Unnumbered Image

A diagram depicts the four-chambered stomach of the ruminant. The left end is marked as the Oesophagus followed by the cardiac orifice and cranial sac of rumen beside it. The dorsal sac is to the right of cranial sac. The caudodorsal sac is on the right end and caudoventral sac of rumen is just below the caudodorsal sac. The cardiac orifice extends down to the ruminoreticular groove followed by reticulo omasal orifice. The omasum is to the right of reticulo omasal orifice and the reticulum is to the left of the omasum. The omasoabomasal opening is to the right of omasum and abomasum, pyloric orifice, and duodenum lies just below the caudoventral sac.

Unnumbered Image

An illustration depicts the proximate analysis scheme for plant and animal tissues. The water includes oven drying at 100 degrees Celsius. The dry matter is classified as ash and organic matter. Ash includes furnace at 500 degrees Celsius followed by H C I digestion, minerals and trace elements. The organic matter is classified as lipid, carbohydrate, and protein. The lipid includes ether extract solvent extraction, carbohydrate includes reducing sugars, enzymatic methods, and C F, A D F, N D F, M A D F, and N

S P. The protein includes C P equals 6.25 N, kjeldahl-N and dumas-N. The empirical composition is as follows: Lipid - C 20 H 38 O 2; Sugars - C 6 H 12 O 6; Starch - C 6 H 12 O 5; Fibre - C 6 H 12 O 5. The approximate gross energy is as follows: Lipid - 39; Carbohydrate - 18; Protein - 23.

Fig. 1.

An illustration depicts the G E gross energy classified as faeces energy (F E) and apparently digestible energy (D E). The apparently digestible energy is classified as methane energy, urine energy, and metabolizable energy. The metabolizable energy is classified as heat increment of feeding and net energy, wherein the net energy is classified as maintenance and production. The heat increment of feeding and maintenance is marked as the total heat production.

Fig. 2.

The graph plots the degradation percent versus time. The horizontal axis represents the time ranging between 8 and 96. The vertical axis represents the degradation percent ranging between 10 and 50. A trend representing c rises from the degradation percent of 10 and peaks to 45 percent passing through 20 percent in 8 hours, 30 percent in 24 hours, 35 percent in 50 hours, and 45

percent in 75 hours. The distance between 10 and 45 percent is marked as b and the distance between 0 and 45 percent is marked as a plus b.

Unnumbered Image

An illustration depicts the raw fish is heated and cooked for around 85 to 90 degrees Celsius. The cooked fish is pressed and converted into oil which is further converted to fish cake and fish juices. The fish juices are decanted and centrifugated to form stick water, wherein the fish cake and stick water are mixed and results in dry fish cake post evaporation and drying. The dry fish cake is grinded to form the fish meal.

Fig. 1.

All three graphs plot g of intramuscular fat per 100 grams of fresh meat. The data inferred for effect of nutritive level is as follows: 150 percent - 3.0; 180 percent - 3.1; 200 percent - 3.15. The data inferred for effect of fattening is as follows: suckling - 0.8; fattened - 2.5. The data inferred for effect of commercial feed addition is as follows: 1.5 kilograms - 0.2; 3 kilograms - 0.7.

Fig. 2.

Both the graphs plots the W B S F expressed in N. The data inferred for effect of nutritive level is as follows: 150 percent - 44; 180 percent - 53; 200 percent - 54. The data inferred for effect of commercial feed addition is as follows: 1.5 kilograms - 28; 3 kilograms - 31.

Fig. 3.

All three graphs plots the percent of total fatty acids. The data inferred for the effect of nutritive level for 150 percent, 180 percent, and 200 percent are as follows: S F A - 48, 46, and 47; M U F A - 24, 28, and 25; P U F A - 28, 26, and 27. The data inferred for the effect of fattening for suckling and fattened is as follows: S F A - 36 and 35.5; M U F A - 20 and 42; P U F A - 37 and 19. The data inferred for the effect of commercial feed addition for 1.5 kilograms and 3 kilograms is as follows: S F A - 36 and 36; M U F A - 31 and 41; P U F A - 33 and 23.

Fig. 1.

An illustration depicts the immunity classified as innate and acquired. Innate is further classified as follows: Barrier - example, skin respiratory cilia gastric acid. Internal - phagocytosis

complement interferon. Acquired is further classified as follows: Active - natural infection vaccination; Passive - colostrum antisera.

Fig. 2.

The trend graph plots antibody levels versus time. A trend rises to the first peak and drops followed a gradually rise to the highest antibody level as time passes. A set of two arrows points to the start point and the drop point of the trend.

Unnumbered Image

The structure of Adenine depicts two six-membered rings, one with two N at top-left and bottom edges and single bonded to N atom on top and the other with two N atoms on top and bottom edges.

Unnumbered Image

A chemical structure of Arginine depicts two N atoms double bonded to one N atom which is linked to one N atom and single bond O double bond O.

Unnumbered Image

The structure of Ascorbic acid depicts a five-membered ring with O atom on top edge, two O atoms single bonded to bottom-left and bottom-right edges, and top-right edge doubled bonded to O atom, wherein the top-left edge is linked to two single bond O atoms.

Unnumbered Image

The structure of Asparagine depicts a chain with two N atoms, double bonded to O atom on the left and linked to single bond O and double bond O on the right end.

Unnumbered Image

The structure of Aspartic acid depicts a chain with N atom at the center and linked to single bond O and double bond O on the left and right ends.

Unnumbered Image

The structure of Alanine depicts a central chain linked to two side chains on left, each with O atoms and two side chains on right, one with N atom.

Unnumbered Image

The structure of retinoic acid depicts a five-membered ring with N atom on top-right and bottom-left, wherein the top-left edge is double bonded to O atom, bottom edge is double-bonded to O atom, and bottom-right edge is single bonded to N linked to single bond N and double bond O.

Unnumbered Image

The structure of Amino nitrogen depicts the N atom at the center linked to R group on the left and single bond O double bond O on the right.

Unnumbered Image

The equation states, Mimosine converted to 3,4-D H P in the presence of microbes or enzymes or H C I, wherein 3,4-D H P undergo further degradation production. The structure of Mimosine includes a six-membered ring with N atom, single bonded to O H and double bonded to O atom, wherein the N atom is linked to N H 2 followed by single bond O H and double bond O.

The structure of 3,4- D H P includes a six-membered ring with N H, wherein the ring is single bonded to O H and double bonded to O.

Unnumbered Image

The structure of Leucine depicts a partial six-membered ring with one edge single bonded to N, and the other edge single bonded to O atom and double bonded to O atom.

Unnumbered Image

The structure of Lignans depicts two six-membered rings, each with O H and O C H 3 linked to two similar chains having C H 2 O, O H, O, O H, C H 2 O H and O H.

Unnumbered Image

Part a depicts the Lucerne plant with clusters of leaves all through the shoot. Part b depicts the Lucerne plant with 2-3 leaflets having a blossomed flower in each of the branches.

Unnumbered Image

The structure of Lysine depicts a trigonal chain pattern with N atom on the left end, N atom on the right end including single bond O and double bond O.

Unnumbered Image

The structure of Lactate depicts two single bonds on top, one with O atom and single bond O minus and double bond O at bottom.

Unnumbered Image

The bonding patter of Lactic acid depicts C atom at the center single bonded to O H on top, single bonded to H at bottom, C O O H at bottom-left and C H 3 at bottom-right.

Unnumbered Image

The structure of Lactose depicts a six-membered ring with all six edges bound to O atoms which are linked to another six-membered ring with six O atoms.

Unnumbered Image

The flowchart depicts that crude protein intake can be quickly degraded protein, slowly degraded protein, and rumen-undegraded protein. 80 percent of quickly degraded protein and 100 percent of slowly degraded protein form microbial nitrogen substrates which are converted into urea reversibly. Urea is excreted in urine. Fermentable energy intake converts microbial nitrogen substrates into microbial true protein, and then to metabolizable protein. Rumen-undegraded protein directly forms metabolizable protein and faecal nitrogen. Metabolizable protein is the source of milk N, growth N, endocrine N secretions, hair N, pregnancy N, and faecal N.

Unnumbered Image

The map has the following data: 0, 1 to 250, 251 to 500, 501 to 750: most of Canada, major parts of North America and Mexico, major parts of South America, most of Africa, Madagascar, Sri Lanka, the Middle East, few parts of U K, some parts of Europe, Scandinavia, Russia, China, Mongolia, Japan, Korea, Malaysia, Indonesia, Thailand, Laos, Vietnam, Australia, few parts of New Zealand, and Papua New Guinea. 751 to 1,000, 1,001 to 1,250, 1,251 to 1,500: parts of U S A, parts of Mexico, north-west and eastern regions of South America, many parts of Europe, some parts of Africa, some parts in south-east China, some parts along the south-west and

eastern boundary of Australia, and few parts in New Zealand. 1,501 to 1,750, 1,751 to 2,000, More than 2,000: many parts in U S A, especially central region, some parts in north-west and eastern regions of South America, most of U K, many parts of Europe, few areas in Africa, most of India and Pakistan, few areas in south-east China, few areas in Indonesia, few areas in south-east Australia, and some areas in New Zealand.

Unnumbered Image

The elements in the structure are as follows: A single-bonded, condensed chain of C H 3, S, C H 2, C H 2, C H single-bonded to N H 2, C double-bonded to O and single-bonded to O H.

Unnumbered Image

The elements in the structure are as follows: A single-bonded, condensed chain of C H 3, S, C H 2, C H 2, C H single-bonded to O H, C double-bonded to O and single-bonded to O H.

Unnumbered Image

The elements in the structure are as follows: A single-bonded,

condensed chain of a five-membered ring, C H 2, C H single-bonded to N H 2 below, C single-bonded to O H above and double-bonded to O. The elements in each position of the five-membered ring are as follows: 1, N or methyl group. Double bond. 2, C H. Single bond. 3, N or methyl group. Single bond. 4, C H. Double bond. 5, C H.

Unnumbered Image

The elements in the structure are as follows: A single-bonded, condensed chain of C double-bonded to O and single-bonded to O H, C H single-bonded to C H 3, C single-bonded to O and double-bonded to O.

Unnumbered Image

The flower is purple in colour. The flower head is surround by bracts which are hairless, with triangular, spine-edged appendages, tipped with a stout yellow spine.

Unnumbered Image

The elements in the structure are as follows: A single-bonded,

condensed chain of C double-bonded to O and single-bonded to O superscript negative, C H 2, C H 2, C single-bonded to N H 2 and single-bonded to O, C double-bonded to O and single-bonded to O N a.

Unnumbered Image

The longitudinal section of a sarcomere has alternate sections of overlapping thick and thin filaments. One sarcomere is flanked by Z line on both sides. The transverse section has many columns made of a repetitive series of one thick filament and thin filaments.

Unnumbered Image

The elements in the structure are as follows: A six-carbon ring in which each carbon is bonded to O. The first, second, third, and fifth carbons are cis oriented and fourth and sixth carbons are trans oriented.

Unnumbered Image

The parts from top to bottom are: lobe made of alveolus, terminal ductule, lobule, and intra-lobular connective tissue, mammary

ducts, gland cistern, teat cistern, and streak canal.

Unnumbered Image

The steps in the reduction of fish are as follows. Fish is ground and cooked, and then pressed to get oil plus stickwater and press cake. Oil plus stickwater is centrifuged to get crude fish oil. Rest of the centrifuged oil plus stickwater is sent to evaporator where water is released and solids form press cake. Drying of press cake releases water and forms fish meal.

Unnumbered Image

The elements in each position of a six-carbon ring are as follows: 1, N. Single bond. 2, C H. Double bond. 3, C H single-bonded to C O O H. Single bond. 4, C H. Double bond. 5, C H. Single bond. 6, C H. Double bond.

Unnumbered Image

The elements in the structure are as follows: A single-bonded, condensed chain of O, C H 2, C single-bonded to C H 3 above and below, C single-bonded to O H above, C double-bonded to O below,

N, C H 2, C H 2, C single-bonded to O H above and double-bonded to O below.

Unnumbered Image

The elements in each position of a single-bonded, five-member ring are as follows: 1, N superscript positive H 2. 2, C single-bonded to C OO H. 3, C H 2. 4, C H 2. 5, C H 2.

Unnumbered Image

The elements in the structure are as follows: A single-bonded, condensed chain of C single-bonded to O superscript negative above and double-bonded to O below, C H 2, C H 3.

Unnumbered Image

The elements in the structure are as follows: A single-bonded, condensed chain of H, C single-bonded to H above and below, C single-bonded to C O O H above and H below, H.

Unnumbered Image

The bar graph has three horizontal lines. The line for apparent points at 78 percent. The line for standardized true points at 84 percent. The line for real points at 90 percent. The area between apparent and standardized true lines is termed as basal. The area between standardized true and real lines is termed as extra. The area above the real line is termed as endogenous protein loss. In vivo, apparently digested protein points upwards in the basal area. In vitro, undigested protein points downwards in the extra area. All data are approximate.

Unnumbered Image

The graph plots nitrogen gain versus nitrogen intake in grams. The line for Mormon cricket meal with unsupplemented protein starts at (0, negative 0.3), peaks to (12, 3.5), and ends at (20, 4). The line for Mormon cricket meal with supplemented protein starts at (0, negative 0.3), peaks to (12, 4), and ends at (20, 4.3). All data are approximate.

Unnumbered Image

The structure is a fusion of a six-membered ring and a five-membered ring. The elements in each position of the structure are as follows: 1, N. Single bond. 2, C H. Double bond. 3, N. Single

bond. 4, C. Double bond. 5, C. Single bond. 6, C H. Double bond between 6 and 1. Single bond between 5 and 7. 7, N. Double bond. 8, C H. Single bond. 9, N H. Single bond between 9 and 4.

Unnumbered Image

The first structure is a single-bonded six-membered ring, in the shape of a chair. The elements in each position of the structure are as follows: 1, O. 2, C single-bonded to H above and O H below. 3, C single-bonded to H above and O H below. 4, C single-bonded to O H above and H below. 5, C single-bonded to H above and O H below. 6, C single-bonded to C H 2 O H above and H below. The second structure is a single-bonded six-membered ring, in the shape of a hexagon. The elements in each position of the structure are as follows: 1, O. 2, C single-bonded to H above and O H below. 3, C single-bonded to H above and O H below. 4, C single-bonded to O H above and H below. 5, C single-bonded to H above and O H below. 6, C single-bonded to C H 2 O H above and H below.

Unnumbered Image

The structure is a six-membered ring with alternate single and double bonds. The elements in each position of the structure are as follows: 1, N. 2, C H. 3, C single-bonded to C H 2 O H. 4, C single-bonded to C H 2 O H. 5, C single-bonded to O H. 6, C

single-bonded to C H 3.

Unnumbered Image

The diagram presents the organs of the human digestive system, such as stomach, liver, gall bladder, duodenum, and pancreas. The pancreas is an elongated organ, tapered from its head to tail. The head is the widest part of the pancreas and lies in the curve of the duodenum. The tail of the pancreas protrudes out of the stomach region.

Unnumbered Image

The structure is a six-membered ring with alternate single and double bonds. The elements in each position of the structure are as follows: 1, N. 2, C H. 3, N. 4, C H. 5, C H. 6, C H.

Unnumbered Image

The elements in the structure are as follows: C double-bonded to O on the left and single-bonded to O superscript negative on the right. Single bond. C single-bonded to C H 3 on the left and double-bonded to O on the right.

Unnumbered Image

The structure consists of a benzene ring. One of its carbons is single-bonded linearly to C H 2, C H single-bonded to N H 2, C double-bonded to O and single-bonded to O.

Unnumbered Image

The elements in the structure are as follows: A six-carbon ring in which each carbon is bonded to O of the phosphate group. The first, second, third, and fifth carbons are cis oriented and fourth and sixth carbons are trans oriented.

Unnumbered Image

The structure is a fusion of three six-membered rings. The first or left ring is single-bonded to two C H 3 groups. The second or middle ring has two N at opposite ends. The N at the top is single-bonded to C with H on either side, which is in turn single-bonded to C with O on left and H on right, C with O on left and H on right, C with O on left and H on right, C H 2, O H. The third or right ring has two N with a C in between. Two carbons next to both N are double-bonded to O.

Unnumbered Image

The elements in the structure are as follows: A single-bonded, condensed chain of C double-bonded to O on the left and single-bonded to O on the right, C single-bonded to N on the left and H on the right, C H 2, C H 2, S single-bonded to C H 3, C H 2, five-membered oxygen ring with two carbons single-bonded to O H, fused six-member and five-member rings with five N.

Unnumbered Image

The elements in the structure are as follows: A single-bonded, condensed chain of O H, C H 2, C H single-bonded to N H 2 above, C H double-bonded to O below, O H.

Unnumbered Image

They have broad ovate purple leaves with pointy ends and serrated margins, arranged oppositely with long leafstalks.

Unnumbered Image

The bone muscle has many muscle bundles containing muscle fibres. Endomysium surrounds the muscle fibre, perimysium separates the muscle bundles, and epimysium encloses the entire skeletal muscle. Blood vessels and nerves are present in the perimysium.

Unnumbered Image

The elements in the structure are as follows: A single-bonded, condensed chain of glucose, glucose single-bonded to bham below, O, fusion of six aromatic rings. All rings are single-bonded. The first three rings are six-carbon, the fourth and fifth rings are five-membered, and the sixth ring is six-membered. N is present at the junction of the last two rings. The rings have C H 3 as side group in four different positions

Unnumbered Image

The tiny flowers are produced in panicles, each flower cluster bears hundreds and thousands of kernels.

Unnumbered Image

The structure is a gonane skeleton made of four fused rings labeled from left to right as A, B, C, and D. A, B, and C are six-membered rings, whereas D is a five-membered ring. The elements in each position of the rings are as follows: 1, C H 2. 2, C H 2. 3, C H 2. 4, C H 2. 5, C H. 6, C H 2. 7, C H 2. 8, C H. 9, C H. 10, C H. 11, C H 2. 12, C H 2. 13, C H. 14, C H. 15, C H 2. 16, C H 2. 17, C H 2.

Unnumbered Image

The leaves and stems are very hairy with stinging and non-stinging hairs. It bears many flowers in dense axillary inflorescences.

Unnumbered Image

The structure of Balenine depicts a five-membered ring with N atom on the bottom-left and top-right edge, wherein the top-left edge is linked to N and H atom, single bond O and double bond O atom, and the N atom is linked to one N atom and double bonded to O atom.

Unnumbered Image

The structure of Biotin depicts two five-membered rings with S atom at position 1 of the left side ring and two N atoms at positions 2 and 5 of the right side ring, wherein position 1 is double bonded to O and the mid part of both the rings is linked to two H atoms, one on top and the other on bottom. The position 2 of the left side ring is linked to a chain terminating with single bond O double bond O.

Unnumbered Image

The structure consists of a benzene ring with one hydroxyl group. The elements in each position of the ring are as follows: 1, C single-bonded to O H above. 2, C H. 3, C H. 4, C H. 5, C H. 6, C H.

Unnumbered Image

The segments of the pyramid from bottom to top are labeled as follows: Grains, Vegetables, 3 or more servings. Fruits, 2 or more servings. Fortified soymilk and alternates, 6 to 8 servings. Beans and bean alternatives, 2 to 3 servings. Other essentials, sources of omega-3 fatty acids, vitamin B 12, vitamin D. The notes read: Eat a variety of foods from each of the food groups. Drink 6 to 8 glasses of water and-or other fluids each day. Limit intake of concentrated fats, oils, and added sugars, if used. Get at least 60 minutes of physical activity each day.

Unnumbered Image

The elements in the structure are as follows: A single-bonded, condensed chain of C H single-bonded to C H 3 above and below, C H single-bonded to N H 2 below, C double-bonded to O above and single-bonded to O below.

Unnumbered Image

The structure is made of a glucose molecule and a pyrimidine ring. The elements in the glucose molecule are as follows: 1, C single-bonded to O attached to a pyrimidine ring above. 2, C single-bonded to O H below. 3, C single-bonded to O H above.4, C single-bonded to O H below. 5, C single-bonded to C H 2 O H above. 6, O. The elements in the pyrimidine ring are as follows: 1, N H. 2, C single-bonded to N H 2. 3, N. 4, C single-bonded to N H 2. 5, C single-bonded to O glucose. 6, C double-bonded to O.

Unnumbered Image

The elements in each position of the structure are as follows: 1, C. 2, C H 2. 3, CH2. 4, C H 2. 5, C single-bonded to C H 3. 6, C. 7, C H.

8, C H. 9, C single-bonded to C H 3. 10, C H. 11, C H. 12, C H. 13, C single-bonded to C H 3. 14, C H. 15, C H 2 O H.

Unnumbered Image

The structure has three rings. The elements in each position of the structure are as follows: 1, C H 2. 2, C H 2. 3, C H wedge-bonded to O H. 4, C H 2. 5, C. 6, C H. 7, C H. 8, C. 9, C H 2. 10, C double-bonded to C H 2. 11, C H 2. 12, C H 2. 13, C single-bonded C H 3. 14, C H 15, C H 2. 16, C H 2. 17, C H single-bonded to a side chain. 18, C H 3. 19, C H 2. 20, C H. 21, C H 3. 22, C H 2. 23, C H 2. 24, C H 2. 25, C H. 2, C H 3. 27, C H 3.

Unnumbered Image

The leaves are dark green above and light green beneath, triangular-ovate, sub-rounded and mucronate at the apex.

Unnumbered Image

The stem is erect. The leaves are cauline and arranged spirally on the stem. The inflorescence has many phyllaries having ray and disk white flowers.

Unnumbered Image

It has a long, thin body, white to silver belly, bluish-green tints on top and vividly colored fins.

Unnumbered Image

The graph plots the milk yield versus time in lactation. A trend ascends and peaks at a point followed by the descending of trend to the lowest point. The second trend ascends from the peak point of the first trend followed by drop. The third trend descends down from the mid time of lactation. The peak point of the first trend is marked as peak yield and the drop point of the trends is marked as drying-off. The region at the mid is labeled response to early lactation supplements and the region at the drying off phase is labeled response to late lactation supplement.

Unnumbered Image

The graph plots the milk yield, fat content, and protein content versus days in milk. The horizontal axis represents the days in milk ranging between 5 and 365 and the vertical axis represents the milk yield in kilograms, fat content in grams, and protein content in

grams ranging from 5 to 50. The trend for far content drops from 47 to 37 between 5 and 40 days, rises from 37 to 47 again between 40 and 365 days. The trend for protein content drops from 40 to 30 between 5 and 30 days, and rises to a value of 38 between 30 and 365 days. The trend for milk yield rises from 22 to 26 between 5 and 35 days and drops to 20 between 35 and 365 days. All the above-mentioned values are approximate.

Unnumbered Image

The first part depicts a rectangular dotted pattern representing continuous grazing. The second part depicts a rectangular pattern split into four, wherein the top-left part is dotted representing rotational grazing, followed by arrows pointing from top-left through top-right, bottom-right, bottom-left, and top-left. The third part depicts paddock grazing wherein the gazing is in the pattern of a vertically elongated rectangle. The fourth part depicts strip grazing, wherein the grazing is in anticlockwise pattern.

Unnumbered Image

The structure of Galactose depicts a six-membered ring with each of its edge linked to O atoms.

Unnumbered Image

The structure of Gizzerosine depicts a five-membered ring with two N atoms, wherein the N atom at the top edge is single bonded to H and top-right edge of the ring is linked to N single bond H and single bond (C H 2)4 which is single bonded to H 2 N and C O 2 H.

Unnumbered Image

The structure of Glutamine depicts a trigonal pattern with N atom linked to single bond O minus and double bond O on left and right ends of the chain.

Unnumbered Image

The structure of Glutamate depicts a chain of trigonal pattern with single bond N and double bond O on the left and single bond N double bond O and single bond O on the right end.

Unnumbered Image

The structure of Glycine depicts N on the left end linked to single bond O and double bond O on the right end.

Unnumbered Image

The structure of Gossypol depicts two interconnected six-membered rings, one single bonded to two O H groups on the left and the top edge is single bonded to H atom double bonded to O atom, wherein the top edge of the six-membered ring on the right is single bonded to O H group. The six-membered ring on the right is linked to a five-membered ring which is further linked to two interconnected six-membered rings, one of which is single bonded to O H group, and the other is single bonded to two O H groups, top edge single bonded to H atom and double bonded to O atom.

Unnumbered Image

The structure of Guanine depicts a six-membered ring with two N atoms, single bonded to N atom and double bonded to O atom, attached to a five-membered ring with two N atoms.

Unnumbered Image

Part a depicts the gastrointestinal tract of horse, where small intestine extends from the stomach followed by rectum which

descends down to caecum and colon. Part b depicts the gastrointestinal tract of pic, where stomach extends through liver, duodenum, pancreas, small intestine and caecum which stretches down to rectum and colon. Part c depicts the gastrointestinal tract of cow, wherein the rumen includes the small intestine, omasum, reticulum, and abomasum, the small intestine extends to the caecum, colon, and rectum. Part d depicts the gastrointestinal tract of hen, where the crop extends down to proventriculus and gizzard beside which the liver extends down to duodenum and pancreas which further stretches beside to small intestine followed by caeca, colon, and cloaca.

Unnumbered Image

The structure of Histidine depicts a five-membered ring with two N atoms linked to a chain of N atom, single bond O atom and double bond O atom.

Unnumbered Image

The structure of Homocystein depicts the S group at the left end linked to N atom at the center, single bond O and double bond O on the right end.

Unnumbered Image

The structure of Hydroxylysine depicts a five-membered ring with one N atom, single bonded to O atom, and linked to a single bond O and double bond O.

Unnumbered Image

The structure of Hypoxanthine depicts a six-membered ring with two N atoms, double bonded to O atom connected with a five-membered ring having two N atoms.

Unnumbered Image

The structure of Isoleucine depicts a chain with N atom at the center linked to single bond O and double bond O at the right end.

Fig. 1.

The graph plots a set of three trends. From the initial period to fourth month is where body reserves used for milk production, from fourth to eighth month is where liveweight is constant, from eighth to twelfth month is where body reserves gained for next lactation, and over 12 months is the dry period rumen

rehabilitation. The trend for liveweight descends from first to third months, rises through third to tenth month, and peaks post 12 months. The trend for milk yield rises from first to fourth month, drops constantly from fourth to twelfth month. The trend for feed intake rises from first to fifth month, drops from fifth to twelfth month and slightly ascends at the end.

Unnumbered Image

The details of the flowcharts are follows. In citric acid cycle, citrate is converted to alpha-ketoglutarate to succinate to fumarate to malate to oxaloacetate to citrate again. During the conversion of malate to oxaloacetate, alpha-amino acid changes to alpha-keto acid, this helps in the formation of aspartate. In urea cycle, citrulline is converted to argininosuccinate to arginine to ornithine to citrulline again. Conversion of citrulline to argininosuccinate requires the breakdown of A T P to A M P plus P P i. Argininosuccinate has its N from aspartate and N H 2 from carbamoyl phosphate. Conversion of argininosuccinate to arginine helps in the formation of fumarate. Conversion of arginine to ornithine requires the addition of H 2 O to urea. C O 2 plus N H 4 superscript positive, addition of H 2 O, and change of 2 A D P plus P i to 2 A T P form carbamoyl phosphate in mitochondrion. Carbamoyl phosphate helps in the conversion of ornithine to citrulline inside the mitochondrion. The coupling of T C A and urea cycles is as follows. In aspartate-argininosuccinate shunt of T C A

cycle, argininosuccinate is converted to fumarate to malate to oxaloacetate to aspartate to argininosuccinate again. Alpha-amino acid changes to alpha-keto acid during the conversion of oxaloacetate to aspartate. In urea cycle, argininosuccinate is converted to arginine to ornithine to citrulline to argininosuccinate again. Carbamoyl phosphate helps in the conversion of ornithine to citrulline. Urea is released during the conversion of arginine to ornithine.

THE ENCYCLOPEDIA OF ANIMAL NUTRITION

2ND EDITION

EDITED BY CLIVE J. C. PHILLIPS

The Encyclopedia of Animal Nutrition covers animal nutrition across a wide range of disciplines, including physiology, biochemistry, veterinary medicine and feed technology. Through approximately 3000 entries ranging from short definitions to more discursive articles, it discusses and illuminates on all aspects of this important topic.

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