

A photograph of two brown cows in a farm setting. The cow on the left is pulling a large amount of dry hay from a metal trough. The cow on the right is also eating hay. The background is slightly blurred, showing more of the farm environment.

Voluntary Food Intake and Diet Selection in Farm Animals

2nd Edition

J. M. Forbes

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DIET SELECTION IN FARM ANIMALS**
Second Edition

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Second Edition

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Preface

The importance of the subject of this book encouraged me to prepare a second edition both to provide up-to-date coverage and to change the emphasis of some sections. The first edition (Forbes, 1995), as with its predecessor (Forbes, 1986b), has been well received, so a broadly similar approach has been adopted for this edition.

The preface to the first edition states that: 'My approach throughout has been to provide examples ... I have given many references to the literature'. This not only cluttered the text and might have interfered with ease of reading, it also resulted in a very long reference list (over 1300 references!) occupying a great many pages. In this edition I have not sought to justify my every statement but rather to provide references to reviews; in many cases only the most recent of a batch of papers is referenced and older literature can be traced through this. Nevertheless, there still remain many references to what I consider to be key original papers. The list of references of the first edition has been made available at <http://www.fbs.leeds.ac.uk/ForbesRef/RefsForFirstEdition> to provide access to some of the information for which references have been omitted from this second edition.

Where I have felt that the text and/or diagrams from the first edition are still appropriate, I have left them in rather than paraphrase for the sake of it. However, there are many new sections and much reorganized material. Chapters have been added and grouped into common themes, and the chapter on intake at grazing has been removed, as that in the first edition did not do justice to the subject. The material on prediction of intake, previously in its own chapter, has now been distributed to relevant sections in appropriate chapters; in this way most of the material on, say, lactation is together rather than being divided between two or more chapters. Prediction of food intake and understanding of how it is controlled should go hand in hand and not be artificially separated as they were in the first edition.

Some areas have seen consolidation but not a great deal of development, especially in physiology, as few are working with farm animals in that area now. There have been expansions in modelling and in molecular biology, but little of the latter has been applied to farm animals yet. It would be logical to include information on laboratory animals where it is missing for farm animals, but this would make an already long book far too long. The classic book of Le Magnen (1985) is an excellent starting point, while that of Dockray and Smith (2006) brings the subject up to date. For those with an interest in fish the book edited by Houlihan *et al.* (2001) provides comprehensive coverage.

I have attempted to provide more structure to the book by using the Minimal Total Discomfort (MTD) concept as a linking strategy. Do not mistake this for a belief that this theory explains everything (or even anything). Simply, the first edition was not as strong as it should have been in structure and direction, and MTD provides a simple way of incorporating several factors affecting intake in a semi-quantitative manner and thereby acting as a framework around which many of the experimental results and ideas can be integrated.

In covering the subject from so many different angles it is unavoidable that there will be some overlap between chapters; in most cases I have cross-referenced between chapters in order to minimize overlap. Nevertheless, it has at times been necessary to present similar information in more than one place. It seems to me that the most obvious such case is in the consideration of diet selection and appetites for protein. Thus, this subject appears in Chapter 7 in the consideration of the principles of diet selection and its methodology, in Chapter 8 where more practical aspects of diet selection are being discussed and in Chapter 13 where the appetite for protein comes under scrutiny. To have put these three sections together in one chapter would have left obvious gaps in the two chapters from which the material was removed.

In describing results of experiments I have not usually given the level of statistical significance; if I say there is an effect then it is significant at $P < 0.05$. If a difference or a relationship is not quite significant then I make this clear.

I am very pleased to acknowledge the advice of Dr Mike Wilkinson on Chapter 14, to my academic colleagues for discussions and collaboration, and to my wife Joan for her patience and understanding.

J. Michael Forbes
February 2007

1 Introduction

The majority of farm animals are fed *ad libitum*; that is, they have food available almost all of the time. This is true whether they are kept intensively – the supply of food being under direct control of their keeper – or extensively, where the herbage available varies in quantity and quality according to the time of year, but is rarely completely unavailable. Despite this freedom of access to food there are many situations in which animals over- or undereat, and ‘voluntary food intake’ and the factors which control and influence it are of great importance to agriculturists across the world. The ramifications of the subject are so great that it is impossible to cover them all in one book, and I have tried to give an even coverage of all aspects although, no doubt, some of my particular interests and prejudices will show through.

The subject of grazing and herbage intake is not covered and readers are referred to books by Hodgson (1990) and Vallentine (2001) and to conference proceedings edited by Hodgson and Illius (1998). Vallentine’s book also includes details of the anatomical and metabolic adaptations of ruminants.

In this brief introductory chapter, we discuss in general terms why studies of the control of voluntary food intake in farm animals are important, the terminology is defined and a little of the history of the subject is described. The techniques used to measure food intake are briefly described while methods of monitoring feeding behaviour are dealt with in Chapter 2.

The Significance of Voluntary Food Intake

If voluntary intake is too low then the rate of production is likely to be depressed, meaning that the requirements for maintenance become a very large proportion of the metabolizable energy in the food and so giving a poor efficiency of food conversion. If there is too high a level of intake then excessive fat deposition may occur, in some species at least. Thus the aim must be to

match food consumption with the required level of production. This optimum level of production depends to a large extent on the relative costs of different types of food and their nutritive values, and on the production response curve to changes in food quantity and quality. For example, depending on the circumstances, it may be economically more efficient to feed a low rather than a high level of compound supplement to a dairy cow, because forage intake increases and milk yield is not seriously depressed.

The quantitative importance of voluntary food intake is illustrated by the fact that poultry, which are mostly fed *ad libitum*, consume some 3.5 million t of food annually in the UK, accounting for some 70% of the total cost of poultry production.

Animals compete with man for food and there is a need to reduce the amount of grain-based food, especially in ruminants, which are able to make use of grass, grass products and by-products of other agricultural and industrial activities; cereals can thus be saved for human consumption and for pigs and poultry which cannot digest cellulose, unlike the ruminant. Because the bulk of a food as well as its nutritive value may limit intake, knowledge of the effects of changes in the type of food offered is essential.

The scientific study of voluntary food intake is important, therefore, and demands a multidisciplinary approach. The nutritionist, the physiologist, the psychologist, the pharmacologist, the modeller and, in the agricultural context, the animal and crop scientist all have to be involved in unravelling the complexities of the subject.

Problems of overeating

While the problems of human obesity are obvious, those concerning farm animals are less so. That proverbial glutton, the pig, is often prevented from eating his fill by restricted feeding of a daily measured amount of food which is expensive in labour. Other species also become obese, however: cattle, sheep and broiler chickens fed *ad libitum* continue to deposit fat until they become grossly 'overweight' (see Chapter 15). For example, Friesian dairy cows offered a food low in roughage *ad libitum* and not remated were seen to increase in weight at the rate of about 1 kg/day and to show no sign of slowing down after 70 weeks, when they weighed 700 kg, some 100 kg above the 'normal' weight for such cattle (Monteiro, 1972).

Do these animals become fat through overeating or because their energy output is too low? There has been much interest in the possibility that brown fat might 'burn off' excess energy intake, but brown fat appears to be absent in farm animals after the first few weeks of life. This then might be why cattle, sheep and pigs do not control their body fat content as well as does the rat. Cattle, sheep, pigs and broilers seem to be more prone to obesity than other species, possibly as a result of selection by man for fast growth (up to the middle of the last century), even if much of the rapid weight gain was in the form of fat.

Consumer preference has been to reduce amounts of fat in meat over the last 60 years or so due, at least in part, to the general decrease in physical

exertion of the human population. It is in the interests of the producer to reduce the amount of fat their animals deposit because of its low sale value and because the high energy content and low water content of adipose tissue make it very expensive to produce – excessive intakes are therefore to be avoided.

Problems of undereating

Animals normally eat that amount of food which satisfies their energy requirements, including continued fat deposition in the adult. There are some circumstances, however, when insufficient is eaten, resulting in loss of body weight or a decrease in a productive process, such as growth or milk secretion (see Chapters 11, 15 and 16). Undereating can occur, in humans at least, even in the presence of adequate availability of food (e.g. the condition of anorexia nervosa). More commonly it occurs when there is a shortage of food (famine).

In farm animals the problem of undereating is most often seen with ruminants where highly fibrous, bulky food is offered. This is digested slowly and its disappearance from the rumen sets a limit to the rate at which more food can be eaten; the mechanisms are dealt with in Chapters 3 and 11. This problem of undereating is at its most acute when other abdominal organs are competing for space (uterus, fat) or when the energy requirements are very high, as in early lactation. Food intake may be depressed also when the food is deficient in an essential component such as protein, a mineral, a vitamin or an amino acid (see Chapter 12).

When the amount of herbage available for grazing is very sparse and each mouthful is small, there may not be enough time in the day for the animal to eat enough to satisfy its nutrient demands. When snow, cold wind or hot weather prevent grazing there will again be inadequate food intake.

Matching Diet with Appetite

Under natural conditions animals such as ruminants, pigs and poultry are 'general' feeders: that is, they eat from a wide range of foods. Initially, they sample most potential foods but as they learn the nutritive (or toxic) properties of each type of material they become more selective. Although energy is probably the main controller of food intake there are other appetites – some innate, others learned – that influence the animal's choice of food and its total intake. The aim of the animal nutritionist is to match the quantity and quality of the diet with the nutrient requirements of the animal. If the diet is offered *ad libitum*, this implies that the composition of the food should be such as to allow enough to be eaten to meet the animal's nutrient needs, but not to over-consume.

In practice, this means offering a highly digestible nutrient-dense food (or foods) when high production is required (growth, late pregnancy, early lactation, egg production), but reducing the nutrient density of the food at other times so as to prevent excessive fat deposition. This control of diet quality is

often achieved with ruminants by varying the amount of a cereal-based compound supplement while allowing free access to a more fibrous forage. With pigs and poultry, the greater degree of dilution with inert or poorly digestible 'fillers' that is necessary to depress intake of digestible nutrients usually renders this approach impractical, and restriction of food must sometimes be practised (e.g. pregnant sows, broiler breeders).

The formulation of diets has become increasingly sophisticated, especially for non-ruminants, so that they meet as closely as possible the requirements of the animals for which they are intended. Because requirements of an animal are for a given amount of a nutrient to be taken in a day, rather than per unit of food, assessment of optimum levels of inclusion of nutrients depends on a knowledge or prediction of voluntary intake if it is intended that the food should be given *ad libitum*, as is usually the case with poultry and pigs. It is unnecessary and impractical to control exactly the composition of ruminant foods because they are going to be modified by ruminal fermentation, which precedes the normal processes of mammalian digestion.

Definitions

Voluntary food intake is the weight eaten by an animal or group of animals during a given period of time during which they have free access to food. In this book, the word *food* describes the materials that animals eat while a *feed* is a portion of *food* offered to an animal, usually of a size and material determined by man. However, for ruminants especially, *feed* is often used to mean food and anyone dealing with practical animal husbandry must be prepared for this.

Distinct eating periods, which may include short breaks but which are separated by longer intervals, are called *meals* and the short within-meal periods of eating are called *feeding bouts*. In analysing feeding behaviour, a *minimum inter-meal interval* is often adopted, meals separated by intervals of less than this value being considered as part of the same continuing meal. This *critical inter-meal interval*, if it is to be applied, should not be selected arbitrarily but only after study of a frequency plot of inter-meal intervals (see Chapter 2). When an animal starts to eat it is said to do so because it is in a state of *hunger*; when it stops eating it does so because it is *satiated*. These two terms have no precise physiological meaning.

Given free access to food of good quality, individuals of many species may eat 10–15 meals/day. Very often the distribution of meals through a 24-h period is not uniform, with more frequent, larger meals being taken during the photophase in those species – including the common farm animals that are more active during that period than at night.

Derived from measurements of meal size and inter-meal interval are the *hunger ratio*, i.e. weight of meal divided by pre-meal interval, and the *satiety ratio* – i.e. weight of meal divided by post-meal interval. *Appetite* is used to describe a drive to eat a specific nutrient, rather than to eat food in general. The word *palatability* has often been used to describe the overall sensory

impression the animal receives from its food. However, there is no precise way of measuring palatability and there seems little point in using the term. However, it is very widely used (e.g. Powell *et al.*, 2000), and it may be better to qualify it rather than to reject its use altogether (see Chapter 6).

The weight of food eaten per unit of time is the *rate of eating*. In this book the term refers to rate of eating during a meal rather than mean rate of eating over the whole day, which is sometimes called *rate of intake*. In some cases it has been possible to measure instantaneous rates of eating at different times during a meal and to show, for example, that rate of eating may decline as the meal progresses.

The total amount eaten during a given period of time (usually one day) is usually called the *voluntary intake*: this is often lower than the potential intake (the weight of food required to fulfil all of the animal's nutrient requirements) due to the physical or chemical constraints within the animal, or to environmental limitations.

Methods of Measuring Food Intake

In order to study factors affecting voluntary food intake and to develop methods of prediction, we need to be able to measure intake in a variety of experimental and farm situations. Much of the more applied experimental work covered in later chapters has relied for measurement of voluntary food intake on single weighings of food at intervals of 24 h, but often at shorter and occasionally longer periods. The method of 24-h weighings is not applicable to the grazing situation, nor is it appropriate to the estimation of individual intakes of animals kept in a group, and Chapter 2 describes methods for monitoring feeding behaviour.

When the fresh food is offered only once per day it is important to offer sufficient so that at least 15% remains; excessive allowance may, however, enable selection of the more preferred parts of food mixtures (see Chapter 8). It is important to recognize that the ability of animals to select an optimum diet (see Chapter 7) allows them to choose between different parts of the same plant and they can select a much more nutritious diet than the overall composition of the forage would provide, if given a sufficient excess of the food. For example, it has been shown that the digestibility of the herbage eaten by goats increases with the amount on offer until this amount on offer reaches about twice the dry matter selected to be eaten by the animals.

Sufficient time should be allowed for animals to become accustomed to new food before voluntary intake is recorded. For ruminants, at least 10 days is required because of the slow rate of passage and adaptation of the ruminal micropopulation, but more prolonged standardization appears to be unnecessary. In view of the variability between individuals it is necessary to use a sufficient number of animals in order to get a reliable estimate of intake.

Variability between animals in a group does not differ greatly between different foods but is less when they are penned individually than when they are penned together (Heaney *et al.*, 1968). These authors observed that: ' ...

while intake is unquestionably an important index of forage value, high variability of estimates (coefficient of variation, 0.16) renders it not so useful as it might appear at first sight'. It has been suggested that the effects of between-animal variation in measurements of voluntary intake can be reduced by using the intake of a standard forage by each animal as a reference point, but this would be very difficult to apply over a long period of time with large numbers of animals.

Marker dilution methods

In situations where it is not possible to measure intakes by individuals directly, such as grazing or group housing, indigestible markers added to, or already present in, the food can be used. Knowledge of the concentration of the marker in the food and measurement of its concentration in the faeces allows digestibility to be calculated. Alternatively, adding a known weight of a marker to the daily diet, followed by measurement of its concentration in the faeces, allows intake to be calculated, as long as digestibility is known. Digestibility is either measured in individuals indoors by weighing the food and faeces or by the use of two markers in the food, one at a known concentration, the other at a known dose. A group of plant waxes, the n-alkanes, possesses the required characteristics and are now widely used for herbivores (reviewed by Mayes and Dove, 2000) and they have also begun to be used in other species, including pigs (Rivera Ferre *et al.*, 2001) and pigeons but not, as far as this author can discover, in poultry.

Each animal is dosed by mouth with a known amount of n-alkanes, given either as a pellet or incorporated in the food. After several days to allow equilibrium to be reached, faeces are collected from each animal, either by grab sampling from the rectum, by collection of faeces identified by observation or by coloured plastic particles which can be given by mouth at the same time as the marker. From the content of the marker in the faeces, total faecal production can be calculated. It is then necessary to know the digestibility of the food in order to calculate the food intake; digestibility varies with level of intake so that ideally the individually penned animals used to determine the digestibility of the food should be of the same species, physiological state and level of intake as those whose intake is being estimated in the group. The cumulative errors involved in these procedures make the results unreliable, but useful for comparisons.

Developments in the use of n-alkanes have included the estimation of concentrate, as well as forage intake, taking advantage of the natural content of some of the n-alkane family in plant material (Mayes and Dove, 2000). Avoidance of regular oral dosing is a major aim of recent research. For example, how well can forage intake be estimated from a known intake of a supplement and an alkane-based estimate of the supplement and roughage proportions in the diet (Ginane and Petit, 2005)? The conclusion is that such a method is valid and will be particularly useful in situations in which individual animals, especially dairy cows, normally receive supplements.

Classical Theories of Intake Control

This section briefly presents hypotheses of the way in which voluntary intake might be controlled. Various aspects are then covered in detail in subsequent chapters.

The history of studies of control of food intake is reviewed by Gallouin and Le Magnen (1987). While there are many references to the subject before the beginning of the 20th century, it was not until around 1950 that much objective scientific study was directed at the problem. Having observed fluctuations in blood glucose concentration in synchrony with meals, and mindful of the central role of glucose in the metabolism of the rat, Mayer (1953) proposed the glucostatic theory, in which he envisaged that the animal attempted to maintain a relatively constant level of glucose in the blood by a central nervous monitoring system.

This has been modified in several ways, as described in Chapter 4, but the concept that it is the supply of energy to the body that the animal attempts to maintain by feeding is still very important. While rats and other simple-stomached animals reduce their food intake when glucose is supplied, as would be expected, ruminant feeding is unaffected by glucose infusion. However, their intake is depressed by infusions of volatile fatty acids, the major products of ruminal fermentation, suggesting that receptors for these acids are involved in control of intake.

It had long been suggested that the capacity of the digestive tract is an important limiting factor in feeding; this seems to be especially true for ruminants, in which fermenting bulky food remains in the rumen for very long periods. In the late 1950s, the importance of gut-fill had been demonstrated experimentally (Balch and Campling, 1962), and the positive relationship between the rate and extent of digestion of a forage and its level of voluntary food intake, which is so important in the utilization of forages, had been established and used as evidence for a 'physical' limit to intake. However, it is also generally accepted that ruminants can control their food intake to meet their nutrient requirements under quite a wide range of circumstances, and there is evidence of sensitivity to the chemical and osmotic properties of the digesta that allow a 'metabolic' control of intake. It is likely that physical and metabolic controls of intake are not mutually exclusive, but additive, and the Minimum Total Discomfort theory is based on the sum of squares of various negative and positive factors affecting intake (see Chapter 10).

While short-term changes in energy supply and gut-fill can be seen to be involved in the control of meal size and frequency, it is unlikely that they would give a perfect balance between nutrient intake and nutrient requirements. A long-term imbalance must lead to an increase or decrease in body energy stores, particularly adipose tissue, and it has been proposed that there is a route whereby the size of fat depots is relayed to the CNS, which uses this information in the control of intake: a lipostatic theory (Kennedy, 1953). This 'long-term' signal must be integrated with the various 'short-term' signals in order that the sum total of the food eaten at a series of meals is appropriate to the animal's long-term requirements. It now appears that leptin might fulfil this role (see Chapter 5).

When requirements change, intake should change in parallel. For example, the onset of lactation creates a massive increase in the requirements for energy, protein and other nutrients. Normally voluntary intake increases to match but sometimes, especially for ruminants offered forages, low voluntary intake limits milk yield and causes mobilization of body fat stores. Climatic changes also modify energy requirements and food intake normally responds appropriately (see Chapter 17); the thermostatic theory of intake control (Brobeck, 1948) envisaged that animals eat to maintain a constant body temperature, but this is now considered to be only a safety mechanism to avoid hyperthermia.

Because the unit of feeding is the meal, it has been suggested that differences in meal size or inter-meal interval must account for differences in food intake over any longer period from a few hours to a lifetime. It was proposed that, if we understand what causes an animal to start and stop eating, then we can claim to understand the control of voluntary food intake. While we know that several occurrences during a meal (stomach distension, accumulation and flow of products of digestion) are able to induce satiety when imposed experimentally, their significance to intake control is uncertain. These negative feedback signals will be considered further in Chapters 3 and 4, and the point will be made that it is likely to be an integration (the sum or sum of squares) of these signals that controls not only satiety, but hunger also.

It must be recognized, however, that feeding behaviour is very plastic and that daily intake can be maintained under a wide variety of meal patterns, voluntary or imposed. It now seems that it is intake over one or a few days that is being controlled, rather than the size of each meal (see Chapter 2).

Nervous pathways from the viscera relay information to the brain concerning such parameters as stomach acidity, abdominal temperature and distension of various parts of the gastrointestinal tract. The lower part of the brain responds with changes in signals controlling metabolic hormones (including growth hormone, insulin and glucagon); it also activates the higher centres to initiate, continue or cease feeding. Information on the environment is relayed from the special senses influencing the basic control of feeding, which is exerted by the lower centres. The identity of the parts of the brain which are involved is covered in Chapter 5.

There are two major reasons for continuing to study the role of the brain in the control of food intake in farm animals: on the one hand there are the agricultural implications of the possibility of manipulating intake by pharmacological or other means to improve animal productivity and welfare. On the other hand there is the possibility of using these species, especially the pig, as a more adequate model than the rat, for gaining deeper understanding of basic feeding mechanisms that will improve chances of combating the human problems of obesity and anorexia.

Prediction of Food Intake

In order to plan a feeding programme or to decide the optimum formulation of a ration to meet the animals' requirements under conditions of *ad libitum*

feeding, it is necessary to be able to predict the level of voluntary intake of a food or foods by farm animals.

There are two general methods for prediction: empirical equations and mathematical modelling, but the division between them is not absolute. The first involves measurement of several parameters, including voluntary intake, followed by regression analysis to find the equation which best fits the data. For example, analysis of live weight (LW), daily gain (LWG), milk yield (MY) and voluntary intake (I) measurements in a large number of dairy cows would yield an equation of the form:

$$I = a + bLW + cLWG + dMY \quad (1.1)$$

which could be used to predict intake in other animals of the same type. Note that this equation is a 'model' insofar as live weight, live weight gain and milk yield might reasonably be expected to be causal factors in the determination of food intake.

The regression approach was adopted by the UK Agricultural Research Council (ARC, 1980) in their summary of voluntary food intake of ruminant livestock. The most comprehensive review of the quantitative aspects of food intake with particular reference to ruminants has been made by the USA National Research Council (NRC, 1987), using predominantly North American data. The reader is referred to this for more detailed coverage of the prediction of food intake.

The second type of prediction method involves incorporation of more basic biological principles and functions that describe the relationships between factors likely to underlie the control of food intake. Such methods are likely to be less accurate at prediction but to be more general in their application. See the book edited by Dijkstra *et al.* (2005) for discussion of modelling in ruminants. A dynamic model is one in which the predictions of one iteration are used as starting values for the next iteration, where time is incremented between successive iterations.

Thus, equations that describe the relationship in ruminants between intake and digestible energy concentration (metabolic control) on the one hand, and intake and rumen capacity (physical control) on the other, can be solved for animals of given live weight, fatness and energy requirement. Whichever intake was the lower would then be used to determine the level of weight gain (or loss) that will change body fatness and live weight for the next iteration, and so on. Such a model might well be constructed using two or more equations derived empirically, as described above. Some examples are given in subsequent chapters.

It is clear that voluntary intake is influenced by both animal and food factors. Many prediction equations are based on one or the other, so it would be surprising if they gave low errors of prediction under conditions somewhat different from those under which the data used in their construction were collected. The major effort in predicting intake has been for ruminants in view of the importance of physical limitations on intake.

Problems and Pitfalls

In case this brief review gives the impression that we understand exactly how intake is controlled, it must be pointed out that there are numerous cases where different experiments and observations lead to contradictory conclusions. This situation can arise for many reasons: first, there may have been differences in experimental protocol such as the type of food offered or the duration of any period of food withdrawal before an experimental treatment or observation. Most studies of peripheral feedback signals either offer food *ad libitum* and add the infused substance to the contents already in the gut or precede feeding tests with fasts of many hours, which put the animal in an abnormal state. The degree of stress to which animals are subjected might also influence the results of experiments on the control of intake.

Secondly, species differences. Hamsters do not increase their food intake after a period of food deprivation while rats invariably do. Would de Jong *et al.* (1981) have reached similar conclusions concerning the role of short-chain fatty acids (SCFAs) in the control of feeding in goats had they been working with sheep as did Anil and Forbes (1980b)?

Thirdly, differences in interpretation. For example, Le Magnen and Tallon (1966) found a close correlation between the size of a meal and the post-meal interval, using an arbitrary minimum inter-meal interval of 40 min, and proposed that the onset of feeding is determined largely by the rate of metabolic utilization of the products of the previous meal. Castonguay *et al.* (1986) have used an objective method, based on a sudden change in the frequency distribution of inter-meal intervals,¹ to determine the minimum inter-meal interval and found it to be between 5 and 10 min. Applying this criterion, they failed to obtain a significant relationship between size and post-meal interval and reached a different conclusion.

It is tempting to think that we can ultimately explain the control of food intake once we know about all the negative and positive feedbacks that pass information to the CNS. However, it is becoming increasingly clear that learning plays a vital role (see Chapter 6). For example, animals learn the difference between two foods offered as a choice and base their relative intakes of the two on what they have learned. Why should the intake of a single food not be subject to the same learning processes? That is, the metabolic consequences of previous meals of that food allow the animal to anticipate the likely consequences of the current meal and to adjust its size accordingly. Thus, the nutritional and metabolic history of the animal is as important in determining when and how much it eats, as are the events occurring in the digestive tract, liver and CNS during the current meal.

The Minimal Total Discomfort Concept of Food Intake and Choice

While accepting the complexities of the control of food intake and choice, many proposals have been made for models encapsulating its major features

¹ See Chapter 2 for a better method of defining the critical inter-meal interval.

(see Chapter 10). The Minimal Total Discomfort (MTD) concept is based on the principle that discomfort is caused by mismatches between what is being eaten and what the animal needs to match its current needs, as well as by physical distension and environmental factors, including social and climatic; it is further proposed that these discomforts are combined into a total signal that the animal tries to minimize. This model will be used as a linking feature in many of the following chapters, as well as being described and discussed in detail in Chapter 10, in order to provide continuity.

2

Feeding Behaviour

The term 'feeding behaviour' generally refers to meal-taking activity, in which the time (and weight) of each meal is monitored. However, it can also encompass events within a meal and the number, frequency and size of individual bites have been monitored and, in some cases, at an even finer scale, the movement of the head and mouth during a bite have been recorded.

Monitoring and analysing feeding behaviour are areas of considerable scientific activity, but their importance in understanding and predicting food intake and selection over longer periods, e.g. a day, is dubious. While the weight of food eaten over periods of a few days can be related to such factors as the animal's nutrient requirements and the composition of the food, there is very considerable variation in biting and meal-taking activity during the course of a day, even between similar individuals within a group. Many factors affect feeding behaviour, including the degree of competition for food and environmental variables – the weather and management system – without having major impacts on food intake over periods of several days.

An example of this disparity between feeding behaviour and long-term food intake is shown in Fig. 7.9, in which it can be seen that daily choices of a cow fluctuate markedly, while weekly intake is very stable. If our interest is primarily in farm animal production, then feeding behaviour may simply be a distraction and, even if it is important in the physiological control of meals, then we need to know how short-term variations in intake can be cumulated into long-term consistency.

The justification for monitoring feeding behaviour is, on the one hand, to allow measurement of daily intake in situations in which it cannot be measured directly (e.g. group housing, see below) and, on the other, to satisfy curiosity and with the hope of gaining understanding about the factors controlling intake over periods of a day or more.

Monitoring Individual Feeding Behaviour

This has traditionally been carried out by many hours of patient observation, noting at regular intervals whether or not each animal is eating, ruminating, standing, etc. While there is no substitute for this in terms of learning about animal behaviour, and certain types of behaviour are not amenable to quantification in any other way, this method suffers from two major drawbacks: it is very time-consuming (this can be overcome to some degree by video recording and observing the playback at a fast speed) and it does not provide information on the weight of food eaten, but only on the timing of meals.

Automated systems

Comprehensive data can be collected by continuous automatic recording of the weight of the food container. If the weight is static the animal is not eating. The duration of a meal is signalled by frequent oscillations in the weight of the container as it is disturbed by the animal's head; the weight of food eaten during that meal is the difference between the weights before and after the meal. It is often possible to obtain intermediate weights during a meal when the animal is not touching the container and thereby to determine the rate of eating at different stages during the meal.

In fully automated systems used at Leeds University, UK, for sheep, pigs and chickens, each balance is programmed to transmit continuously the weight as a string of digits through a multiplexer to a PC. Each time a weight is obtained it is compared with the previous weight from that balance. If there has been no change then it is initially assumed that the animal is not eating; if previously the animal was eating then a potential end of meal is stored. However, in case this is just a pause in a meal, a series of stable weights over the period required for an inter-meal interval is necessary to confirm that the meal has indeed ended.

If, on the other hand, there is a difference between two successive weights on the same balance, then the animal is detected as eating; if this follows a period of stable, i.e. non-eating, weights, then the start of a meal is signalled. Each pen or cage can be provided with more than one weigher, so that the intake of two or more different foods and water can be monitored.

Operant conditioning

In the systems just described, the animal has free access to the food; an alternative is to teach the animal to 'work' for a reward of food (reinforcement) by pressing a button (response), a technique known as *operant conditioning* (pigs and sheep, Baldwin, 1979; chickens, Clifton, 1979; cattle, Matthews and Kilgour, 1980). The number of responses the animal has to make before a reward is given (the *reinforcement schedule*) can be increased in order to see how strong is its desire for food. The use of operant conditioning techniques ensures that the animal eats only when it has a definite urge to do so, and not

simply when it happens to find itself near to food. The apparatus used to control the reinforcement schedule can easily be adapted to keep a record of the timing of responses for subsequent analysis of meal occurrence.

Perhaps operant conditioning, in which the animal has to 'work' for food, might be a method of avoiding the social eating so often seen when animals are penned in sight of each other – one animal's eating often triggers that of another when the second would not have otherwise taken a meal at that time, thus confounding a strict 'physiological' experimental design. It must be recognized, however, that single confinement may induce abnormal behaviour. Savory (1989) has suggested that having to do a moderate amount of work for food avoids eating from boredom and gives more natural patterns of feeding under laboratory conditions.

Monitoring of jaw movements

The timing of eating and ruminating can be monitored by means of a small balloon or a pressure transducer held on the animal's lower jaw by means of a bridle. In the upper half of Fig. 2.1 can be seen patterns typical of eating, showing both long and short timescales. At the left, eating bouts can be seen while at the right the individual jaw movements are clear and allow differentiation to be made between prehension (1) and mastication (2). In the lower part of the figure can be seen rumination jaw movements, at low and high resolution, the latter demonstrating the very regular movements compared with the irregularities of eating. Some progress has been made in analysing such records by computer (S.M. Rutter, personal communication).

Monitoring Feeding Behaviour in Groups

The relatively simple methods available for automatically recording the meals taken by individuals penned by themselves are not all suitable for monitoring

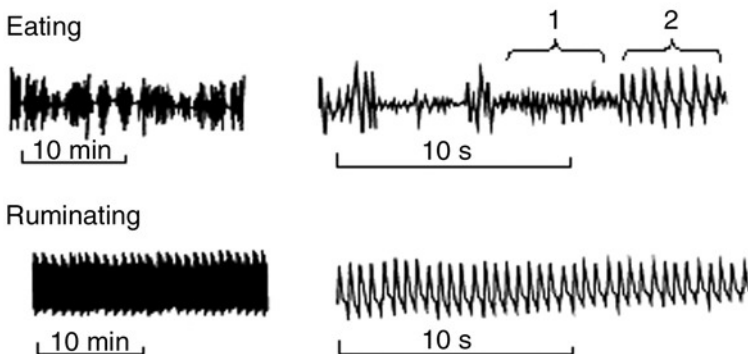


Fig. 2.1. Recordings of traces of jaw movements of sheep using a small foam-filled balloon in the submandibular space connected to a pressure transducer (from Jarridge *et al.*, 1995).

the behaviour of individuals in a group. Observation, either direct or by video recording, is still possible for animals in groups when individuals can be identified by sight. With modern electronic equipment, recognition of individuals is possible and a food dispensing system can identify animals and record the amount of food eaten by each individual. Such systems are available commercially for the recording and/or control of the concentrate allowance to individual dairy cows kept in groups (out-of-parlour dispensers) and for groups of growing pigs for genetic selection purposes on breeding farms. While these systems are suitable for pelleted foods, they cannot be used to dispense long roughages.

Full details of meal patterns of forages by individuals in a group can be monitored by continuous automatic weighing of the box containing the food, with animals identified as they eat by means of transponders worn on their ear tags or collars. An example is that developed by Forbes *et al.* (1986), in which cows wear collars with transponders of the type available commercially for identification in the milking parlour or at out-of-parlour concentrate dispensers. The food is placed in boxes mounted on top of load platforms which are capable of weighing to the nearest 0.1 kg. Both food weighing and identification systems are multiplexed to a PC with software to collect meal patterns at each weigher and also for each cow. A controlled-entry, solenoid-controlled door can be provided for each feeder (e.g. a Calan[®] door), which allows certain animals to be prevented from eating from some or all of the food boxes for some or all of the day.

Thus, it is possible to have a group of animals, managed as a herd, in which different individuals have access to different foods; it is also possible to restrict animals to eating within given periods of the day and/or to predetermined weight of food(s). Figure 2.2 illustrates an example of the feeding pattern of one cow obtained using this system (known as the LUCIFIR system).

Other systems have been developed elsewhere (e.g. Insentec, <http://www.insentec.nl/>). Equipment such as this is expensive but yields a very large amount of detail about feeding behaviour; it also allows animals to be kept in groups for the measurement of intake and thus avoids the likely effects of individual confinement. In addition to its use for research, it is being used by breeding companies to enable the intakes and thus efficiencies of individual animals to be used in the selection index. Several pig breeding companies are using automated food intake recording systems to monitor daily intakes of individual pigs kept in a group.

We have recently developed a system (Leeds University Pig Intake System, LUPINS) for monitoring feeding of weaned piglets, in which small weighed food hoppers are suspended from electronic balances alongside which are antennae for detection of piglet identity from transponders carried in their ear tags. Figure 2.3 is a diagram of the system, while Fig. 2.4 is a photograph showing the feeders in a pen of pigs. The output is similar to that for the bovine system, but the advantage of using commercial digital balances is that they provide an additional signal (stable/unstable) that assists in the analysis of the data; sometimes animals change so quickly at a given feeder that it is impossible to obtain a stable weight. In this case, an 'unstable' signal accompanies the weight, which can then be 'corrected' (i.e. the best estimate calculated) during the subsequent analysis phase.

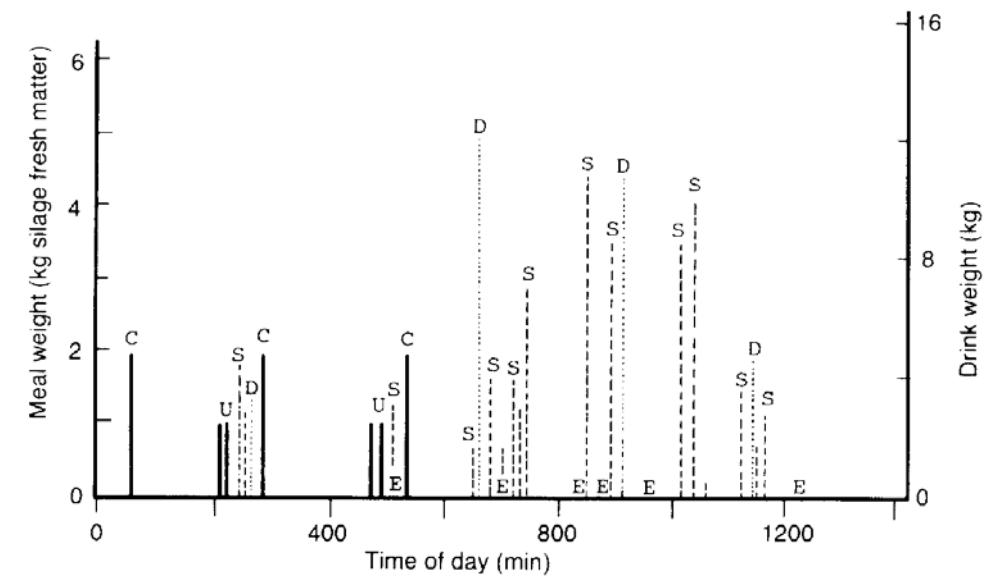


Fig. 2.2. An example of the meals of silage and concentrates and the drinks of water taken by a lactating dairy cow during a 24-h period using the LUCIFIR system (D.A. Jackson, J.M. Forbes and C.L. Johnson, unpublished results). S, meals of silage; C, meals of concentrates; U, visits to the concentrate dispenser that go unrewarded as the requisite time since last dispensation has not elapsed; D, drinks of water; E, visits to the concentrate dispenser that go unrewarded as the daily allowance has been exhausted.

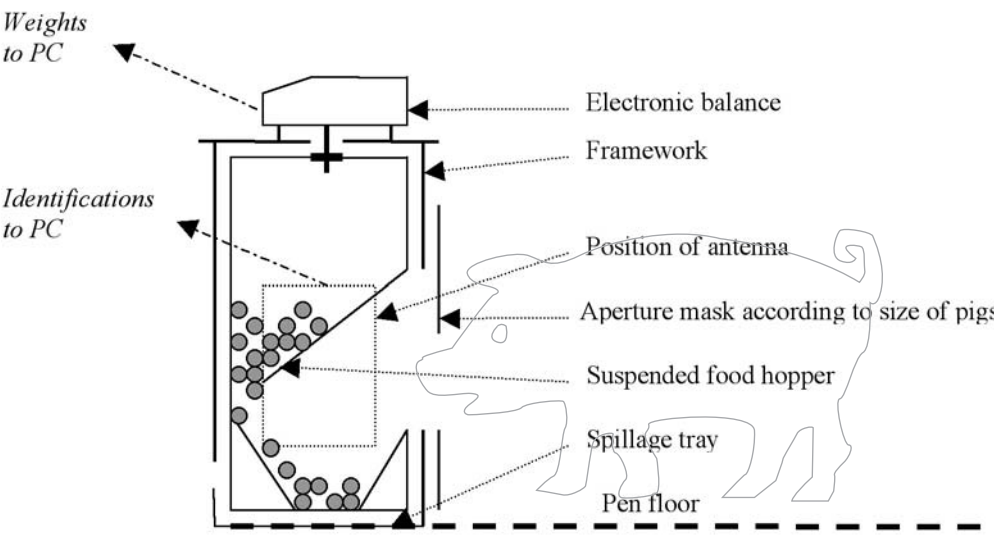


Fig. 2.3. Diagram of side view of a LUPINS feed station for young pigs.



Fig. 2.4. Piglets in pen with four-station feed monitoring system. Balances are protected by a lid and feeding apertures are adjusted according to the size of pigs with masks, through which the feed hoppers can be seen.

Analysis of Meal Data

Reduction of meal data: calculation of inter-meal interval

Typically, the data generated by automatic recording systems are of the form: (i) animal identity; (ii) serial number of feeding station; (iii) times of start and end of meal; and (iv) weights of start and end of meal, with each meal forming a record in a computer file. These data can be manipulated by statistical analysis programs, by purpose-written software or by means of a spreadsheet or database program. Calculation of total intake per day or during particular periods of the day is straightforward, as is calculation of inter-meal interval, rate of eating, hunger and satiety ratios.

However, it is first necessary to consider 'When is a meal not a meal?' Animals invariably take short pauses during a meal and these must be differentiated from the longer gaps between separate meals. Sometimes an arbitrary period has been used. However, examination of the frequency distribution of inter-meal intervals often shows that these intervals form two distinct populations. In several species of bird, for example, intervals of more than a few minutes between feeding bouts are distributed in the form of negative exponentials, implying that there is a constant probability of a meal starting. However, the shortest intervals between meals do not follow this pattern and can be regarded as breaks in a meal, rather than true intervals between meals.

Duncan *et al.* (1970) plotted the frequency distribution of inter-meal intervals for domestic fowl and noted that there were far more intervals of ≤ 2 min than would be predicted from the negative exponential of the rest of the data, and 2 min was therefore adopted as the minimum inter-meal interval. For lactating cows fed grass silage at the Leeds University farm, the critical inter-meal interval was found to be close to 7 min (Forbes *et al.*, 1986), and this varied little between animals or with season or physiological state of the cows.

However, these approaches to defining meals have been seriously questioned by Tolkamp and colleagues (1998c), based on the convincing argument that if meals are satiating then the probability of an animal starting to eat again after a meal should initially be low, but then increase as the satiating properties of the meal decline. Thus, there would be a large number of short (within-meal) intervals and a large number of long (inter-meal) intervals, with relatively few of intermediate length. They tested this proposition with data collected from 16 dairy cows and compared the following methods of deriving the inter-meal interval (Tolkamp and Kyriazakis, 1999):

- 'Broken stick' (two straight intersecting lines, both with a negative slope) to the frequency distribution.
- Log(e)-transformed cumulative frequency distribution (the log-survivorship curve).
- Log(e)-transformed frequency distribution.
- Two Gaussians fitted to the frequency distribution of log-transformed interval length (log-normal models).
- Three Gaussians fitted to the frequency distribution of log-transformed interval length (log-normal models).

They found that the frequency of intervals to visits to feeders was much better described by two log-normal distributions than by a random probability. Inter-meal interval was estimated as 1.9, 6.0, 7.5, 32.4 and 49.1 min by these methods, respectively, while meal number was between 5.7 and 12.1/cow/day and meal size from 4.0 to 8.4 kg. The two log-normal models fitted the data most closely, and it can be concluded that they are the most useful for estimating meal criteria in cattle and probably in other species as well.

It was noted that there was a small third peak, seen as an irregularity on the descending part of the first, and this was traced to intervals between meals and drinks, which often occur in close association. Inclusion of a third distribution representing these intervals – including drinking – gave an even better fit than the two-peak model (Tolkamp and Kyriazakis, 1999). These three segments of the relationship can be seen in Fig. 2.5, which was generated from almost 80,000 pauses between automatically recorded meals of dairy cows offered completed foods. They represent: (i) intra-meal pauses; (ii) intervals between eating and drinking; and (iii) true inter-meal intervals. Once the critical inter-meal interval has been determined or estimated for the animal(s) in question, raw meal data can be merged into 'true' meals.

This log-normal approach has been used for growing pigs by Morgan *et al.* (2000a), who analysed visits to feeders by 16 individually housed growing pigs for 35 days. Intervals between visits were described by two log-normal distributions,

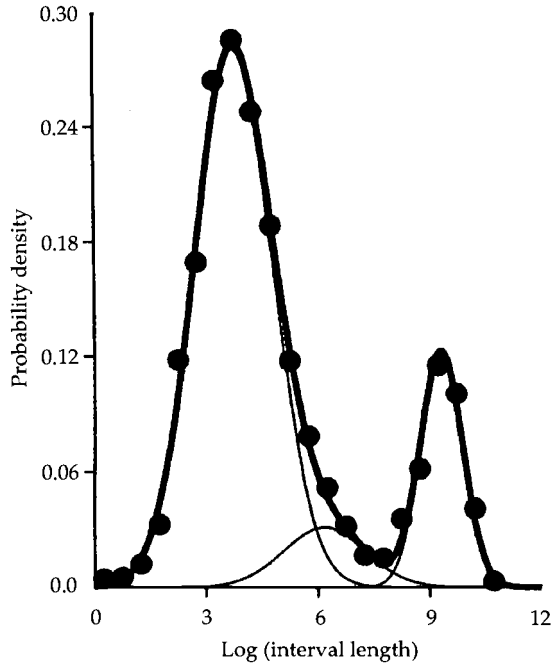


Fig. 2.5. Observed frequencies of inter-meal intervals for lactating cows offered concentrate/silage mixtures (●) and probability density functions for the three-Gaussian curves (—), with their summation (—) (from Tolkamp and Kyriazakis, 1999).

as described for cows, above. For all the animals, the mean intra-meal interval was 11.2 s and the mean inter-meal interval was 110.1 min; the critical interval separating the two types of intervals was 1.29 min. The three-Gaussian model gave an improved fit to the interval distribution and an estimate of the inter-meal criterion of 2.78 min. Although this was more than twice the criterion from the two-Gaussian model, this has little effect on the number (approximately 14/day) and size of meals as there are relatively few intervals in this part of the distribution – most intervals are short (< 30 s) or long (> a few min). The probabilities of meals of these pigs starting were different between daytime and night-time (Morgan *et al.*, 2000b), so that pooling data for all times of the 24-h cycle introduces a false appearance of randomness.

Meal Patterns

Farm animals feed in discrete meals and considerable effort has gone into trying to discover what causes them to start and stop eating, on the premise that if we understand this then we will understand how food intake is controlled. However, despite the discovery of numerous factors that influence meal onset and cessation, we have to take on board the fact that intakes over

longer periods are invariably much more stable than those over short periods of one or a few meals. Stability of intake over several days is observed in the face of extreme variability of meal size and interval.

This is shown nowhere more clearly than in the results of Savory (1989), from a study in which chickens were trained to respond in order to obtain access to food. As the number of pecks required for access (the fixed ratio, FR) was increased, so the meal size increased, the number of meals decreased and the rate of eating increased, but the daily intake of food remained stable (except at the very high FR of 160) (see Fig. 2.6).

Nevertheless, meal size and inter-meal interval must be co-controlled in order that daily intake be regulated, and there has been considerable speculation as to which of these is modified. Are meals initiated at random and their size controlled, or is the interval between meals controlled by the size of previous meal(s)? These questions will be addressed below in a discussion of hunger and satiety ratios.

Even when the food, the environment and the animal itself do not change significantly, there can be considerable differences in the patterns shown by different individuals, even when conditions are similar (e.g. Barrio *et al.*, 2000). Clearly, variability in meal patterns is enormous and its analysis features in studies of feeding behaviours (below), as well as in the use of feeding parameters in animal breeding programmes (see Chapter 15).

It has been suggested that grazing animals are not meal-eaters because they often seem to spend most of the day eating. This is because the slow rate at which they can harvest herbage means that they have to take very long meals in order to try to satisfy their hunger but, with more easily harvested foods, where the rate of eating easily outpaces the rate of utilization of nutrients, meals are

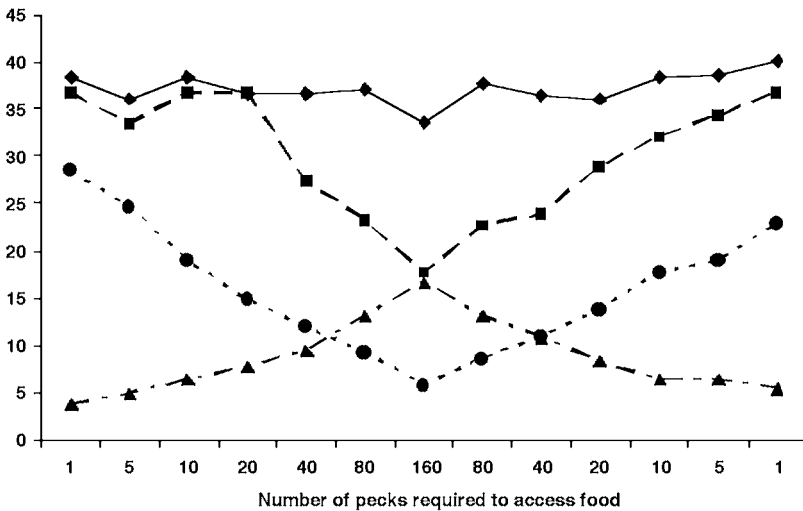


Fig. 2.6. Food intake (♦, g/day), time spent eating (■, min/day), meal size (▲, g) and number of meals per day (●) for chickens with different numbers of pecks required to gain access to food (from Savory, 1989).

discrete. Our assumption is that the various classes of farm animal, ruminant and non-ruminant, have similar basic mechanisms of controlling their food intake, although differences in anatomy and metabolism that have evolved to suit them for particular niches have resulted in emphasis on different mechanisms in different species and in different physiological states.

The study of feeding behaviour has been given a great boost by the development of automated methods of monitoring meal timing and weights, described above. While the primary purpose of such methodology is to allow daily intakes of food by individual animals kept in a group to be monitored, it has resulted in some development of our understanding of feeding behaviour.

Movement between feed stations

When housed in groups with access to several food hoppers, animals usually move between feeders during a meal. To what extent should this be taken into account in determining meal occurrence? Tolkamp *et al.* (2000) analysed visits to feeders by cows offered two foods of differed protein content and those with access only to one of the two foods. Single-visit characteristics were poorly correlated with daily intake and the probability of cows ending a visit did not change greatly with visit length.

Visits were then grouped into meals according to the log-normal model described above; neither inter-meal interval (44.7 \pm 2.1 min), meal duration (36.9 \pm 1.3 min) nor daily number of meals (6.1 \pm 0.1) were affected by treatment, and the probability of cows ending and starting a meal increased with meal length and interval between meals, as predicted by the satiety concept. It can safely be concluded, therefore, that it is meals rather than visits to feeders that are the more meaningful description of short-term feeding behaviour.

Statistical Analysis of Meal Data

Various ways of analysing meal pattern data are discussed by Panksepp (1978). This section covers some of the more commonly used methods.

Univariate analyses

Methods such as t-test and analysis of variance have usually been used to compare means of parameters such as daily intake, meal size and rate of eating. However, because many feeding characteristics, such as meal duration, meal size and inter-meal interval, are inter-correlated, the use of univariate tests for each variable is likely to yield some false significant differences. It is, therefore, often advisable to use multivariate methods of analysis. Where intake has been measured at several intervals during and after an experimental treatment, the intakes during each time interval should be analysed rather than cumulative intakes (Fitts, 2006).

Multivariate analyses

These methods include multiple analysis of variance, discriminant analysis and multiple regression analysis, in which more than one meal-related variable can be included. This is a complex area of statistical analysis (see Geiselman *et al.*, 1980, for examples).

Sometimes, to reduce the huge amount of data collected by automatic systems, calculations are made of mean meal size and inter-meal interval. When done for whole days this disguises the fact that there is a circadian rhythm of feeding behaviour, so the day can be divided into periods of, say, 4 h and means calculated for each period (Forbes *et al.*, 1989).

Figure 2.7 shows the number of meals, meal size and rate of eating by sheep during the six 4-h periods of the day during late pregnancy, lactation and after weaning. The number of meals/4 h declined from the time when fresh food was offered, as did meal size. However, rate of eating did not differ between different periods of the day. The increase in total food intake between pregnancy and lactation was due to an increase in meal numbers, while the slight fall in intake after weaning was due to fewer meals of larger size than in lactation, eaten at a faster rate.

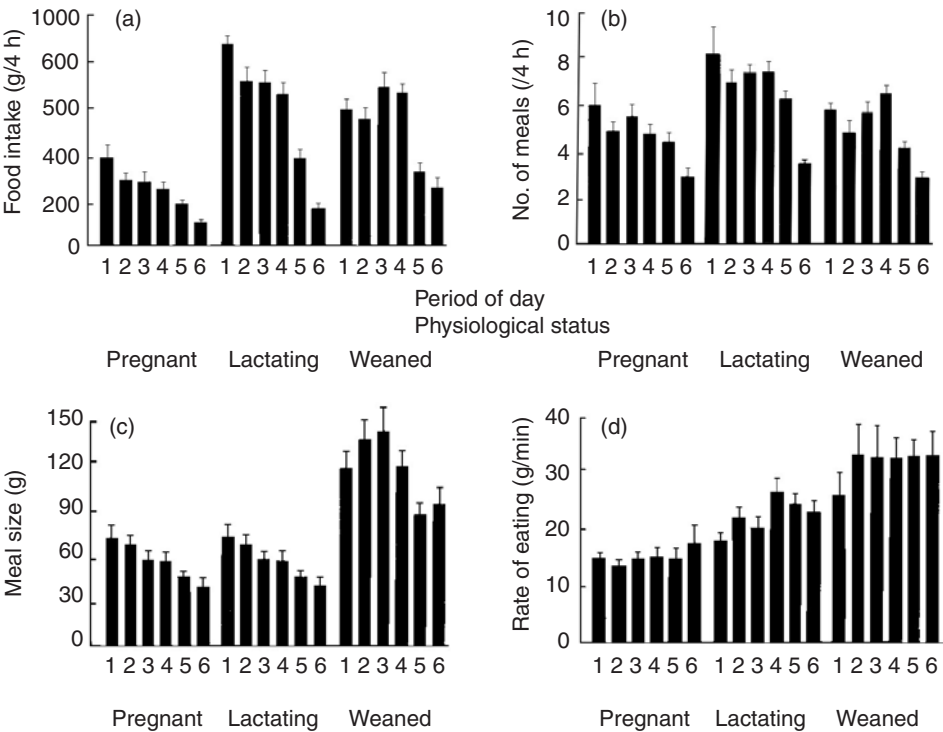


Fig. 2.7. (a) Food intake, (b) meal numbers, (c) meal size and (d) rate of eating by pregnant, lactating and weaned ewes during different periods of the day (from Forbes *et al.*, 1989).

Forbes *et al.* (1989) confirmed that feeding behaviour of ewes was markedly affected by physiological state using discriminant function analysis, which showed that there was very little overlap between pregnancy, lactation and weaning in the characteristics of eating as described by total daily intake, rate of eating, meal weight, number of meals, satiety ratio and time spent eating.

Division of the day into arbitrary periods is an artificial procedure, and methods that adopt a more continuous approach have been developed. Deswysen *et al.* (1989) used Fourier analysis to extract rhythms from meal patterns recorded from heifers offered maize silage. There were large and consistent cycles with phases of 24, 12 and 8 h; the authors speculate about the physiological significance of these rhythms, but only the 24-h cycle is clearly explicable as it is related to the diurnal light cycle and the daily offering of fresh food.

Barrio *et al.* (2000) noted that individual water buffalo had different feeding patterns but that any one animal had a similar pattern on consecutive days. They used cluster analysis to characterize these patterns and saw that the first meal after fresh food (hay) had been offered was longer and heavier than subsequent meals.

Hunger and satiety ratios

Close correlation between the size of meals and the length of the preceding inter-meal intervals implies that there is a mechanism that determines when feeding should stop, i.e. that satiety mechanisms predominate. If, on the other hand, there is a significant correlation between meal size and post-meal interval, this implies that there is a mechanism for determining when feeding should start, i.e. a hunger mechanism. The hunger ratio has usually been found to be more important than the satiety ratio in chickens, as in rats. It has been suggested that using a fixed schedule operant situation gives more 'normal' feeding patterns with more reliable hunger ratios. In cattle, Metz (1975) found a positive correlation between meal size and the length of the pre-meal interval, as did Baile (1975) with sheep offered a 0.6 concentrate:0.4 forage mixture, i.e. the hunger ratio was thought to be more useful than the satiety ratio.

Note, however, that statistically significant ratios between meal weight and prior or subsequent intervals might be a consequence of using inappropriate inter-meal intervals. If arbitrarily defined inter-meal criteria are used that are shorter than the 'true' biologically defined interval (as in the two examples cited immediately above), there will be many small meals separated by short intervals, which will give closer correlations between meal size and pre- or postprandial interval than if the more biologically meaningful interval is used. It is important, therefore, that a method with biological integrity be used for the calculation of inter-meal intervals if false conclusions are not to be drawn from data on feeding behaviour.

In Tolkamp's observations, lengths and weights of meals by cows were distributed according to negative exponentials, suggesting that the termination of

meals was largely random and not tightly controlled by the animal reaching a threshold level of satiety. Although statistically significant, pre- and postprandial correlations were associated with very small proportions of the variation in meal size (Tolkamp *et al.*, 2002). Preprandial correlations, although low ($r \approx 0.12$) were about four times higher than postprandial correlations. This is a sign that feeding behaviour is determined more by satiety than by hunger mechanisms, and means that cows manage their daily intake by means other than inter-meal interval, i.e. feeding behaviour is flexible but, the longer the time over which meals are summed, the more stable and predictable is intake. Therefore, detailed studies of feeding behaviour are of little direct help in improving our understanding of what physiological mechanisms underlie the control of voluntary food intake on a longer timescale.

Description of Feeding Behaviour and its Development

In this chapter we do not describe in detail the many and various methods animals use to harvest food. The book by Fraser and Broom (1997) gives a useful introduction to feeding behaviour, while considerable detail of the feeding process can be found in that edited by Bels (2006). It is, however, appropriate to describe briefly some of the main features.

Poultry

For the first 2 days after hatching, chicks are not dependent on eating food as they have sufficient reserves from the yolk sac. In the first few hours they eat little or nothing, although they are exploring their environment and pecking at small, round objects.

Chickens peck jerkily at food items, pick up the grain in their beak and then lift the head back before swallowing (see Appleby *et al.*, 1992b for a detailed description of feeding behaviour in poultry). Yo *et al.* (1997a) provide very detailed studies based on high-speed video recording and Picard *et al.* (2000) follow this up with further observations that demonstrate the rapid learning of day-old chicks to associate nutritional effects with the sensory properties of the food, based on both their visual and tactile senses.

A novel analytical technique has been applied to describe the patterns of activity during pecking at food by chicks, in which hidden (i.e. not obvious to the human observer) time patterns of behaviours not randomly distributed in time are exposed (Martaresche *et al.*, 2000). It was seen that some pecking at food is organized in regular patterns while other pecking, which increases when the physical form of the food is changed, is not so organized. It was suggested that the latter might be a way in which the chick gathers information about novel foods.

Isolated birds feed in frequent, brief bouts from which it is difficult to define a meal (Kaufman and Collier, 1983). However, when the cost of feeding is

increased, chickens exhibit similar patterns of feeding to mammals, and similar functional relations between foraging cost, meal frequency and meal size, i.e. meal frequency and, eventually, daily intake, decline with increasing difficulty of obtaining food. The authors conclude that: 'Meal patterns do not reflect momentary fluctuations in the internal environment; rather, they appear to be a behavioural device that animals adjust to exploit the available resources in their current habitat efficiently'. Savory (1989) has suggested that feeding behaviour should be studied in conditions where birds have to do a modest amount of work to get food, as this provides more clearly defined meals than when food is easily available all the time.

Although broiler chickens eat almost twice as much as layers of the same age, they spend only half as much time eating and take more meals of shorter duration (Masic *et al.*, 1974).

Feeding data of poultry have not yet been subjected to the rigorous analytical methods of Tolkamp and colleagues to define the critical inter-meal interval. However, analysis of a modest amount of data – from 11 individually caged male chicks of a layer strain, 9 weeks of age with an average body weight of 1115 g – has been performed (Hannah, 2001, using data from M. Picard). The food provided 13.0 MJ ME and 190 g protein/kg. In every bird there were two peaks of interval frequencies, and an example is given in Fig. 2.8. Note that intervals of ≤ 5 s have been filtered out before analysis, so the left-hand distribution is artificially truncated at 1.6 (natural logarithm of 5).

It is clear from these relative frequency distribution plots that two populations of intervals are present, i.e. intervals within and between meals. These initial observations suggest that the log-normal model incorporating two Gaussian distributions can be used to analyse the data to obtain the critical interval time between meals in chickens, which was found to be 1 min 49 s for the bird shown in Fig. 2.8. The proportion of intervals in the first distribution was calculated to be 0.82. To calculate how many meals/day this bird was

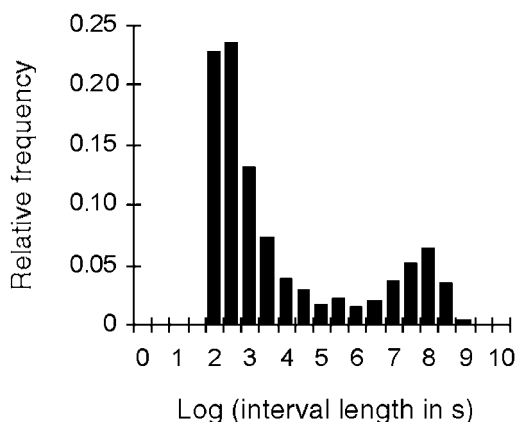


Fig. 2.8. Relative frequency distribution of natural log-transformed intervals between feeding activity (interval length in s) of an individual chicken (from Hannah, 2001).

eating, the number of intervals/day between feeding activities must be multiplied by the proportion of intervals in the second distribution ($1 - 0.82 = 0.18$). The total number of intervals recorded for this chicken was 175/day, so the number of meals/day eaten was $175 \times (1 - 0.82) = 31.5$. Ten other birds in the same study had critical inter-meal intervals of 18–163 s and took 30–70 meals/day.

The mean critical interval time between meals is therefore just under 3 min. The relative paucity of intervals in the middle of the distribution (between 1 and 20 min) means that changes in the critical interval within this range do not have a very large effect on the calculated number of meals.

Beak trimming

While beak trimming, sometimes carried out on laying hens to overcome fighting, does not affect daily food intake or meal number or size (Persyn *et al.*, 2004), beak-trimmed birds spent more time per day eating (3.3 versus 2.0 h/day), so ate more slowly ($0.43 \text{ g/min-kg}^{0.75}$ versus $0.79 \text{ g/min-kg}^{0.75}$). Trimmed hens seemed to be more selective as there was a higher proportion of large particles in the food refusals, suggesting that they found it more difficult to pick up particles, for which the tip of the beak is required. Because of this selection the food actually eaten by the trimmed birds had somewhat higher crude protein and mineral contents than for the untrimmed hens.

Pigs

Pigs grasp at food with their mouths and chew vigorously to mix it with saliva before swallowing the bolus. When kept outdoors, they spend a lot of time rooting in the soil with their snouts. Pregnant sows with nose rings to inhibit rooting ate pellets more slowly than did those without rings, especially when they had to root in turves for the food pellets, putting them at a disadvantage if a mixed group is given a limited amount of pelleted food (Horrell *et al.*, 2000).

Stolba and Wood-Gush (1989) described the behaviour of domestic pigs in a semi-natural environment. Concentrates were given, as the paddocks were not large enough to support the groups with natural food. Even so, on average, 31% of the day was spent grazing and 21% rooting, i.e. over half of the time was spent in ingestive activity. The animals turned turves over to get at worms and prized certain types of root, especially tree roots and those of sedge. Stereotypies and vices, common in indoor confinement, were absent.

Individually housed pigs have shorter and more frequent visits to the feeder than do pigs kept in groups. Nielsen *et al.* (1996) initially housed growing pigs in groups of ten for 14 days and then moved selected animals into individual housing. Contrary to expectations, the animals' feeding behaviour did not appear to change greatly within this new social environment. The individual housing resulted in only a small increase in the frequency of feeder visits. The authors suggested that the feeding pattern of growing pigs may be less flexible than expected.

Cattle

Dulphy *et al.* (1980) and Dulphy and Faverdin (1987) have reviewed the feeding behaviour of ruminants in detail. A characteristic of grazing cattle is that they wrap their tongue around herbage and pull rather than biting cleanly. They walk slowly forward, moving their head from side to side to take mouthfuls as they go.

The feeding behaviour of housed cattle depends to a large extent on the ratio of animal numbers to length of trough. If there is sufficient space for all animals to eat at once then this they will do, especially when fresh food has been given or when they have just returned from milking. At other times a proportion will be eating leisurely. If, however, there is insufficient space for all animals to eat simultaneously then a great deal of manoeuvring takes place, dominant animals displacing timid ones, and meals tend to be a succession of brief episodes interspersed with movement to other feeding positions. Those cows lower in the social dominance order are forced to eat at less popular times of day, including late at night.

Using a critical inter-meal interval of 9 min, it was found that Friesian-Holstein cows in early lactation ate an average of 8.7 meals/day, irrespective of whether the silage dry matter (DM) content was high (H, 449 g/kg) or low (L, 215 g/kg) or whether the supplementary compound food was high in starch or high in digestible fibre (Romney *et al.*, 2000). The results show that chewing indices (time spent eating silage, ruminating and total time chewing/kg DM ingested) were significantly greater for the L silage, while time spent eating, and duration and number of meals were similar for either silage. The most likely explanation for the greater intakes of H is a faster particle breakdown in the rumen, allowing larger meal sizes before animals became constrained (see Table 2.1). Factors affecting silage intake are discussed in Chapter 14; the information given here is as an example of eating parameters in dairy cows.

In a similar experiment, intake reached a peak in mid-lactation, while the number of meals per day reached a nadir around week 15 of lactation (Jackson *et al.*, 1991). The daily intakes of silage for the two supplement types were 10.8 and 13.0 kg DM, respectively, eaten in 209 and 229 min. Thus the higher silage intake was achieved on the digestible fibre supplement by eating

Table 2.1. Food intake parameters derived from 48 h continuous recording of intake for dairy cows consuming low (L) or high (H) DM silage supplemented with 9 g/day concentrates (from Romney *et al.*, 2000).

Silage	L	H	Significance
Silage intake (kg DM/day)	9.0	13.8	+++
Time spent eating (min/day)	183	200	ns ^a
Rate of eating (g/kg)	49	69	+++
Number of meals	8.4	8.6	ns
Intra-meal pauses (min/day)	27.6	36.8	

^a Not significant.

larger, longer meals. Figure 2.2 shows an example of a 24-h meal pattern of one cow. In this case, nine meals of silage were taken and three allocations each of 2 kg concentrates were dispensed. At 230 min, she tries to get concentrates but is not allowed and diverts her attention to eating silage. Some of the silage meals are protracted and fragmented (e.g. those at 650–750 min), while others are continuous (e.g. that starting at 840 min).

Dado and Allen (1994) have monitored feeding, ruminating and drinking behaviour in lactating cows offered a total mixed ration and have concluded that a Latin Square design with 12 cows monitored for 5 days would be sufficient to detect a 10% difference between means for feeding-related behaviour variables with a probability of 80%.

Sheep

From 2 or 3 weeks of age, lambs spend increasing amounts of time nibbling at food. After weaning they eat by prehending food with their lips and tongue, pulling it back into the mouth for extensive chewing.

Sheep can select well as they have a narrow bite. However, they have a blind area about 30 mm in front of the nose so they can't see clearly what they are eating! Perhaps they use touch to decide exactly what to eat. When they are selecting actively, e.g. green material from a predominantly dead sward, rate of eating is greatly reduced. The best way to monitor what sheep are selecting is to collect oesophageal extrusa from fistulated animals, although it is then difficult to identify the various parts of the plants. Lynch *et al.* (1992) cover feeding behaviour of sheep in detail.

Dulphy *et al.* (1980) reported a mean total eating time of 305 min/day for wether sheep fed fresh-cut green forages, with a mean rate of eating of 4.3 g DM/min. These animals took 7.5 meals/day and spent an average of 537 min/day ruminating.

Rate of Eating

When it is possible to measure intermediate weights of the food during the course of a meal it can be seen that rate of eating sometimes declines towards the end of the meal.

Poultry

Growing broilers eat faster than layers of the same age (Masic *et al.*, 1974), but it is not clear whether this is because they are bigger and heavier or have a greater need of nutrients. Rates of eating were significantly faster for pellets than for the same food in powdered form, and declined during the 30 min after giving food after a 0–4-h fast (Savory, 1988). The weight eaten in the first 5–10 min was proportional to the length of the previous deprivation period (see below).

Pigs

Auffray and Marcilloux (1983) observed a deceleration in the rate of eating as the meal progressed. 'Unpalatable' foods are eaten more slowly than 'normal' ones and rate of eating often increases over a period of several weeks as the animals learn that the food is completely safe. It had been assumed that rate of eating would be influenced by the bitter-tasting glucosinolates present in rapeseed meals but, in the work of Lambert *et al.* (1992), the food eaten most slowly was that lowest in glucosinolate!

Cattle

Faverdin (1985) observed that the rate of eating of a complete food by a lactating cow increased linearly from 50 g/min in the first few days of lactation to 90 g/min in week 9 of lactation. The rate declined as a large meal proceeded, from 120 to about 50 g/min due to longer pauses in actual chewing as the meal progressed. Intake rate at the beginning of the meal is four to five times higher than at the end for cows eating maize silage.

The mean rate at which lactating mature cows ate grass silage (54 g DM/min, Jackson *et al.*, 1991) was very similar to that for lactating heifers eating a complete silage/concentrate mixed food, with an average rate of approximately 50 g DM/min (J.M. Forbes, unpublished observations).

Presumably in systems where food is limited, e.g. dairy cows fed concentrates in a group, the fastest eaters will consume more and produce more milk, thus rendering themselves more likely to be selected as the mothers of future cows, i.e. selection for fast rate of eating. However, the rate of eating by cows low in the dominance order was found by Kenwright and Forbes (1993) to be significantly faster during the 40-min peak periods after each milking (300 g fresh matter/min) than at a quiet period (10.00–12.00 h) (200 g/min) and the time spent eating significantly less (14.6 versus 18.7 min/h).

The most dominant animals did not eat significantly more quickly during these peak times than at other times of day (270 versus 250 g/min), but spent a little more time eating than at other times of day (19.9 versus 17.6 min). Thus, the dominant cows did not feel under pressure to eat quickly at busy times as they were confident of being able to continue eating when they were hungry.

Rate of eating of concentrates is particularly important when cows are fed in the parlour at milking time. Any cow not having eaten all her allowance when her group has finished milking will hold up the whole group, or miss part of her ration which will then be eaten by the next cow to come into that position in the milking parlour. Inclusion of rapeseed meal in a dairy compound food slows rate of eating, but only to a marked extent during the first two or three foods after the rapeseed is introduced (Frederick *et al.*, 1988). A familiar flavour incorporated in the food successfully prevents this initial slow rate of eating.

Wet food is eaten more quickly than the same food given in the dry form, and Clough (1972) found that cows that ate loose meal at 323 g/min ate pellets at 455 g/min and slurry at 1670 g/min; even though the slurry contained water, the rate of DM intake was considerably higher with the food in this form.

Sheep

Pregnant ewes fed throughout on a complete, pelleted food ate at an average rate of 15 g/min and this increased to around 20 g/min during lactation and to over 30 g/min after weaning (Forbes *et al.*, 1989; Fig. 2.7).

Rates of eating during the first 30 min of the large meal taken after offering fresh hay, chopped dried grass or pelleted dried grass were 7.3, 9.4 and 10.8 g/min, respectively (Forbes *et al.*, 1972). During the second and third 30-min periods there were progressive reductions in the rate of eating. In a further experiment, the same authors penned ewes either singly or in groups of six and fed them on hay either *ad libitum* or at two-thirds of *ad libitum*. Rate of eating in the 30 min after giving fresh hay was significantly higher for the lower level of feeding (9.7 g/min) than for *ad libitum* (8.4 g/min), but only slightly higher for group-fed ewes (9.3 g/min) than for those penned individually (8.8 g/min).

The fact that restricted-fed sheep ate more quickly than those fed *ad libitum* shows that the latter were not eating at their maximum rate, and therefore that neither jaw fatigue nor lack of saliva were likely to have limited *ad libitum* intake.

Detailed studies of long meals have shown an exponential slowing of rate of eating. In the example given in Fig. 2.9, the sheep was allowed access to lucerne for only 6 h/day and would therefore have been very hungry at the start of this meal (Baumont *et al.*, 1989).

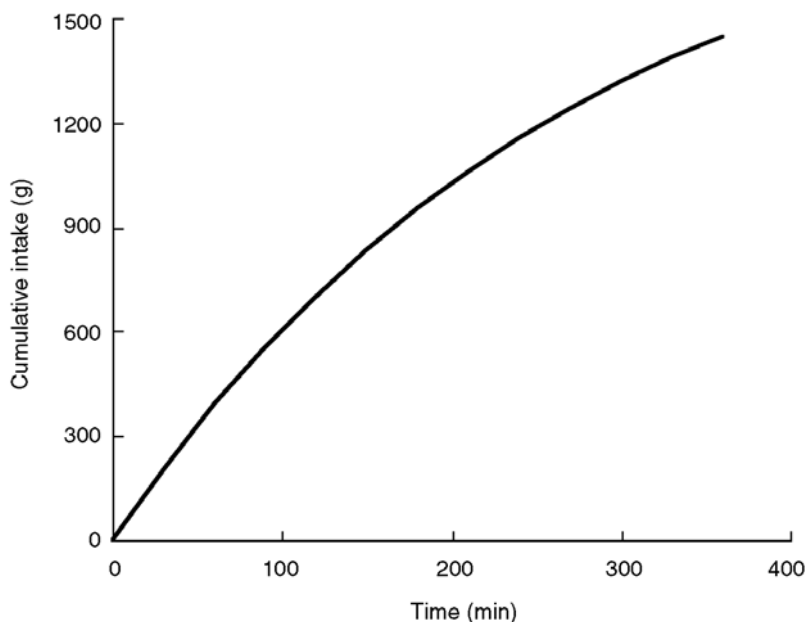


Fig. 2.9. Cumulative intake of lucerne by a sheep given access for 6h/day: intake (g DM) = $1975(1 - e^{(-0.0044 \cdot \text{time})})$ (from Baumont *et al.*, 1989).

Short-term Intake Rate

It has been suggested that foods that are initially eaten more quickly than others will have a higher daily intake, and Short-term Intake Rate (STIR) has been proposed as a way of predicting intake, or at least of ranking the intake potential and as a test for intake potential of foods initially only available in small quantities (e.g. from plots of new varieties of herbage plant) (Harrison *et al.*, 1998). STIR was defined for cows as the amount eaten in 4 min after a 4-h fast. Although there was some evidence that STIR predicted rank order of intakes of different forage mixtures, there were quite marked effects of the order in which forages were offered on test days. However, many factors are likely to affect STIR, including starvation time, length of ingestion period, form of presentation of food, fibre concentration, DM content, feeding level, body condition of animals and physiological state of the animals.

One very important consideration is the experience the test animals have had of the tested foods, or of foods with similar sensory properties (see Chapter 6). For example, lambs that had received intra-ruminal infusions of starch just after feeding increased intake, intake rate, bite rate and intake per bite of the food available just after the infusion, compared with lambs that had received only intra-ruminal infusions of the vehicle (water) (Villalba *et al.*, 1999).

This demonstrates that STIR is influenced to a great extent by the post-ingestive consequences of food ingestion, so that it is not suitable for testing foods that are only available in sufficient quantities to make one or two tests, i.e. insufficient experiences to allow learning.

Rate of eating silage or grazed herbage was found to increase with length of pre-fasting, mainly through increases in biting rate and dry matter intake (DMI)/bite (Patterson *et al.*, 1998, Fig. 2.10). Extending the fasting period from 6 to 13 h did not cause any further increase in rate of eating, however, suggesting a physical limit to the frequency and size of bites. Intake rate was found to decline during an eating bout, as the hunger drive declined.

Circadian Rhythms of Feeding

Rats eat more frequent and larger meals at night than during the day, as they are nocturnal animals, while farm mammals are more active during the day and eat a greater proportion of their meals in daylight than at night.

Poultry

Unless the nights are very long, poultry do not eat during the hours of darkness, so there is a very marked diurnal rhythm of feeding. Savory (1979) observed a peak of feeding activity and intake during the hour before dusk, presumably to fill the crop as a reservoir of food to last the bird through the night. It is not necessary for the light to dim slowly for this feeding to occur, as the peak of feeding still occurs when the lights are extinguished abruptly.

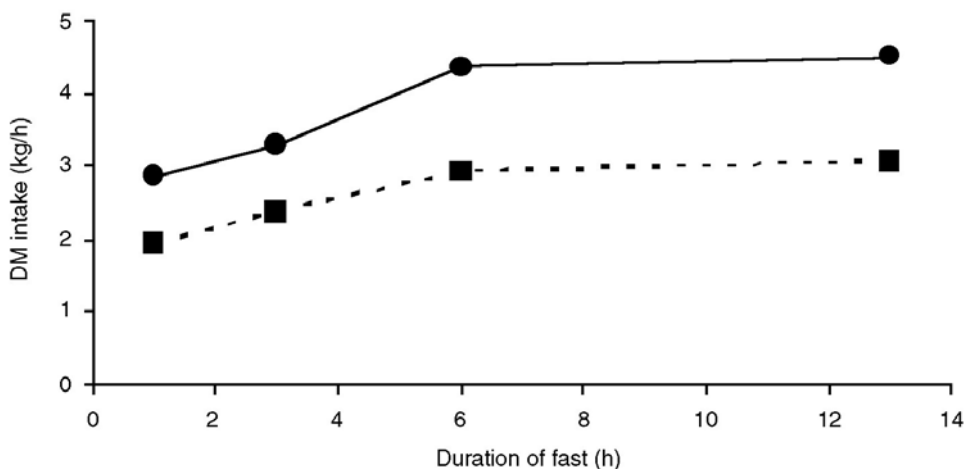


Fig. 2.10. Intake of grazed herbage (●) and silage (■) by lactating cows after various lengths of fast (from Patterson *et al.*, 1998).

In order to see the extent to which birds learn to anticipate a fast, Petherick and Waddington (1991) housed pullets individually in a circadian-free environment and, on days 17–47, 50% were shown a coloured card during the final hour of food availability, prior to food deprivation of 8 or 12 h. There was no indication of increased intake during this period and so no suggestion that they could learn to use the colour cue to anticipate a fast. Do they learn when dusk is approaching by the number of hours since dawn?

Pigs

There are two peaks of feeding, one in the morning and one in the early afternoon (de Haer and Merks, 1992) but Fig. 2.11 shows that the second is by far the greater. Note that some feeding still takes place at night and that there is little effect of single versus group penning. However, examination of the data in more detail showed that, in groups, 69% of meals accounted for 87% of intake and 83% of eating time. With individual housing, only 39% of meals contributed 90% of the food eaten and 79% of the feeding time.

In other words, there were a lot of small, short meals when pigs were kept individually, compared with when they were in groups; with group feeding there can be considerable competition for a single feeder, resulting in many interrupted meals and therefore fragmented feeding behaviour. The repeatabilities of day-to-day recordings of intake traits were high within 2-week periods compared with months or the whole fattening period, indicating a steady change in feeding behaviour as pigs grow.

The difference in behaviour between day and night is likely to be a result of social constraints, but may also represent a reluctance by the animals to feed

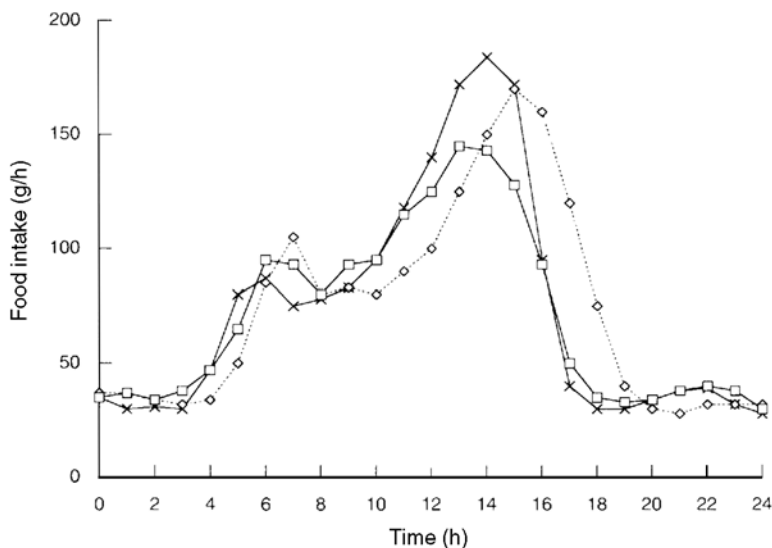


Fig. 2.11. Diurnal patterns of feed intake in group-housed growing pigs. The three lines represent different batches of animals (from de Haer and Merks, 1992).

at night. The two daylight feeding peaks may be coincidental with the entrance of the stockperson into the animal house or may be the preferred feeding times of the pigs.

Cattle

A high level of feeding activity is usually observed after fresh food is offered. A smaller peak often occurs before sunset and another just after midnight. Data from individual young bulls fed from automatically recording feeders showed that the sunset peak moved according to the time of year and that the night-time quiet period was longer in winter (Stricklin, 1988). In another trial, cattle were either trough-fed or fed from a single automatic feeder. While those fed from the trough showed a normal diurnal pattern of feeding, those on the single-space feeder ate at any time of day or night, presumably due to competition. Trough-fed cattle spent about 120 min/day feeding compared with 80 min/day for those on the single feeder.

Under conditions where little competition for feeder space exists, dairy cows eat few meals from around 01.00–06.00 h. When there are more animals than feeder spaces there is strong competition at busy times, particularly after milking and when fresh food has been delivered. Kenwright and Forbes (1993) observed a clear triphasic pattern of eating in cows milked three times per day, peaks of feeding activity occurring during the periods after return from milking, including large meals, which shows that some cows were monopolizing feeders, thereby preventing others from eating at that time. The more dominant animals

ate less at night (01.00–06.00 h) than those at the bottom of the ‘pecking’ order. Therefore, heifers low in the social dominance order might not be able to satisfy fully their desire to eat when the level of competition for feeding space was high. The high incidence of aggressive interactions during the period immediately after return from milking has implications for the health and nutrition of the animals.

The fact that lower-yielding cows were lower in the dominance order (calculated according to Rutter *et al.*, 1987) than high yielders but ate more at night suggests that high demand for nutrients was not the prime cause of nocturnal eating, although it is possible that low dominance caused low intake, resulting in lower milk yield. It is more likely that those lower in the dominance order were prevented from meeting their needs during the day and were thus forced to satisfy their requirements by eating in the middle of the night. When they did manage to eat at the most popular times of day it was in short meals, eaten at a rapid speed and terminated by the arrival of a more dominant animal.

What are the implications of these findings for the management of dairy herds? Jackson *et al.* (1991) suggested that, up to a ratio of 3.5 cows/feeder, there was no effect on daily intake of silage, while Elizalde and Mayne (1993) have shown that, although feeding behaviour is affected with 5 or more cows/feeder (increased rate of eating and shorter total feeding times), it is not until there is a ratio of 7 cows for each feeder that daily intake of silage becomes depressed.

Sheep

Sheep show similar light-entrained circadian rhythms of feeding to cattle (see Fig. 17.7). Another factor affecting feeding rhythms is environmental temperature: sheep do not eat in the hottest part of the day when the heat load is so great that they must seek shelter.

Food Restriction and Fasting

Periods without food leave the animal in a different state than when fully fed. It is important to measure fully this state in order to predict how the animal will respond when fully fed again. Care needs to be given to the choice and description of the treatment(s) during the rehabilitation period.

Poultry

Pecks at food become faster, stronger and less accurate after increasing periods of deprivation (Wood-Gush and Gower, 1968) but, when food is unavailable for 1 day in 5, there is complete compensation of intake and growth. Petherick *et al.* (1992) trained hens to run down a 14.4-m alley for food after being deprived for 0, 6, 12 or 18 h. The speed of running was significantly increased by deprivation,

but there was no difference between deprivation periods (0.29, 0.62, 0.65, 0.57 m/s, respectively), suggesting that 0.65 m/s was the fastest they could run.

Food restriction is sometimes used to delay puberty in pullets. When pullets were subsequently restricted to that weight of food eaten voluntarily at 6 weeks of age (45 g/day), the birds ate and pecked at empty feeders for the same amount of time per day as ad libitum controls spent eating, i.e. there was no increase in attempts to get food, as is seen in more severe types of underfeeding.

Broiler breeder stock are usually restricted to less than one-half of ad libitum intake. Such animals have a high rate of working for food, even just after their ration has been consumed, and are highly motivated to eat at all times (Savory *et al.*, 1993). If offered food ad libitum after a period of restriction, at first they eat up to three times the restricted daily level, gradually falling to about double the restricted level (de Jong *et al.*, 2003).

When food was returned to cockerels of an egg-laying strain after food deprivation, the rate of eating was higher after a 24-h fast than after a 2-h fast, but there was no further effect of 48 h (Wood-Gush and Gower, 1968). It is likely that the size of the first meal after a long fast is limited by the capacity of the crop, which acts as a storage organ, the distension of which inhibits feeding.

Rather than restrict intake by offering weighed amounts of food, it is often more convenient to give access to unlimited amounts of food for limited periods of time. Cockerels of a layer strain allowed food for one or two periods of 2 h each per day ate 65 and 80%, respectively, of the amount eaten by control groups with 24 h/day access and, somewhat surprisingly, they did not increase their intake as they became accustomed to the situation (Barach *et al.*, 1992).

In a review of the welfare of poultry in modern production systems, Mench (1992) discusses food deprivation and restriction which pose a welfare dilemma as, if fed ad libitum, broiler breeders experience reduced fertility and health problems, yet if fed at the usual severely restricted level they are hungry for most of the time. The welfare aspects of feeding restricted amounts of food or imbalanced foods are discussed further in Chapter 18.

Pigs

There was a linear increase in the weight of food eaten by growing pigs during the first meal after deprivation of 1–6 h (M. Corbett, S. McNicholas and J.M. Forbes, unpublished observations).

Restriction of protein intake in pigs has been shown to cause increased rooting and general activity, suggesting that specific nutritional needs increase foraging motivation (Lawrence *et al.*, 1993). Restriction of food intake gives rise to increases in 'working' for food in an operant conditioning situation, but normal farm environments do not provide facilities for foraging. Therefore, animals develop stereotypies such as chewing chains; ingestion of even a small amount of food stimulates such activities. Pregnant sows are usually restricted to about 60% of their ad libitum intake and such animals have a high rate of working for food, even just after their ration has been consumed. In order to

give sows a more natural way of getting food by working for it, a feeding ball has been developed that delivers food pellets at random intervals if it is rolled around (Young and Lawrence, 1993). The lower the level of feeding, the more sows push the ball around.

Quite severe food restriction of boars makes them much more willing to press a button to obtain small rewards of food, compared with those fed almost *ad libitum* (Lawrence *et al.*, 1989). When the bulk of the restricted ration is increased by incorporating straw, there is no reduction in operant responding, showing that the mere presence of bulk in the digestive tract is not satiating. However, pregnant gilts and sows given restricted amounts of food with different levels of fibre showed a significant reduction in stereotypies with higher fibre foods, and so Robert *et al.* (1993) concluded that bulky food may be beneficial for the welfare of pregnant sows.

Pigs spend a considerable amount of time chewing materials in their environment, but it is unclear whether this reflects motivation to feed, to explore or a combination of both. By providing a tube containing water, saccharin solution or sucrose solution, Day *et al.* (1996a) were able to separate these possibilities. They observed that chewing at the plain water tube was at a low level and not affected by the degree of food deprivation. Saccharin only slightly increased chewing whereas sucrose, which provided energy as well as a sweet taste, caused large increases in chewing activity, especially in food-deprived animals, demonstrating that nutritional feedback during exploration modifies foraging behaviour towards correction of energy deficiency.

Cattle

The intake of hay by cows increased by 20% as the increase in time of access to food was increased from 5 to 24 h/day, in contrast to an 80% increase in intake when the food was a concentrate mixture (Freer and Campling, 1963), suggesting a physical limit to intake of the hay. Daily access for at least 6 h is necessary for maximum intake of silage by beef cattle (Wilson and Flynn, 1974). Dry cows ate 8.0 kg/day when given access to silage for 5 h/day, while those with continuous access ate 10.1 kg (Campling, 1966).

Sniffen and Chase (1987) observed that mildly intake-restricted cows (100% of calculated net energy requirement) ate an average of 4.4 meals daily, compared with an *ad libitum* group (111% of net energy (NE) requirement) that ate 12.4 meals.

Sheep

When sheep were given access to hay cubes for 3, 6, 12 or 24 h/day, intakes were 1502, 1869, 2086 and 2413 g/day (Hidari, 1981). With fasts of 1–6 h, sheep fed on a pelleted 0.5 dried grass:0.5 barley compound food compensated for the fasting period in the first two or three meals after the food had been

replaced and there was no effect on daily intake (J. Black, F. Carey-Wood and J.M. Forbes, unpublished observations).

Abnormal Feeding-related Behaviour

In intensive husbandry it is not uncommon for abnormal feeding-related behaviours to occur. While these have been ascribed to boredom, it is also possible that such behaviours as tail biting and feather pecking are expressions of a desire to obtain nutrient(s) not provided in sufficient quantities by the diet.

A stereotypy is 'a repeated, relatively invariable sequence of movements which has no obvious purpose' (Fraser and Broom, 1997), such as repeated chewing of metal bars by individually penned sows. They are mostly performed during the post-feeding period and are initiated by giving a small amount of food. This, and the fact that they are not normally elicited by non-food-related stimuli, suggests that they are due to underfeeding and exacerbated by the lack of alternative possibilities for exploration and activity.

Excessive water consumption is sometimes seen in poultry, pigs, sheep and horses, the latter taking up to 140 l/day. When this occurs, it is usually in confined animals and can be overcome by provision of more space and exercise. Often, the apparently high consumption of water is due to excessive waste, as bored animals stand with their noses on nipple drinkers, allowing most of the water to go to waste.

Poultry

Feather pecking can occur in all types of poultry, especially if insufficient trough space is provided. This can be alleviated by giving birds something to search for, e.g. by giving some whole grains in the food or on the floor, but this does not necessarily alleviate hunger (de Jong and Jones, 2006). Feather pecking sometimes leads to body pecking and wounding.

Egg eating by hens may be an indication of mineral deficiency in the diet, as it is reduced by providing grit, although this again may be a question of lack of variety of activities rather than a nutrient deficiency. Birds eat shavings on which they are bedded if they have insufficient trough space; this can result in gizzard compaction and eventual death if not forestalled by increasing the availability of food.

Pecking at metal or wood in a stereotypic manner is sometimes observed in birds, again when the environment is monotonous. It has been noted that the amount of time spent stereotypically pecking was negatively related to plasma corticosterone levels, and it has been suggested that such activity relieves stress.

Pigs

It is natural for newly weaned animals to explore their environment and they often lick and chew objects, including other animals. However, this sometimes

develops into biting each other's tails if pigs are heavily stocked in a boring environment. The use of straw bedding and/or the provision of 'toys' is helpful as it gives the pigs more interest and activity. Belly nosing in early-weaned piglets is a response to the lack of the mother. Pigs also show increased tail biting when the diet is deficient in salt or protein. This is probably a general increase in oral activity rather than a specific alleviation of the nutrient deficiency, as the little blood obtained would not significantly improve their salt or protein status (Fraser and Broom, 1997).

Stereotypies by pigs are increased by low levels of feeding, leading to persistent feeding motivation. Bar chewing or sham chewing in sows, common in individual pens or stalls when restricted feeding is practised, is usually reduced if straw or sawdust is provided (Lawrence *et al.*, 1993). Sows often eat dead piglets but occasionally a sow may attack, kill and eat a piglet. Usually only first litters are affected and in the first few hours after parturition.

Cattle

Calves spend about 1 h/day sucking naturally from their mothers, but can drink milk replacer much more quickly than this, leading to boredom and sucking of other calves, particularly the navel. The use of dispensers that deliver the milk slowly to simulate natural suckling is helpful, as is the provision of straw bedding.

Many calves in crates lick their own hair, a symptom of boredom and possibly of nutrient deficiency. This often creates hairballs in the stomach, which can occasionally become so large that they block the digestive tract.

Restricted-fed heifers sometimes show stereotypies in the post-feeding period, and those individuals spending less time eating spend more time exhibiting stereotypies. Feeding-related activities such as sniffing or licking the feeding trough are seen more frequently around the time that stereotypies are exhibited, suggesting that oral stereotypies are indicative of frustrated feeding behaviour. Although lactating cows are usually fed *ad libitum*, they are often in negative energy balance and higher-yielding cows, which typically lose more weight in early lactation, have been seen to show more stereotypies.

Redbo *et al.* (1996) studied the effect of mild restriction of food on oral stereotypies in lactating cows. A total mixed ration was given *ad libitum* from weeks 3 to 26 of lactation or *ad libitum* from weeks 3 to 14, with restriction to Swedish standards for maintenance and lactation from weeks 17 to 26, while the third treatment was restriction throughout. When food was available *ad libitum* there were almost no stereotypies, while with restricted feeding the amount of time spent in stereotypic activities was noticeable (see Fig. 2.12). Those cows that were restricted in both periods showed distinctly more stereotypies in period 2, i.e. when they had been on restriction longer. It seems as if stereotypic activity is caused by underfeeding, but it is not always clear whether it is hunger or boredom that is the main determinant.

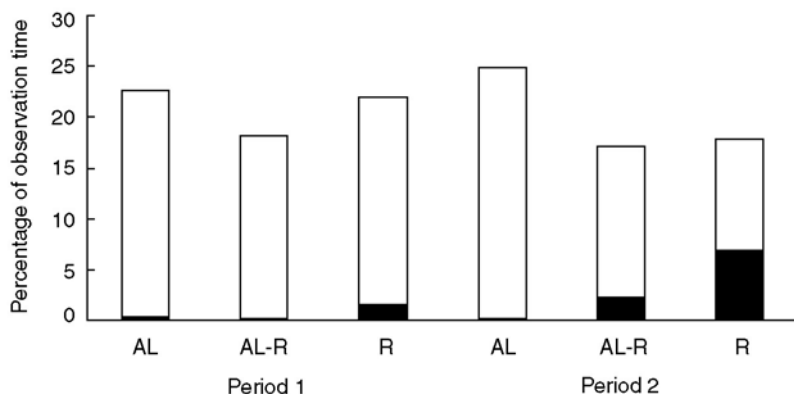


Fig. 2.12. Time spent feeding (blank) and performing stereotypes (filled) by lactating cows fed on a total mixed ration. Period 1, weeks 3–14 of lactation; period 2, weeks 17–26. AL, ad libitum throughout; AL-R, ad libitum in period 1, restricted in period 2; R, restricted throughout (from Redbo *et al.*, 1996).

Sheep and goats

Sheep will pull and eat the wool of others if too tightly penned, but this can usually be prevented by providing roughage for them to chew. Agile, young goat does can suck their own teats.

Marsden and Wood-Gush (1986) fed individually penned lambs aged 8 weeks either high (174 g/kg DM) or low (110 g/kg DM) protein foods ad libitum or restricted to 1 kg/day. More time was spent in abnormal activities (such as biting empty food bins, wood or wool, 'star-gazing') by those on the restricted level of food but, when hay was offered in addition, there was much less abnormal behaviour. Blackface lambs chewed wool more when on low-protein than when on high-protein food, while there was no difference in Suffolk crosses. The former spent less time eating than the latter when on ad libitum feeding and more time in abnormal food searching. These ad libitum fed animals grew at a very high rate, thus showing that high performance is not necessarily an indication of good welfare.

Conclusions

There are various ways of monitoring food intake, but some of the indirect ones have a large amount of variability associated with them. Automation allows the collection of large amounts of data without the presence of a human observer to disturb the animals. It is possible to monitor the feeding behaviour and food intake of individual animals kept in a group, which allows monitoring under realistic farm conditions.

This has paved the way for the use of food intake and efficiency of utilization in selecting breeding stock. It has also allowed better statistical

methods of defining inter-meal intervals to be developed. Feeding is characterized by relatively stable food intakes over periods of several days, but also by widely different meal patterns between individuals on the same food and within individuals with different foods.

The feeding behaviour of an animal in a barren experimental environment might be quite different from that of the same animal in more natural surroundings, and it has been suggested that the use of operant systems that make the animal work to obtain food encourage the animal to adopt a more natural feeding pattern. Unnatural feeding-related behaviour is seen in animals that are frustrated, either by lack of food or by being kept in a restricting environment.

There are strong circadian rhythms of feeding, but these are not inflexible: for example, chicks will eat during the dark if that is the only time food is available, even though they normally eat nothing at night. Short periods without food can be compensated for when food becomes available, but longer periods of fasting result in a significant reduction in daily intake.

3

Feedbacks from the Gastrointestinal Tract

In searching for hunger/satiety signals we are looking for changes in the body that go in one direction during a meal, may continue in that direction for some time after the meal, but eventually return to the pre-meal level. There are numerous changes that fit these criteria, including physical and chemical factors in the gastrointestinal tract, and hormones and metabolites in the bloodstream. These changes, and the routes by which information concerning them is carried to the brain, are referred to as negative feedback pathways. It is unlikely that, under normal circumstances, only one factor is involved in the termination of feeding, or satiety. Rather, satiety is proposed to occur when the combined strength of signals from gastrointestinal and liver receptors reaches a threshold (MTD hypothesis, see Chapter 10).

Even this is a simplification, however, as it does not allow for long-term balancing of food intake with requirements; in order to achieve this match, feeding must terminate long before the animal knows how much of the various nutrients have been absorbed. In order to provide ways of predicting nutrient availability, learned associations between the organoleptic properties of a food and its eventual nutritive value are developed (see Chapter 6). However, the considerable variation in meal size and number within a day, both between and within animals, throws great doubt on the importance of short-term negative feedback signals as the only determinant of the amount of food eaten over periods of 1 day or more. This has already been alluded to in Chapter 2, and we will return to this theme in later chapters. This chapter deals with the gastrointestinal tract, while metabolites and hormones are covered in Chapter 4.

There is particular emphasis in this chapter on ruminant animals because of the great economic importance of their having evolved a large and complex set of stomachs in which digesta are stored for many hours for microbial fermentation (Church, 1988). This long period of storage makes the physical capacity of the stomachs a potential limiting factor to intake and gives considerable importance to the rates of digestion, breakdown and onward passage of particles of food. In

addition, there are several unusual products of digestion, particularly the volatile fatty acids (VFAs), which the host animal must metabolize and which are therefore potentially important controllers of voluntary intake.

Altering the digestibility and rate of passage of a forage food causes parallel changes in intake (Van Soest, 1994). For example, supplementation of low-protein forages with urea increases the rates of digestion and passage and allows a greater intake. Grinding a forage food also increases its rate of flow out of the rumen and allows increased voluntary intake. Although the digestibility of the food is reduced by grinding, since the food is in the rumen for a shorter time, the total weight of nutrients absorbed daily is increased. Such treatment of poor forages, accompanied by pelleting, is sometimes practised commercially. Relationships between the digestible energy concentration of food and level of intake by ruminants and simple-stomached animals are discussed in Chapter 11.

The Mouth

The first point at which intake might be limited is the mouth or, more precisely, the teeth. While this is not likely to be an important limit under most circumstances, Illius *et al.* (1995) have observed that wild Soay sheep on the small island of St Kilda off the Scottish coast show 3–4-year cycles of population due to high mortality from starvation and intestinal parasites when the population gets too great to be supported by the available herbage. The survival rate is significantly related to the incisor arcade, animals with wide mouths being better able to harvest the short grass.

These authors wondered why this natural selection did not lead to ever-widening mouths, and proposed counter-selection for arcade width in the years of plenty following the population ‘crash’. According to their theory, an excess of herbage leads to poor-quality pasture and it is the animals with narrow mouths that can more successfully select the more nutritious shoots from amongst the bulk of stemmy grass, thus obtaining a more nutritious diet on which their chances of survival are improved compared with wide-mouthed individuals. Thus, over a period of many years, mean arcade width remains relatively constant.

It has been suggested that the jaw muscles become fatigued in species such as ruminants that have to spend a long time chewing each day, leading to slowing of the rate and eventually to the cessation of eating. Such fatigue is not of importance in normal satiety, however, because cows continued to eat for much longer than usual when ingested food was removed via a gastric fistula (Balch and Campling, 1961). It is not necessary, therefore, to consider the mouth as a generator of negative feedback signals, except in helping the animal to identify the food with learned associations.

Oropharyngeal Receptors

Receptors in the buccal cavity and throat are important in the animal’s sensory perception of food; the sensory properties of a food are as likely to encourage

further feeding as they are to cause feeding to stop. De-afferentation of the buccal region in the pigeon, by section of the trigeminal nerves, leads to loss of interest in food, although drinking and grooming are unaffected; clearly, in this species the taste and texture of food in the mouth is an important reinforcer of feeding.

Gastric Receptors

The first internal changes to be correlated with feelings of hunger were the so-called hunger contractions of the stomach. However, vagotomy, which abolishes these contractions, does not seriously interfere with the regulation of food intake in poultry or pigs. In the chicken hunger contractions occur in the crop and in the proventriculus and gizzard, whereas with ruminants there is a decrease in the frequency of contractions during periods without food.

Distension of a balloon in the stomach depresses intake, but does not completely abolish feeding, while intra-gastric administration of the amount of food normally taken in a meal also depresses, but does not totally inhibit, feeding showing that stomach distension is not the only controller of intake. Clearly, the presence of food in the stomach and/or its passage through and absorption from the intestines are important factors in inducing satiety, but not the sole factors.

Dilution of food with non-nutrients, or 'dietary bulk', reduces the concentration of nutrients in the food so that more food is eaten before nutrient-induced satiety occurs. However, the volume accumulating in the stomach, and later passed to the intestines, may be limited by the capacity of these viscera and a physical, distension-induced satiety may result. This is particularly true in ruminant animals with foods high in fibrous constituents that have to stay in the rumen for many hours. Chapter 11 discusses this aspect in more detail.

Poultry

Stimulation of the crop by filling it with water, saline or a balloon, or cooling the crop, all depress food intake (Richardson, 1970). Such treatments involve considerable disturbance and there would have been less stress if the crop were loaded via a surgically implanted cannula. Introduction of 12 or 20 ml of a paste of food into the crop via a cannula depressed food intake (Shurlock and Forbes, 1981b). To determine whether bulk or nutrients were involved in this response, glucose solutions were given into the crop. Amounts > 1.5 g in 10 ml of water significantly depressed food intake during the 1 h after injection, while at least 3.8 g was necessary to depress intake over a 3-h period. The effect of additional amounts of glucose was greatest with loads of up to 4 g, and with greater weights there was little additional effect on food intake, suggesting that the receptor(s) involved are maximally stimulated by 4 g. Even so, intake was only depressed by one-half of that of the control during the 1 h after injection and by one-third during the 3 h after.

Although the results of this experiment might indicate the presence of receptors sensitive to glucose in the crop, or lower down the digestive tract or post-absorptively, they do not rule out the possibility of distension receptors, because more concentrated solutions take up more water and therefore occupy more space; osmoreceptors might also be present. Shurlock and Forbes (1981b) therefore compared the effects on feeding of glucose and the non-absorbable substances, sorbitol and potassium chloride, all at an osmolality of 3 osm. During the 3 h after injection into the crop, the food intakes were depressed to an equal extent by all three solutes. It was concluded that glucose introduced into the crop was probably not, therefore, influencing intake by stimulating post-absorptive receptors, but by an osmotic or distension effect.

Mechanoreceptors are to be found in the muscular stomach of the chicken, and both the crop and the gizzard are well innervated by branches of the vagus nerve. The crop is, however, a diverticulum, and food often bypasses it; thus it cannot be the main controller of meal size. Following surgical removal of the crop, daily intake is normal once the immediate effects of surgery and the adaptation period are over (Savory, 1985). Cropectomy is followed by decreased meal size and increased feeding frequency, although eventual oesophageal dilation often leads to a gradual return to normal meal frequency.

Introduction of food slurry into the intestines of growing turkeys increased the proportion of boli entering the crop during an evening meal by decreasing the proportion of boli travelling directly to the gizzard (Jackson and Duke, 1995). A slowing of stomach emptying by the presence of digesta in the intestines is a general feature of the control of the digestive tract, making it difficult to pinpoint the site of effects of artificial or natural changes.

Pigs

Indirect evidence of a physical limit to intake in the pig has been obtained from observations of the effects of dietary dilution. Pigs attempt to compensate for dilution of the food by increasing their intake when its energy concentration is reduced. Although there appear to be no reports in the literature of balloon inflation in the porcine stomach, loading young pigs with hypertonic saline or water equal in volume to the volume of milk taken voluntarily after a 3-h fast depressed intake. As pigs grow older they can compensate better for diet dilution (see Chapter 11).

Pekas (1983) loaded the stomachs of young pigs daily through a cannula, which led to a reduction in voluntary intake that almost exactly compensated for the weight of food introduced. When loading was carried out on 4 days/week, compensation was incomplete on these days so that total intake increased. However, a reduction of voluntary intake on the other three days of each week led to weekly intakes, growth rates and carcass compositions indistinguishable from those of controls. Long-term (or at least medium-term) control mechanisms are involved, therefore.

The rate at which the stomach discharges its contents into the duodenum has an important influence on the signals generated by that part of the intestine

and is partly controlled by the quantity and quality of duodenal contents. Infusion of fats and products of lipolysis into the stomach was compensated almost exactly by reduced food intake, suggesting that the rate of stomach emptying plays a major part in determining meal size. Glucose infusions into the stomach similarly depress intake, but this effect can be ascribed to intestinal osmotic or caloric effects of the glucose that delay stomach emptying and prolong gastric distension.

Ruminants

As already mentioned in Chapter 1, a considerable body of evidence had been built up by about 1960 to support the concept that the food intake of ruminants was restricted primarily by ruminal capacity; this was reviewed by Balch and Campling (1962). It is clear that there are also effects of the VFAs produced by fermentation, and of the osmolality of ruminal contents, and it is proposed in Chapter 10 that these various factors are integrated in an additive manner. Dietary effects on intake mediated by the rumen are covered in Chapters 11 and 12.

Physical aspects

It is generally considered that the voluntary intake of forages is limited by the capacity of the digestive tract, particularly the rumen, to store and allow passage of digesta (see review by Allen, 1996). This is based on observed relationships between intake and digestibility, rate of digestion, fibre content and other indicators of the residence time of material in the rumen. In addition, placing bulky objects such as water-filled balloons in the rumen results in reductions in forage intake, and mechanoreceptors have been demonstrated in the ruminal wall whose firing rate is increased by stretch, with afferent neurones in the vagal nerves carrying information to the gastric centre of the *medulla oblongata* in the CNS, as described by Leek (1986).

CORRELATIONS BETWEEN RUMINAL CAPACITY AND INTAKE Not only is intake affected by the rates of digestion and passage, but also by the capacity of the digestive tract, principally the rumen. Positive correlations have been found between level of intake and the weight of the empty reticulo-rumen, but cause and effect are difficult to establish. There are positive correlations between the weight of voluntary intake of forage just before slaughter and the weight of ruminal contents at slaughter in cattle (Tayler, 1959), but the causality cannot be established with certainty.

Increases in the volume of other abdominal organs, such as abdominal fat or the pregnant uterus, can apparently cause compression of the rumen and a reduction in food intake. Tayler (1959) found a negative correlation between the weight of abdominal fat and the intake of herbage in cattle. In late pregnancy there is an increase in the girth of the abdomen, but this is not always great enough to accommodate the growth of the uterus. Although the rate of passage

of particles of forage food through the digestive tract is increased during pregnancy, under some circumstances this is not enough to prevent a limitation of voluntary intake (see Chapter 16).

For animals of any given size, the fatter they are the heavier they are, so intake is often inversely correlated with body weight. On the other hand, there is a positive relationship between intake and body weight in growing animals, and between mature animals of different skeletal sizes but of equal fatness.

ADDITION OF MATERIAL TO THE RUMEN Addition of food material directly into the rumen through a fistula reduces subsequent intake (Hodgson, 1971a) but, of course, supplies nutrients as well as bulk. Removal of digesta from the rumen is followed by increased intake, but this removes a source of nutrients as well as physical bulk, so that physical and metabolic factors are again confounded in such situations.

In the early 1960s, Campling and Balch conducted a series of experiments using a more critical approach. One of their methods was to insert balloons via a fistula into the rumen of non-pregnant, non-lactating mature cows; the balloons were then filled with water and the effect on intake during a 4-h period of access to food was noted. When 50–100 l of water-filled balloons were introduced for 10–14 days, there was a 0.54 kg/day decrease in dry matter intake (DMI) for each 10 l of water (Campling and Balch, 1961). If the water was added directly into the rumen of cattle there was no effect on intake, even when large quantities were involved (45 l). With sheep, addition of 8 l of water directly into the rumen had no effect on forage intake, while inclusion of only 2 l in a balloon depressed intake by 27% (Davies, 1962). There is often a negative relationship between the water content of grass or silage and voluntary intake; water trapped in stems and leaves acts more like water in balloons than free water.

It is likely that physical aspects were unduly emphasized as a result of the approach adopted in the work of Balch and Campling, because the 20-h fast that preceded each feeding period would leave the animals in considerable nutrient deficit, causing them to need to eat a much larger amount than would otherwise be eaten during such a small part of the day. Also, the use of ruminal DM as a measure of fill is inappropriate, as volume is related more closely to total weight, i.e. wet weight, of the ruminal contents.

More recent studies using balloons in the rumen of lactating cows fed grass silage (Anil *et al.*, 1993) showed that there was a 70 g DM decrease in intake for every additional litre of water put in the balloon over a 3-h period, and that this response was approximately linear over the range 0–25 l – similar to the 54 g DM/l decrease noted by Campling and Balch (1961) with non-lactating cows fed on hay. This approach has been extended to include gradual increases in the volume of balloons in the rumen of cattle by Mowatt (1963), who found little evidence of a compensatory increase in ruminal capacity. However, some recovery of DM intake towards pre-treatment levels was seen in sheep with balloons maintained in the rumen when fed on a pelleted diet, but not when fed on straw (Egan, 1972).

A single, large balloon in the rumen might interfere with the normal flow of materials and, at worst, block the reticulum and prevent onward flow of digesta.

An alternative is to use many small balls, and tennis balls have been used for this purpose (Schettini *et al.*, 1999). Steers fed a low-quality forage diet had 50 or 100 balls placed in the rumen, with a specific gravity (SG) of either 1.1 or 1.3, for 18-day periods, of which the first 10 days were for adaptation. There were significant effects on intake of both number of balls and of SG, even though increasing the SG did not increase the volume (see Fig. 3.1).

As both SGs used were higher than the SG of ruminal fluid, it is assumed that all the balls eventually sank to the bottom of the posterior ventral sac of the rumen, where they would directly stimulate the mechanoreceptors in that region, as well as exerting a stretching effect on the ruminal wall more dorsally, where receptors are more numerous. The effects of volume and SG were approximately additive, supporting the additivity hypothesis proposed in Chapter 10. Note, however, that the authors conclude by saying: 'The large change in ruminal mass and volume as a function of the experimental treatments in our study ... resulted in a relatively small change in the voluntary intake of a hay diet. This suggests that factors other than distension of the gut have a large influence on voluntary intake of low-quality forage diets by ruminants.'

The effect on food intake of balls or balloons in the rumen would be predicted to be greater with a more fibrous diet than with a more concentrated one, given the belief that physical factors are more important in the control of forage intake as compared with concentrates. When lactating cows were fed on diets containing either 250 or 350 g NDF/kg (low- and high-fibre, respectively), and plastic containers of water (each of 500 ml) were inserted into the rumen to occupy 25% of pre-trial rumen volume for each cow, food intake was significantly decreased by the addition of ruminal inert bulk when the high-fibre diet was fed, but had no effect with the low-fibre diet (Dado and Allen, 1995).

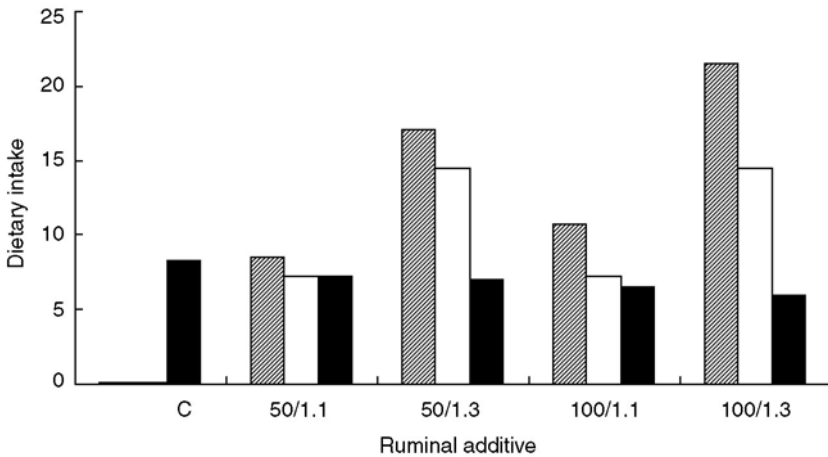


Fig. 3.1. Effects of adding 50 or 100 tennis balls, SG 1.1 or 1.3, to the rumen on daily intake of low-quality hay. Shaded bars, weight of balls (kg); open bars, volume of balls (l); solid bars, intake (kg DM/day); C, control (from Schettini *et al.*, 1999).

With the former food, the objects displaced an equal volume of ruminal contents, suggesting that this food 'filled' the rumen; food intake was depressed.

Overall, therefore, as far as the voluntary intake of long forages is concerned, ruminal distension with balloons and similar objects has consistent and predictable effects, but ones that are not as large as might be expected from the volume displaced.

As an alternative experimental technique for demonstrating effects of ruminal fill on intake, Welch (1967) introduced into the rumen via a fistula 150 g of polypropylene fibres, each 30 cm in length, which were too long to exit the rumen. Intake of hay was depressed to 33% of control values and remained low. With shorter fibres (3.5 or 7 cm), regurgitation was possible so that the fibres were broken down by re-chewing and fragments were found in faeces; intake was initially depressed, but recovered during the few weeks after administration of the fibres. Such manipulations are apparently not unpleasant, as sheep voluntarily consume polypropylene fibres when offered a fibre-free diet.

Muscular activity of the reticulo-rumen causes particles of digesta to rub against the papillae, stimulating the epithelial receptors, but the role of these receptors in the control of feeding is unclear. Baumont *et al.* (1990) placed blocks of expanded polystyrene in the rumen that floated on top of ruminal fluid so that they would stimulate tactile responses as well as increasing the bulk of ruminal contents. Hay intake was significantly reduced by 2 l of cubes, but there was no effect on the frequency of reticulo-ruminal contractions during eating. However, the frequency of contractions during rumination was increased and more periods of rumination occurred. The polystyrene blocks became rounded during their stay in the rumen, showing that they must have been rubbing on the ruminal papillae, but their bulk meant that they were also likely to have been stimulating the distension receptors.

Baumont *et al.* (1990) provided tactile stimulation of the dorsal ruminal papillae without distension by means of a stiff brush via the fistula. This induced pseudo-rumination and extra-reticular contractions in sheep given a non-stimulating liquid diet to a similar extent as did a small amount of hay or 1 l of polystyrene cubes. On the other hand, insufflating the rumen with air for 5 min or adding 2 l of a buffer solution – which would cause distension but not stimulate tactile receptors – did not induce pseudo-rumination and had no effect on contractions. These results suggest that the use of a balloon in the rumen might not mimic all of the effects of forage, especially if the balloon gets dragged down into the rumen away from the sensitive areas of the reticulum and the cranial dorsal sac of the rumen.

DIGESTION AND PASSAGE OF FOOD There is an overwhelming amount of literature on positive relationships between extent and/or rate of digestion of forages and voluntary intake by ruminants. In interpreting these data it is necessary to remember that the evidence from such relationships, that intake is limited physically, is circumstantial.

The more digestible the food, the less indigestible material remains to occupy space in the rumen. By the mid-1960s it was becoming clear that this positive relationship did not continue to hold true with foods of very high

digestibility, and Baumgardt (1970) reviewed the evidence that intake is controlled to balance energy requirements when the food is highly digestible and of small particle size. With highly digestible long forages, however, intake continues to be positively related to digestibility, even at the very highest level of digestibility (see review by Minson, 1982).

Ruminants eating forages have to trade off the advantage of holding the food in the rumen for a long time to allow extensive digestion against the advantage of moving digesta along the tract to allow for further food intake. While relationships are found between the digestibility of the diet and voluntary intake (see Chapter 11), the total extent of digestion by the whole alimentary tract is not sufficient to give an adequate understanding of the physical limit to intake, as it depends not only on the physical form of the food, but also on its potential to be digested. Digestibility is the product of the retention time in the rumen and the degradation characteristics of the food concerned. The longer a portion of food stays in the rumen, the closer it will come to being digested to the maximum extent possible, i.e. its potential digestibility, but factors such as level of feeding and ruminal capacity cause variations in residence time and therefore in actual digestibility. Increasing the rate of passage of food particles by grinding forages results in increased levels of voluntary intake, while the extent of food digestion is reduced due to the decreased time spent by each particle in the digestive tract.

The degree to which food particles are digested in the rumen could be as important as whole-tract digestibility. Several studies have found that the intakes of different hays were closely related to the rate of disappearance of hay from Dacron bags in the rumen (potential ruminal degradability). Intakes have often shown a much closer relationship with this than with digestibility or rate of degradation, making ruminal degradability a useful predictor of intake. For example, a very close fit was obtained for browse plants fed to goats, when the independent variables included the digestion rate constant (c from the equation $p = a + b(1 - e^{ct})$, see Chapter 11), the soluble fraction of the food and the insoluble but fermentable fraction of the food. As Dacron bag studies are tedious, the measurement of the rate and amount of gas production of samples of foods incubated *in vitro* with ruminal contents as a measure of degradation is a very promising method for predicting intake of forages (Getachew *et al.*, 1998).

Rates and extents of breakdown of forage particles depend in part on the animal – the time and vigour devoted to chewing, for example – but are to a great degree dependent on the physical and chemical characteristics of the plant material being eaten. The subject of relationships between plant structure and breakdown in the rumen is well covered by Wilson and Kennedy (1996). They make the vital point that genetic modification of herbage plants to make their tissues more readily digested by ruminants is certain to reduce the strength of stems and leaves during growth, leading to increased likelihood of lodging, i.e. collapsing in heavy wind and/or rain. Thick cuticles, inimical to digestion, are very protective during drought conditions; plant toxins reduce attacks by pests; endogenous antimicrobials deter infections of the living plant but may also reduce microbial attack in the rumen.

Nevertheless, there are strategies for improving particle breakdown, e.g. breeding animals to spend more time per day chewing. Increasing activity of ruminal microbes by genetic engineering is another possibility – but will the introduced bacteria survive (Flint and Scott, 2000)?

RELATIONSHIPS WITH DIETARY FIBRE Cellulose and hemicellulose are degradable by the ruminal microorganisms, but the rate of digestion and the time spent by a particle in the rumen are variable, so there is no close relationship between the level of voluntary intake and a forage’s content of these carbohydrates. It might be rather that the bulk of plant cells would be a good predictor of intake of forages, and the cell-wall constituents (CWC) fraction (Van Soest, 1994) – as measured by the NDF method – was found to give an almost constant intake of NDF for a wide range of grasses, including many tropical species:

$$I = 110 - 1716/(100 - \text{CWC}) \tag{3.1}$$

where I is the voluntary intake (g DM/kg LW^{0.75}) by sheep and CWC is the proportion of CWC in the dry matter (%). The amount of time spent in rumination is much more closely correlated with the intake of NDF than it is with the weight of food eaten, and NDF is now widely accepted as being a good indicator of the bulk properties of forages. Figure 3.2 shows the relationship between the NDF content of forages and their organic matter intake by sheep, after adjusting for the intake by each sheep of a standard reference forage (Osbourn *et al.*, 1974).

While most research into the relationships between intake and forage composition has been with sheep, which show an approximately constant intake of NDF, cattle increase their intake of NDF as its content in food increases (Van

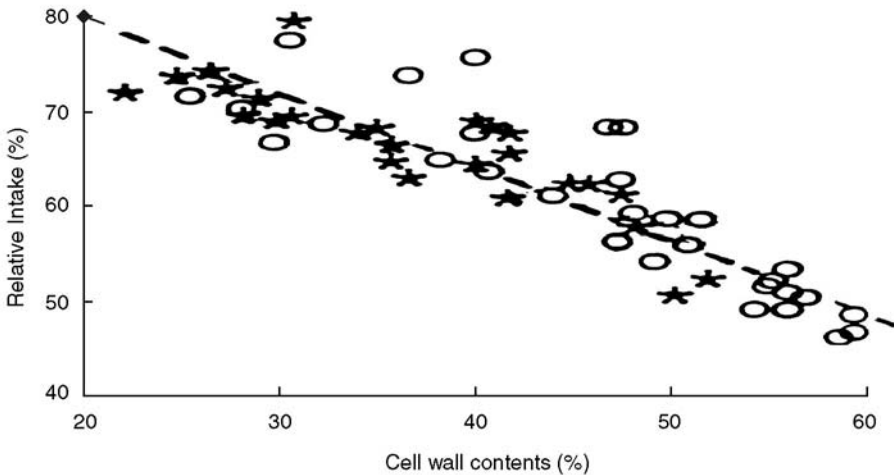


Fig. 3.2. Intake by sheep of a range of forages with different cell wall (NDF) contents relative to intake of a standard forage by the same animals. *, legumes; o, grasses (from Osbourn *et al.*, 1974).

Soest, 1994). For any given level of NDF, sheep eat more DM/kg^{0.73}, but less/kg^{1.0}, than cattle because of the lower ratio of gut capacity per unit of metabolic rate in the smaller species. Maximum forage energy intake for ruminant species of different mature body sizes has been estimated to be related to live weight^{0.87} (Taylor *et al.*, 1987). Further discussion on the effects of fibre content of the diet on voluntary intake is to be found in Chapter 11.

Much of the evidence for physical limitation of forage intake is circumstantial and has been challenged (e.g. Ketelaars and Tolkamp, 1992a). However, the sheer weight of the evidence, and the lack of any sustainably credible alternative, means that many still view stimulation of ruminal stretch and mechanoreceptors as a critical part of the intake control system of the ruminant.

Involvement of receptors in the physical control of intake

There is irrefutable evidence of mechanoreceptors in the wall of the rumen with afferent fibres to the CNS. The ruminant fore-stomachs are innervated by branches of the vagus and splanchnic nerves (see Leek, 1986 for detailed review). There are rapidly adapting mechanoreceptors in the epithelial lining of the reticulo-rumen, concentrated in the anterior dorsal rumen and the reticulum, and slowly adapting tension receptors in the muscular layers throughout the gastrointestinal tract. One important role of mechanoreceptors is in the control of gastrointestinal motility. However, since the epithelial receptors found in the reticulo-rumen and duodenum also respond to chemical stimuli (see below), it is likely that chemical effects are also involved in the control of motility. Central projection of these receptors is to the gastric centres of the *medulla oblongata*, which have afferent fibres projecting to the nucleus of the solitary tract of the hindbrain.

RETICULO-RUMINAL MOTILITY There are spontaneous biphasic cyclic contractions of the rumen that mix the digesta, the contractions being weaker when ground and pelleted diets are fed than with long forages. Reduction in the strength or frequency of ruminal contractions does not necessarily mean a decrease in tension, however. Pentagastrin infused into the coeliac artery caused an increase in reticular tension receptor activity without an increase in pressure as measured by a balloon in the lumen. Intra-ruminal pressure is, therefore, not a reliable indicator of tension.

If the reticulo-rumen were an inert elastic sphere, then it would be a simple matter to calculate the degree of stretch for any given load of digesta. However, the muscular activity of the ruminal wall complicates the situation, especially as eating (or even teasing with food) stimulates more frequent contractions. If stimulation of the in-series stretch receptors by distension of the rumen depresses voluntary food intake, then this increased muscular activity during feeding will act to inhibit feeding. However, increased motility, as during feeding, increases the rate of outflow of digesta, leading to decreased distension and, potentially, to increased food intake.

Rumination increases the breakdown of particles of food and thus increases the rate of emptying of the reticulo-rumen. When rumination was prevented

with a face mask to impair jaw movements (10 h on and 2 h off, successively during 4 days), food intake in steers was significantly reduced (Welch, 1982). Rumination is also accompanied by increased ruminal muscular activity, and therefore helps to maintain voluntary intake by reducing the bulk of digesta in the reticulo-rumen.

To test whether drug-induced changes in ruminal motility affected intake in dwarf goats, Van Miert and Van Duin (1991) gave several drugs that inhibited ruminal contractions, but found they did not affect food intake. Other drugs induced hypophagia but yet stimulated intestinal propulsion. Therefore, there is no direct connection between gut motility and food intake.

Temperature receptors

Increasing the temperature of ruminal contents depressed intake of cattle, whether by means of heating coils in the rumen or by addition of warm water (Bhattacharya and Warner, 1968a). Conversely, adding cold water to the rumen of cattle, which reduced intra-ruminal temperature by about 10°C, caused a large increase in the intake of a pelleted diet. Note, however, that the addition of water might in itself increase intake (see below), but the fact that warm water depresses intake while similar volumes of cold water stimulate intake shows that temperature can play a role in controlling food intake. Temperature receptors have been demonstrated in the abdomen of sheep with afferent fibres in the splanchnic nerves, and this could be the route through which ruminal heating or cooling affects intake.

Chemical receptors

VOLATILE FATTY ACIDS It has been reported many times that VFAs, particularly acetate, can depress food intake when infused into the rumen (see de Jong, 1986). As the effect was either greatly reduced or absent when the VFAs were infused into the jugular vein, it was assumed that they were sensed by receptors in the ruminal wall. This idea was strengthened when it was demonstrated that a local anaesthetic, when infused into the reticulo-rumen along with acetate, prevented most of the intake-depressing effect of the latter (see Baile and Forbes, 1974, for references to work in this section). However, the effect of the anaesthetic need not have been on 'acetate receptors' but on 'osmoreceptors' (see osmolality, below).

Baile and colleagues infused VFA mixtures into the rumen or other sites during spontaneous meals by means of pumps triggered by their sheep breaking light beams as they ate. They observed significant relationships between the amount of VFAs infused, in the range 2.5–20.0 mmol/min of a mixture in physiological proportions (0.55% acetate, 0.30% propionate, 0.15% butyrate), and the depression in food intake:

$$\text{DEPR} = 0.38\text{VFA} + 8.74 \quad (3.2)$$

where DEPR is the percentage reduction in intake compared with pre-treatment control periods and VFA is the mean amount of a mixture of the three salts

infused (mmol/meal). Similar results were obtained in goats and cattle. Separate infusion of the three acids showed that the effect of the mixture was due mainly to acetate and propionate.

ACETATE The effects of intra-ruminal acetate have been shown many times; for example, with sheep:

$$\text{DEPR} = 0.39\text{Ac} - 5.18 \quad (3.3)$$

where DEPR is the percentage reduction in intake and Ac is the amount of acetate infused (mmol/meal). For dairy cows (Anil *et al.*, 1993):

$$\text{Hay} = 2.85 - 0.085\text{Ac} \quad (3.4)$$

$$\text{Silage} = 2.25 - 0.07\text{Ac} \quad (3.5)$$

where Hay and Silage are the weights of food eaten during the infusion (kg DM/3 h) and Ac is the amount of acetate infused (mol/3 h) (see Fig. 3.3).

Intravenous injection of acetate has less effect than intra-ruminal administration in cattle, and has no effect on the intake of sheep, suggesting that receptors to acetate are in the ruminal wall. Selective infusions made into different areas of the rumen showed that the biggest effect on intake was in the dorsal part; infusion of acetate into isolated 'Pavlov' pouches made of 5% of the rumen was sufficient to depress intake significantly. Direct comparison of intra-ruminal versus jugular infusion in goats and of intra-ruminal versus ruminal vein infusion in sheep confirmed that the main effect of acetate is on the ruminal wall.

As mentioned above, local anaesthetic infused into the rumen of sheep along with acetate prevented most of the intake-depressing effect of the latter. Infusions of local anaesthetic around the ruminal vein had a similar effect in goats, and it was concluded that signals transmitted in response to increased ruminal acetate concentrations were neurally transmitted to the CNS. It is now

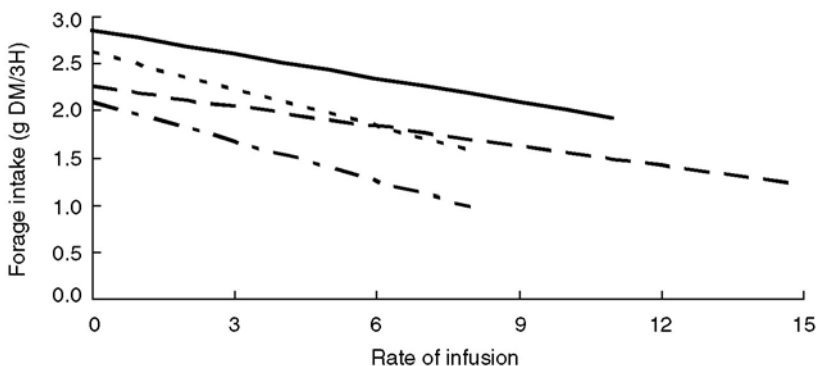


Fig. 3.3. Effects of intra-ruminal infusions of solutions of sodium salts of acetate (Ac) or propionate (Pr) on the intake of hay or silage by lactating cows. Solid line, hay Ac; dashed line, silage Ac; dotted line, hay Pr; dot-dash line, silage Pr (from Anil *et al.*, 1993).

accepted that the major effect of acetate on intake in ruminants is via receptors in the ruminal wall. However, it has been shown that the type of infusion used by Baile and others induces large, probably unphysiological, changes in ruminal fluid and blood composition, and de Jong (1986) could not reproduce the results of Baile's group with infusions made to demonstrate that these unphysiological changes were avoided.

Continuous infusion of sodium acetate for 3 h into the rumen of lactating cows had small and non-significant effects when the doses were less than the rate at which it is calculated that acetate is normally produced, even though this led to greatly elevated concentrations of acetate in ruminal fluid (Anil *et al.*, 1993). The depression in intake only became obvious and significant at rates of infusion considerably above the normal production rate that elevated the concentration of ruminal acetate to at least twice the normal. However, the significant, linear relationship between the dose of acetate administered and the depression in food intake suggests that the effect of physiological amounts is real, albeit small.

Infusion of acetate into the rumen avoids oral effects during ingestion. However, when rumination occurs there will be a higher concentration of acetate than normal in the regurgitated bolus. It has been shown that acetate added to food reduces the rate of eating of that food and, by implication, its acceptability, using a sophisticated method whereby the effects of additions of a range of levels of acetate on rate of eating were compared with several foods (Gherardi and Black, 1991). Surveys have shown a negative relationship between the acetate content of silages and their daily intake by ruminants (Tayler and Wilkins, 1976) but, at the present time, we have no way of knowing the relative significance of oral and ruminal effects of acetate. In general, however, oral effects are of little significance when only one food is on offer; palatability effects come into play in determining the food to be eaten when a choice is available (see Chapter 7).

A further complication in ascertaining the effects of acetate on food intake arises from the fact that acetate inhibits ruminal motility, which would be likely to reduce the intake of forage foods by reducing rate of passage and increasing the occupancy of the rumen (see above). However, infusions of acetate that significantly depressed silage intake in cows did not affect the frequency or amplitude of ruminal contractions (S.B.J. Dunne, M.H. Anil and J.M. Forbes, unpublished results).

PROPIONATE Propionate is approximately as effective, mole for mole, as acetate in depressing intake when infused into the rumen of sheep:

$$\text{DEPR} = 0.36\text{Pr} - 0.27 \quad (3.6)$$

where DEPR is the percentage reduction in intake and Pr is the amount of propionate infused (mmol/meal). However, propionate was rather more effective than acetate when infused into the rumen of lactating cows (Anil *et al.*, 1993):

$$\text{Hay} = 2.61 - 0.13\text{Pr} \quad (3.7)$$

$$\text{Silage} = 2.09 - 0.14\text{Pr} \quad (3.8)$$

where Hay and Silage are the weights of food eaten during the infusion (kg DM/3 h) and Pr is the amount of propionate infused (mol/3 h) (see Fig. 3.3).

Sodium propionate is particularly effective in depressing intake when incorporated in foods for sheep. Seeking its site of action, Baile and McLaughlin (1970) infused propionate into the dorsal rumen, ventral rumen, abomasum or duodenum of goats; intake was depressed to the same extent by each infusion, which shows that, in contrast to those for acetate, the receptors are not specifically in the rumen. Comparison of infusion into the lumen of the rumen, ruminal vein, mesenteric vein, portal vein and carotid artery showed the biggest effect on voluntary intake with ruminal vein infusion, and it was concluded that receptors sensitive to propionate were in the wall of this vessel. In the light of later work this seems unlikely, as sensitivity to propionate has been demonstrated in the liver (see Chapter 4) but, of course, ruminal vein infusion would elevate the levels of propionate entering the liver.

Propionate effects on intake of a total mixed ration by lactating cows have been studied by Oba and Allen (2003b). Rather than simply infusing propionate at different rates, they used mixtures of sodium propionate and sodium acetate so that the total amount of VFA infused was constant, given into the rumen continuously for 14 h at rates of 16.7 and 25 mmol/min, respectively, for experiments 1 and 2. In both experiments, as the proportion of propionate increased, there were linear decreases in DM intake (see Fig. 3.4a) and total ME intake (see Fig. 3.4b), meal size tended to decrease and inter-meal interval tended to increase linearly. Thus, the depression in food intake was greater than compensation for the energy yield of the infusate. Also, propionate had a greater effect on feeding than did acetate (cf. Fig. 3.3), given that the 'control' was acetate, and this adds further weight to the proposition that propionate plays an important role in food intake regulation.

BUTYRATE When injected intravenously or intra-ruมินally, butyrate has smaller and more variable effects on feeding than either acetate or propionate (Baile and Mayer, 1969):

$$\text{DEPR} = 0.17\text{Bu} + 11.4 \quad (3.9)$$

where DEPR is the percentage reduction in intake and Bu is the amount of butyrate infused (mmol/meal).

Although intravenous infusion of butyrate sometimes reduces feeding, this is probably of little physiological significance as butyrate is produced by fermentation at a much lower rate than acetate; it is converted to 3OH-butyrate in the ruminal wall, so that plasma levels are very low. For these reasons there have been few studies on the effects of butyrate on voluntary intake. However, butyrate appears to be more slowly absorbed from the rumen than either acetate or propionate, and is more effective in causing ruminal stasis. Butyrate improves the acceptability of foods to which it is added (Gherardi and Black, 1991). It is not possible to say whether the positive effect of butyrate on palatability might override its negative effect on ruminal chemoreceptors nor, indeed, whether its attractiveness to sheep is due to its metabolic effects.

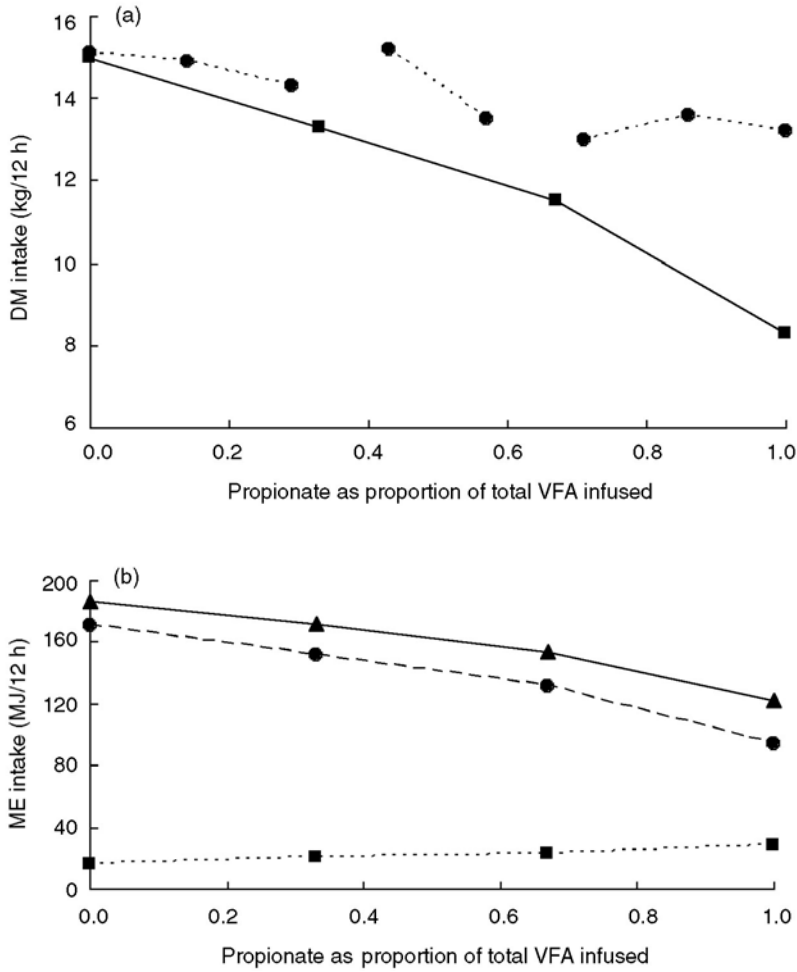


Fig. 3.4. Dose–response effects of intra-ruminal infusion of propionate relative to acetate on (a) food intake of lactating dairy cows for experiments 1 (●) and 2 (■); (b) energy intake (MJ/12 h): in diet (●), infusion (■), total (▲) for experiment 2 (from Oba and Allen, 2003b).

Difficulties of interpretation of work with sodium salts of VFAs

Most studies of the effects of VFAs on feeding have used infusions of their sodium salts. In addition to elevating the concentrations of the VFA(s) in question, they also elevate sodium levels and osmolality of ruminal fluid. The use of the acids themselves has been restricted by the discomfort apparently induced in the experimental animals. Thus, there has been considerable confounding of the specific effects of VFAs and the more general osmotic effects of intra-ruminal infusions. Grovum (see Carter and Grovum, 1990b) has been particularly active in highlighting doubts about the specificity of VFA effects on feeding, and the effects of ruminal osmolality are reviewed below. In addition, changes in short-

chain fatty acid (SCFA) production are small during and after the relatively small meals that are taken with *ad libitum* access to food, which also casts doubt on their importance in the physiological control of intake in ruminants.

Further doubt has been cast on the relevance of VFA concentrations in the rumen on the control of meal size when, following fasting overnight, sheep were given a meal of concentrates 30, 60 or 120 min before hay was offered *ad libitum*; there was no effect on the intake of hay in the 1 or 3 h following, despite different levels of ruminal VFA concentrations when hay was offered (Duranton and Bueno, 1985). However, the daily intake of hay was significantly reduced.

Another concern is the rate at which VFAs are infused. In much of the work of Baile and his colleagues, infusion into the rumen was carried out at high and unphysiological rates for the duration of each spontaneous meal, and this would cause a very rapid elevation in VFA and sodium concentrations. It would be more appropriate to use slowly rising and falling rates of infusion in order to achieve increases similar to those occurring naturally during fermentation of meals taken previously.

Experimental addition of chemicals into the rumen via a fistula is a widely used technique that appears to avoid sensory evaluation by the animal. However, we rarely consider the effects of such materials on the taste, smell and physical form of the boluses of digesta regurgitated during rumination. In assessing the effects of the characteristics of the food on intake we must be careful to differentiate between their influence on the taste of the food and its post-ingestional effects (see Chapter 6).

Despite these difficulties, the facts that: (i) VFA concentrations, osmolality and distension increase during feeding; (ii) food intake is depressed by experimentally increasing VFA concentrations, osmolality or distension in the rumen; and (iii) there are receptors sensitive to these changes, encourage the belief that there is a physiological role for gastrointestinal receptors in the control of food intake in ruminants. The theory of Minimal Total Discomfort (see Chapter 10) can incorporate changes such as these as discomforts, along with the effects of other food characteristics and animal factors. One such additional set of factors is protein, amino acids and their metabolites.

NITROGENOUS COMPOUNDS Although under some circumstances ammonia or amines depress intake, there is as yet insufficient information about their site(s) of action or the receptors which might be involved, although many of these compounds are of types that are known to be biologically active. This subject is addressed in more detail in Chapters 12 and 14.

Propionate can decrease the ability of the liver to detoxify ammonium, and Oba and Allen (2003a) investigated whether intra-ruminal infusion of propionate, compared with acetate, had more than an additive effect on the reduction in food intake caused by infusion of ammonium salts into the rumen of lactating dairy cows. The results (see Fig. 3.5) show that the effect of ammonium was significantly greater when infused along with propionate, compared with ammonium and acetate, both on weight eaten and number of meals.

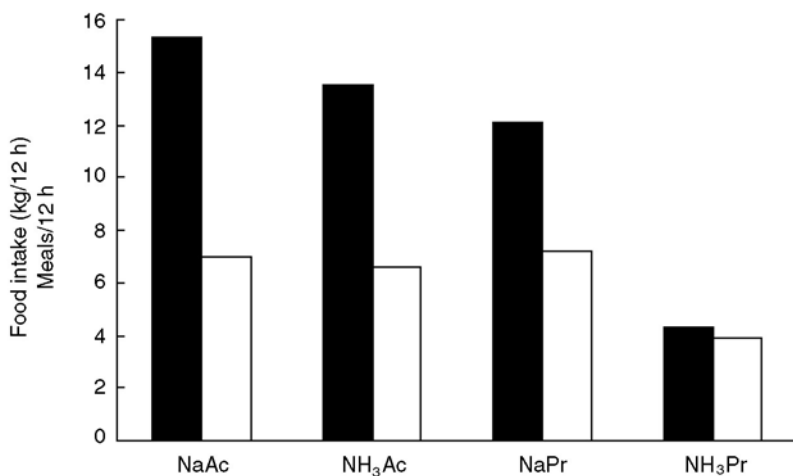


Fig. 3.5. Effect of sodium (Na) or ammonium (NH₃) salts of acetate (Ac) or propionate (Pr) infused intra-ruminally at 17 mol/min on food intake (solid bars, kg/12 h) and number of meals (open bars, meals/12 h) by lactating cows (from Oba and Allen, 2003a).

PH AND ACIDITY It has been suggested that the fall in ruminal pH towards the end of large meals is involved in the cessation of feeding, but relevant experimental work has yielded conflicting results. On the one hand it has been reported that the activity of chemoreceptors is changed according to the pH of ruminal fluid, irrespective of the type of acid applied (Crichlow and Leek, 1981) while, on the other, VFAs – but not lactic, citric or hydrochloric acids – given into the reticulum at concentrations of 100–200 mM inhibited ruminal contractions (Ash, 1959) (when ruminal pH falls below about 5.0, ruminal stasis occurs and the hypophagia that follows is more likely to be due to that ruminal stasis than to low pH per se).

With regard to effects on intake, acetic acid depressed intake but there was no effect of potassium acetate given intra-ruminally (Hutchinson and Wilkins, 1971). However, Baile and Mayer (1969) found a similar depression of intake by sheep whether the pH was lowered by acetic acid or by infusion of sodium acetate that did not affect ruminal pH.

Bhattacharya and Warner (1967) infused various acids, including phosphoric, lactic and citric, into the rumen of steers, maintaining the ruminal pH at about 6.0. They observed significant reductions in food intake, but this effect might be an indirect one because acidity, even when pH is maintained within the normal range for the rumen, is known to have strong inhibitory effects on reticulo-ruminal motility.

It is therefore likely that the titratable acidity of silage is more important than pH, and attempts to stimulate the intake of concentrates by incorporating buffers in the food have sometimes been successful. The inclusion of sodium bicarbonate (25 kg/t) in concentrates for dairy cows increased hay intake and the fat content of milk, with no effect on total milk yield (Edwards and Poole, 1983). With inclusion at 20 kg/t of a complete food in another experiment,

intake increased (13.9 to 19.0 kg/day) and weight loss was reduced, but no effect on milk yield or composition was observed.

Inclusion of 25 g/kg of calcium hydroxide in a complete food containing 30% hay and 70% concentrates increased intake by sheep significantly from 920 to 1120 g/day, while in cattle the increase was from 11.0 to 16.3 kg/day (Bhattacharya and Warner, 1968b). Sodium carbonate (25 g/kg) and sodium bicarbonate (50 g/kg) were as effective as calcium carbonate in cattle but less so in sheep. Other experiments have not always shown an effect, however, and these additives are not widely used in practice.

OSMOLALITY Many of the effects that have been attributed to chemoreceptors could be due to osmotic effects rather than to specific chemical effects on the gut wall. There are significant changes in the osmolality of ruminal contents depending on the intakes of DM and water. In general, osmolality increases during and after a meal. Osmolality of the ruminal contents increases from a pre-feeding level of 250–300 mosmol/kg to as much as 500 mosmol/kg in the few hours after a large meal, and thus it must be considered as a candidate for involvement in the control of food intake.

However, some have concluded that osmolality does not play a significant role in the control of food intake unless it is increased above the physiological range but, in a critical review of the control of food intake, Grovum (1987) suggested that osmolality can account for many of the effects of intra-ruminal or intravenous infusions of VFA salts on food intake. By increasing the osmolality of ruminal contents with either sodium chloride or PEG (polyethylene glycol), Carter and Grovum (1990a) found a linear reduction in food intake during the first 10 min of 3.49 g food/g NaCl. The local anaesthetic lidocaine injected intra-uminally just before the sodium chloride did not reduce the response. When given into the abomasum, sodium chloride had no effect in the first 10 min, and there was no consistent relationship between osmolality of plasma collected from the jugular vein and the reduction in intake following either loading or drinking. Thus, it was concluded that osmolality is sensed in the rumen rather than in the abomasum or vascular system.

In comparisons between equimolar sodium acetate and sodium chloride infusions into the rumen of cows (Forbes *et al.*, 1992) and sheep (Engku Azahan and Forbes, 1992), a somewhat greater inhibitory effect of the former has been shown. Figure 3.6a shows the dose–response relationship between rate of infusion of sodium acetate and silage intake and also the silage intake during infusion of 15 mol of sodium chloride/3 h. While chloride depresses intake to a lesser extent than the same number of mol of acetate, this difference is not significant. It should also be noted that the osmolality and sodium concentration of rumen fluid at the end of the infusion period are similar for the 15 mol of sodium chloride and 12 mol of sodium acetate, suggesting that chloride is absorbed more quickly than acetate, or else stimulates outflow from the rumen. Thus, the results of this experiment are inconclusive as far as demonstrating a greater effect of acetate than chloride.

However, a second experiment, the results of which are summarized in Fig. 3.6b, gives much clearer evidence for this effect, acetate depressing intake more than chloride, mole for mole, across the range of doses studied.

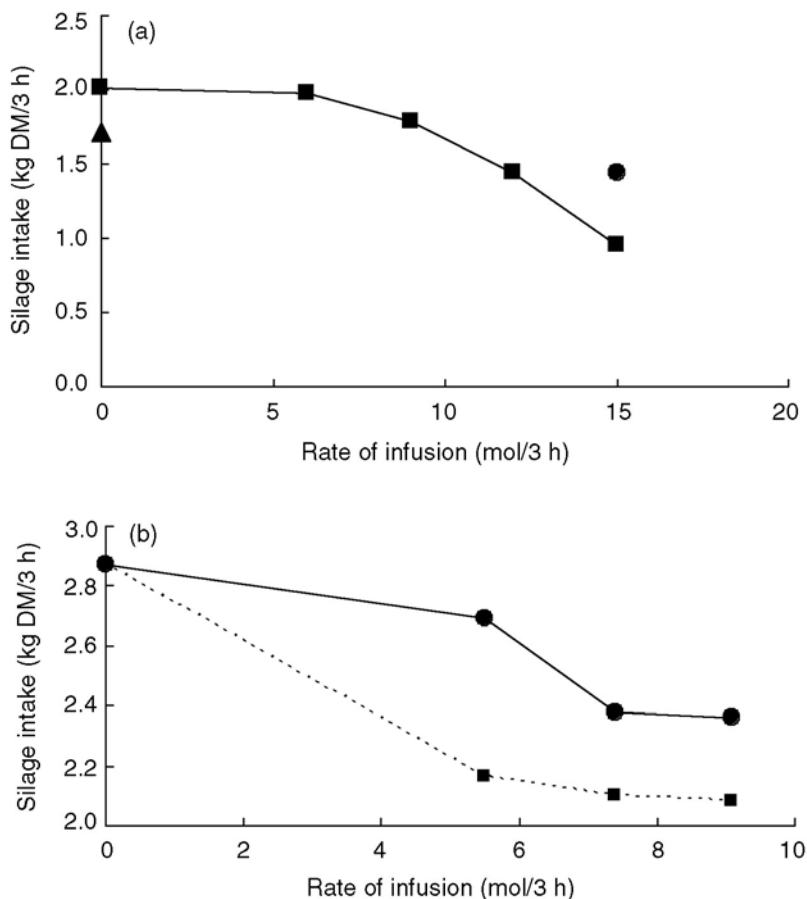


Fig. 3.6. Effect of infusing sodium chloride or sodium acetate solutions into the rumen of lactating cows on silage intake. (a) The seven infusion treatments were: none (▲); 0, 6, 9, 12 and 15 mol sodium acetate (■), 15 mol sodium chloride (●) in 4.5 l water over 3 h; (b), the seven infusion treatments were: 0, 5.5, 7.4 and 9.1 mol Ac (■), 5.5, 7.4 and 9.1 mol Cl (●) in 4.5 l water over 3 h (from Forbes *et al.*, 1992).

One difficulty in interpreting these results is that raised ruminal tonicity normally stimulates voluntary drinking, thereby attenuating the effects of the infusion, but can only do so if animals have access to water. Grovum and colleagues withheld water during their experimental periods, so it is understandable that Grovum should place such emphasis on the importance of osmolality of ruminal fluid as a controller of food intake.

In the experiments of Baile and Mayer (1969), infusions of sodium salts of VFAs into the rumen reduced voluntary food intake but stimulated water intake; there was no effect on drinking when the acids were infused. Because VFAs are naturally produced in the rumen without such large increases in tonicity as have been induced by most of these experimental manipulations, and any increases in tonicity of ruminal fluid induce increased water intake, it is

likely that Grovum has exaggerated the involvement of osmolality in the control of food intake in ruminants.

Nevertheless, it seems likely that osmoreceptors exist in the rumen in order to stimulate drinking when this is required to maintain ruminal osmolality within the normal range. However, there is no consistent experimental evidence of osmoreceptors located in the ruminal wall and/or duodenum. One explanation for this, proposed by Forbes and Barrio (1992), is that osmotic changes in the rumen induce changes in the concentration of sodium and potassium in the extracellular fluid of the ruminal mucosa. An increase in extracellular sodium, as would occur during and for some time after an infusion of sodium salts into the rumen, should increase the likelihood of transmission of an action potential in view of the fact that removal of sodium from the extracellular fluid abolishes transmission. Thus, osmolality would only affect the frequency of afferent impulses in the vagus nerve if the receptors were themselves being stimulated.

Under the conditions of Leek's experiments, in which solutions were gently sprayed on to the exposed ruminal mucosa of anaesthetized sheep, there would be little nervous activity and therefore little chance to show a modifying effect of osmolality. In the conscious sheep, on the other hand, in which epithelial receptors are being continually stimulated, both physically and chemically, there is plenty of opportunity for osmotic changes to attenuate or amplify the action potentials passing along the axons, hence the observed osmotic effects on feeding.

One indirect effect of osmotic changes in the rumen on intake might be by inhibition of ruminal microfauna, but this is not likely to be important in short-term responses to treatments. Nevertheless, a normal ruminal osmotic pressure near 260 mosmol/kg is favourable for ciliate protozoan activity. Cellulose degradation is inhibited *in vitro* at osmolalities > 400 mosmol/kg, but such high tonicity is unlikely to occur as long as drinking water is available.

Almost all experiments involving infusion of salts into the reticulo-rumen have been performed using sodium salts, other cations rarely having being used. However, Warner and Stacy (1965) stated that the post-feeding rise in ruminal osmotic pressure, when sheep were fed on equal amounts of lucerne chaff and wheaten chaff, was largely due to increases in the concentration of potassium and, to a lesser extent, ammonium. J.P. Barrio, S.T. Bapat and J.M. Forbes (unpublished results) have observed a closer relationship between osmolality of ruminal fluid and potassium concentration than between osmolality and sodium concentration in sheep with free access to a pelleted, complete diet and drinking water.

Ruminal osmolality can indirectly affect voluntary food intake by altering salivary secretion. Large amounts of saliva are secreted and swallowed by the ruminant in order to keep stable the ruminal pH, which tends to be lowered by the continuous production of VFAs. When strongly hypertonic solutions of sodium or potassium salts were infused into the reticulo-rumen of sheep, or sodium salts or urea were infused into the bloodstream, saliva production was found to decrease (Warner and Stacy, 1977). Marked decreases in plasma volume have been shown during feeding, and the state of hydration of the body probably plays a part in the control of feeding, as giving a diuretic before feeding

reduced food intake while a preload of isotonic saline given intraperitoneally in sheep increased intake (Ternouth and Beattie, 1971). It can be concluded that the relative importance of osmolality as a satiety factor in ruminants is still uncertain.

Physiology of chemoreceptors

Acids affect the epithelial receptors according to their titratable acidity and molecular size (but not pH) to cause ruminal stasis. Butyric acid has a more potent effect than would be predicted from the effects of a mixture of VFAs. Leek (1986) questioned whether epithelial receptors have a physiological role as chemoreceptors, in view of the high concentration of chemicals required to activate them and their long response times. However, the inhibition of reticulo-ruminal motility by intra-ruminal infusion of VFAs or arising pathologically during the ruminal acidosis syndrome is undoubtedly attributable to reticulo-ruminal epithelial receptor excitation.

It has been reported that ruminal fluid samples taken from sheep, immediately after the contractions of the reticulo-rumen had been inhibited by intra-ruminal infusion of VFAs, were able to elicit responses in the ruminal epithelial receptors of another anaesthetized sheep (Crichlow, 1988). Decreasing the pH enhanced the potency of this fluid, while raising it decreased activity, showing that it was undissociated acid affecting the receptors. VFAs are transported through the ruminal epithelium mainly as un-ionized molecules, and the pH-partition hypothesis of membrane permeability predicts faster transport for un-ionized substances, suggesting that weak organic acids have to diffuse through cell membranes in order to affect epithelial receptors.

The Omasum

The reticulo-omasal orifice is very sensitive to mechanical stimuli and its distension evokes rumination and parotid salivary secretion via the vagus nerves. As the only exit for particles of food not digested in the rumen is via this orifice, and in view of its small size, it might be thought that control of rumen emptying, and thus of voluntary intake, could reside at this site. Laplace (1970) observed a correlation between feeding and omasal activity and proposed a role for the omasum in the control of food intake and rumination.

The Abomasum

Mechano- and chemoreceptors are to be found in the stomach of non-ruminants, and the abomasum – as the equivalent organ in the ruminant – also possesses such sensitivity. There are mechanoreceptors in the epithelium of the abomasum, which give a rapidly adapting response to stimulation but continuous discharge if sufficient stimulus is provided. These abomasal receptors also respond to chemicals. The effects of acids on abomasal mucosal

receptors are very similar to those in the rumen (Leek, 1977), being positively related to their titratable acidities rather than to pH and inversely related to molecular weight. Thus, acetic acid had the same effect whether buffered or unbuffered. Alkalis also stimulate these receptors, as do hyper- and hypotonic solutions and water. The effect of tonicity is very variable, however, application of the same stimulant to the same unit generating different latent periods on successive occasions.

Intra-abomasal infusion of VFAs reduces abomasal activity and emptying, butyric acid being the most potent. This suggests that total VFA content and the relative proportions of VFAs may be important factors in the induction of the abomasal hypomotility preceding abomasal displacement in dairy cattle. Whether the composition of abomasal fluid and the degree of activation of the receptors has any influence on ruminal emptying and food intake is not clear.

Abomasal motility is increased during rumination, which might account for the increased rate of outflow from the rumen during the night – which is when most rumination takes place.

Infusion of fat into the abomasum of sheep reduces food intake, presumably by inhibiting ruminal outflow. Infusion into the abomasum of dairy cows of a mixture of rapeseed and sunflower oils, supplying predominantly unsaturated long-chain fatty acids (LCFA), significantly depressed DMI, but only to the extent of the ME (metabolizable energy) content of the oil, so there was no effect of oil infusion on milk yield (Benson *et al.*, 2001). Comparison of this result with the results of other trials involving post-ruminal fat infusion suggests that polyunsaturated non-esterified fatty acids have the most potent effect on DMI. The mechanisms of the effect of fats and oils in the abomasum are as yet unclear (Ingvarsen and Andersen, 2000), but may involve gastrointestinal hormones and fatty acid oxidation (see Chapter 4).

Intestinal Receptors

Chyme is likely to reach the jejunum before the end of the meal, and the distension which results may play a part in the initiation and maintenance of satiety. The effects of digesta reaching the duodenum and jejunum could be mediated by stretch receptors, osmoreceptors or chemoreceptors. Although there is adequate neurophysiological evidence for receptors sensitive to several chemical types, that for osmoreceptors is weak. However, there is much circumstantial evidence that they are important in the control of food intake.

In later chapters, the role of learned associations between the sensory properties of foods and the consequences of eating those foods will be emphasized. Most research with simple-stomached animals has been carried out with hormones and metabolites, but Bardos (2001) demonstrated aversion in rats to a food taste that had been paired with mechanical stimuli (balloon distension) applied in both small and large intestinal loops. Distension of the intestines is not simply, therefore, the affector of a primary negative feedback, it also contributes to the secondary, learned feedback complex, which is now viewed as being of the utmost importance in the control of food intake and choice.

Poultry

Duodenal infusion of glucose solutions inhibits feeding but potassium chloride and sorbitol solutions, which are not absorbed, have a more prolonged effect (see below) suggesting that it is the physical presence rather than the chemical nature that is important.

Distension of the cloaca or rectum results in reduced food intake, so that it seems reasonable to conclude that stimulation of stretch receptors at any point along the digestive tract will result in hypophagia, and that this distension during and after meals is a factor in the control of meal size and frequency.

Some of the solutions injected into the crop (Shurlock and Forbes, 1981b) probably found their way further along the digestive tract and might have affected food intake by means of gastric or intestinal stimulation. This was investigated by slowly injecting 10 ml of 3 osm solutions of glucose, sorbitol or potassium chloride into the duodenum of cockerels through permanently implanted cannulae. Compared with control (no injection), water had no effect on intake, nor did glucose, while sorbitol and potassium chloride caused highly significant decreases in intake. Neither did intra-duodenal glucose infusions affect food intake in the work of Lacey *et al.* (1986). Glucose is absorbed quickly from the small intestine and would not be present for long enough to result in prolonged stimulation of gut distension or of osmoreceptors, while the non-absorbed solutes would continue to stimulate these receptors, resulting in depressed voluntary intake. In birds that had been fasted overnight before these same treatments were given, glucose injection into the duodenum did significantly depress feeding, perhaps because the liver content of glycogen was depleted so that it took up glucose, which stimulated liver receptors (see Chapter 4).

Vagotomy at the level of the proventriculus prevented the effects of glucose solutions infused into the duodenum of chickens (Shaobi and Forbes, 1987) but, as the nerve section included fibres to and from the liver and pancreas as well as the duodenum, it is not completely clear whether the glucose was acting primarily on the duodenum or elsewhere. It seems likely that osmoreception is important in birds, although it is possible that the effects of hypertonic solutions are due to physical distension of the duodenum by the increase in volume as water is drawn from the blood. It is also worth noting that hypertonic solutions stimulate gut motility, this being likely to stimulate mechanoreceptors in the gut wall.

Pigs

Food intake by hungry growing pigs is reduced by injection of 250 ml of a 150 g/l solution of glucose into the duodenum. When the treatment was given 3 min after food had been offered following an overnight fast, intake was 445 g compared with 782 g for control, whereas 250 ml of a 15% solution of neutral fat or a 10% solution of amino acids had no effect (Stephens, 1980). This suggests that there are specific glucose receptors in the duodenum rather than

osmo- or distension receptors. The effect of 250 ml of a 150 g/l glucose solution into the duodenum was prevented by prior bilateral thoracic vagotomy (Stephens, 1985), confirming that there is a neural link with the CNS rather than a humoral one in this context.

2-deoxy-D-glucose (2DG, a glucose antimetabolite) did not affect feeding when given just after the start of the meal, but it did block the effect of glucose, suggesting that some of the hypophagic effect of glucose solutions infused into the duodenum is not osmotic unless, of course, the glucose has to be absorbed before gaining access to the osmoreceptors.

Duodenal infusions of solutions of non-absorbable sugars such as mannitol have a more prolonged action than glucose, presumably due to the osmotic drawing of water into the intestinal lumen, which causes greater stretch of mechanoreceptors. Infusion of a fat emulsion also depressed intake, but this was blocked by local anaesthetic as was the effect of glucose given into the duodenum. A large increase in the osmolality of duodenal contents occurs during a normal large meal, so that these receptors could be of physiological importance in the termination of meals (Houpt, 1983). Xylose solutions, which are not absorbed, are less effective than glucose or sodium chloride when given into the duodenum, which suggests that the osmoreceptors are not on the surface of cells exposed directly to the infusate. Most of these effects can be blocked by a local anaesthetic given in the infusion, so the receptors are not thought to be deeper than the mucosal layer.

Houpt (1983) suggested that good control over food intake in the pig could be exerted by a combination of three factors working largely in the duodenum: (i) osmotic sensitivity, which is precise but not directly related to nutritive value; (ii) CCK (cholecystokinin) responses to protein and fat in duodenal digesta; and (iii) glucoreceptors in the intestine. The satiating effect of glucose infused into the duodenum of young pigs has been apportioned as follows: 20% due to fluid movements from blood to gut, 55% is osmotic within the gut, while the remaining 25% is hormonal, perhaps involving CCK.

Despite the emphasis on osmolality as a major factor in intake control in pigs, with normal feeding and free access to drinking water, osmolality of duodenal fluid never exceeded 300 mosmol/kg. It is uncertain, therefore, whether osmolality normally plays a significant part in the control of feeding.

Protein infused into the stomach or protein hydrolysate into stomach, duodenum, jejunum or ileum all decrease intake approximately in proportion to the amount of energy infused. Glucose infusion into the duodenum slowed gastric emptying so that the total flow of energy through the duodenum was unchanged, but the mechanisms for this apparent control of energy flow are not understood. Infusion of fat into the stomach or duodenum, or fat, bile salts and lipase into the upper jejunum, depressed intake in pigs (Rayner and Gregory, 1989). Fat, bile and lipase infusions into the ileum had no effect on that meal but did tend to reduce the size of the next meal. Older pigs, > 60 kg body weight, still respond to glucose and fatty acid infusions, so their 'overeating' is not due to lack of sensitivity to nutrients in the gastrointestinal tract.

Ruminants

There are tension receptors with vagal afferent fibres in the duodenum of the sheep that also respond to chemicals (Cottrell and Iggo, 1984). In view of the evidence of important roles for intestinal mechano- and chemoreceptors in the control of food intake in other classes of animal, it is likely that such receptors are also important in the ruminant. There are two different types of duodenal chemoreceptor: one is excited by potassium chloride solutions, the response increasing with the concentration of the salt (12.5–450.0 mmolar), while the other is insensitive to potassium chloride but excited by acetic, butyric or propionic acids (10–150 mmolar). The responses elicited were directly related to molecular weight but not to pH or osmolality; both were excited by sodium hydroxide solutions but not usually by sodium bicarbonate. Considerable quantities of potassium ions and VFAs leave the rumen and might, therefore, be expected to stimulate the abomasal and duodenal chemoreceptors and act in the negative feedback control of feeding.

Dynes (1993) studied the effect of duodenal osmolality on feeding in sheep by injecting 5 ml/kg of 6.5% NaCl or mannitol into the duodenum 5 min before feeding and without access to drinking water. There was almost complete inhibition of feeding in the first 15 min, an effect not alleviated by local anaesthetic. When water was made available 30 min after feeding had commenced, the sheep immediately drank a large volume and between 1.5 and 3 h food intake was significantly higher than when water was not available. The amounts of salt, mannitol and anaesthetics were similar to those used by Houtp *et al.* (1983), who did find that anaesthetic reversed the intake depression by mannitol in pigs. It seems unlikely that there would be basic differences between the intestinal physiology of pigs and sheep, but no explanation has been proposed for these different experimental results.

In adult ruminants offered dry foods, osmolality can be up to 585 mosmol/kg in the duodenum, but not so high further along the intestines. The osmotic effect of digesta in the duodenum could be an important contributor to satiety under many circumstances, but little relevant research has been carried out with ruminants.

Although there have been suggestions on several occasions that flow through the intestines limits voluntary intake by ruminants, this is not a generally important factor. Suspensions of sawdust or methylcellulose infused into the abomasum at rates which doubled the volume of faecal production had no effect on voluntary food intake and it should be concluded, therefore, that intestinal capacity is not a limiting factor in feeding.

The role of *gut hormones* such as cholecystokinin is covered in Chapter 4.

Integration of Multiple Signals from the Gastrointestinal Tract

There are several instances of stimulation of receptors in one part of the digestive tract having consequences elsewhere that might influence voluntary intake indirectly. Chemical or acid factors in the rumen affect motility and

therefore the stimulation of mechanoreceptors by local contractions so that, for example, loss of reticulo-ruminal motility occurs when epithelial receptors in the rumen become stimulated by high levels of VFAs. Lactic acid may facilitate the inhibitory effects of VFAs, as it has been reported that activation of reticulo-ruminal epithelial receptors by low levels of undissociated VFAs occurs after exposure of the luminal surface to dl-lactic acid. Thus, the intake-depressing effects of lactic acid on food intake may be indirectly related to the inhibition of reticulo-ruminal motility.

There is presumably a concentration gradient in digesta for such things as VFAs, with the highest levels in the centre of the rumen and lower levels at the ruminal wall, from where they are absorbed. Such a gradient is difficult to confirm experimentally in view of the contractions that move the tips of sampling tubes, and may be quite small in magnitude. However, the increase in frequency of ruminal contractions during feeding, speeding up the mixing of ruminal contents, may significantly increase the level of intake-depressing activity at the ruminal wall.

Leek (1977) points out that one stimulus excites several types of receptor and one type of receptor is excited by several types of stimulus. Thus, no single stimulus/receptor combination is likely to explain the effects of the physical and chemical properties of digesta in the gastrointestinal tract on motility and food intake. The experimenter measures fullness of a part of the tract as the volume of its contents, whereas to the CNS this may be:

a composite quality depending not on the absolute volume of the contents but on the rate of change of volume, the tonic state of the visceral muscle, the texture and chemistry of the contents and the extent to which the contents displace the viscus on its mesenteric attachment; such possibilities illustrate the difficulty of defining and quantifying a visceral stimulus.

(Leek, 1977)

If these are the difficulties involved in understanding receptor involvement in signalling to the CNS, how much more difficult will it be to understand the control of voluntary food intake, in which many more factors must be taken into account?

The great complexity of the signals reaching the CNS from the digestive tract makes it necessary to aggregate the effects of different types of food according to measurable features such as fermentability, nitrogen content, fibre characteristics and energy yield in order to describe and predict their effects on voluntary food intake. Modelling of the convergence of such aggregated signals can then be attempted, for example by the theories discussed in Chapter 10.

Conclusions

There are stretch receptors in most or all parts of the gut that relay information on fill to the brain via the nervous system to inhibit feeding. Hypertonic solutions infused into the gut inhibit feeding but it is not certain whether there are osmoreceptors or whether water drawn in by the hypertonic solution

stimulates the stretch receptors. There is evidence for chemoreceptors in the duodenum, but the relative importance of distension, stretch or chemical effects probably varies depending on the type of food.

The capacity of the rumen to hold digesta clearly sets a limit to how much the ruminant can eat, but rarely is this the only factor controlling food intake. Those receptors in the ruminal mucosa sensitive to chemical influences cannot be envisaged as ceasing to inform the CNS about pH, VFA concentration and osmolality when the mechanoreceptors are being strongly stimulated. In fact chemo- and mechanoreception are properties of the same neurones and it seems likely that chemical and stretch information are dealt with in an additive manner (see Chapter 10).

The osmolality of ruminal contents has an important influence on feeding when it is raised above the normal range, and this changes the interpretation of results from experiments in which the sodium salts of the VFAs were infused. The situation is clouded by the difficulty of demonstrating receptors sensitive to osmolality, and new experimental approaches will have to be developed to resolve this difficult area.

We can rarely be sure of the exact mechanism(s) being brought into play when intake is affected by a change of diet or an experimental treatment. It is difficult to design experiments to isolate one factor at a time, but such experiments are necessary if progress is to be made in understanding more fully the control of food intake. It might be technically possible, for example, to manipulate the composition of ruminal fluid while maintaining normal conditions in the rest of the tract by preventing the flow of digesta from the rumen and infusing artificial digesta of normal composition into the abomasum. However, a multiplicity of cannulae and tubes, even if ethically acceptable, will undoubtedly increase the risk of inappetence in the experimental animals.

4

Metabolites and Hormones

Digesta in the stomach(s) and intestines stimulate mechano- and chemoreceptors (Chapter 3), but it is unlikely that the total of the information from these receptors is sufficient for the CNS to gain a complete picture of the quantities of nutrients ingested in order to balance intake with output. The liver is the first point at which most of the absorbed nutrients can be monitored by a single organ but, even then, lipids are absorbed via the lymphatic system and bypass the liver. The general circulation transports nutrients between organs and is also the medium whereby hormones, secreted by endocrine organs, pass to their target tissues. Many of the hormones have metabolic functions and have been implicated in the control of food intake (e.g. insulin, leptin), while others have primary roles in other bodily functions but influence intake secondarily (e.g. oestrogens).

Early theories of food intake control gave a prominent place to the monitoring of blood metabolite levels such as glucose, suggesting that they were sensed by the CNS. However, many of the functions of the body have evolved to protect the CNS from fluctuations in its supply of nutrients. A parallel can be made with the regulation of body temperature, where it appears that the temperature sensors in the periphery are more important than central receptors under normal conditions, so that the CNS is made aware of potential changes in deep body temperature and can set in motion actions to balance environmental changes before brain temperature itself has changed. So, with nutrient supply, we can envisage a more important role for peripheral receptors, with those in the CNS only being stimulated under severe conditions of nutrient shortage or excess. This will be explored further in Chapter 5, and it is sufficient here to say that blood concentrations of metabolites or hormones are unlikely to be the only factors taken into account by the CNS circuits controlling voluntary intake.

This is not to say that blood-borne nutrients and hormones cannot exert marked influences on feeding, as changes in their concentrations induce changes in the metabolism of tissues and organs. Satiated sheep began to eat soon after the start of blood exchange with hungry donors; the intake of hungry

sheep was reduced when blood was exchanged with satiated donors (Seoane *et al.*, 1972).

The levels of many metabolites and hormones in the blood have been suggested to inform the brain of the animal's metabolic state and to be involved in the short-term control of feeding. Of these, insulin and glucagon are the most likely candidates despite the attention that has been directed at other hormones, particularly cholecystokinin. In the longer-term control of intake and body weight, leptin is prime candidate as the link between adipose tissue and the CNS.

Glucose

Mayer (1953) suggested that voluntary intake is controlled by blood glucose levels. He pointed to the facts that blood glucose concentration rises after a meal, then falls before the next meal and that injection of gold thioglucose into mice caused hyperphagia and obesity. At autopsy, gold was found in the ventromedial hypothalamus, which had been damaged by its toxic effects; this was used as evidence that glucose had been taken up by this part of the brain. It was later shown that the uptake of gold thioglucose into the ventromedial hypothalamus was dependent on the presence of insulin. These findings supported the theory that the hypothalamus monitored blood glucose concentration in order to control intake.

Subsequently, there has been very great attention paid to glucose as a negative feedback signal, some of it concluding that it is just one of many oxidizable substrates that can act in this way, others finding evidence for specific effects of glucose. Rather than attempt here what must needs be a very inadequate coverage of the subject from the point of view of laboratory animals and humans, the reader is referred to the comprehensive book edited by Stricker and Woods (2004).

Poultry

Infusion of glucose into peripheral veins has no effect on intake but, when infused into the hepatic portal vein, it has a potent suppressing effect (Shurlock and Forbes, 1981a). The quantities of glucose required to depress intake when infused into the portal vein are within the physiological range, and the effects are blocked by bilateral vagotomy at the level of the proventriculus (Rusby and Forbes, 1987b). This shows that the flow of glucose from the digestive tract is monitored by the liver, which relays its information to the CNS via peripheral nerves. The liver is the first organ to be presented with an overall picture of what is being absorbed; also, with its role as a buffer in the maintenance of blood glucose concentration, the liver takes up glucose from the portal blood when it is in excess of the requirements of the rest of the body and releases it when necessary. Thus, it can transmit a signal that contributes to satiety when glucose (and other metabolites such as amino acids) are becoming available in

excessive quantities, this signal being reduced or reversed in times of need. The role of the liver in the control of food intake is discussed further below.

It has proved difficult to affect feeding in chickens by manipulation of blood glucose concentrations with insulin. Injection of mammalian insulin, for example, caused decreased blood glucose in birds, but intake was depressed (e.g. Smith and Bright-Taylor, 1974) rather than elevated as in mammals; perhaps avian insulin would give different results. 2-deoxy-D-glucose (2DG), which prevents the uptake and utilization of glucose in mammals and stimulates voluntary intake because of glucoprivation, actually depresses feeding in the chicken (Rusby and Forbes, 1985); unfortunately, it is not yet known whether 2DG has the same metabolic effects in birds as in mammals.

Incorporation of 100 g glucose/l in the drinking water for growing chickens does not depress food intake, nor does it increase live weight gain. There is, however, an increase in carcass fatness (Engku Azahan and Forbes, 1989). Thus, apart from osmotic effects, only hepatic infusion of glucose suggests that it is specifically involved in the control of intake in chickens.

Pigs

Glucose infused into the jugular vein or hepatic portal vein had no effect on food intake by young pigs (Houpt *et al.*, 1979), but the conditions of the experiment (10 min access to food after an overnight fast) would not necessarily allow an effect to be shown – severe hunger might far outweigh the effects of infused glucose. In the young pig, 1 unit/kg insulin causes increased intake during the 6 h after injection (Houpt and Houpt, 1977).

Infusion of glucose solution into the duodenum of fasted pigs depresses intake (Chapter 3) but the effect is not specific to glucose, as similar depression of intake was induced by infusion of hypertonic saline. Thoracic vagotomy, or concurrent infusion with local anaesthetic, largely blocked the effect of duodenal infusion of glucose (Stephens, 1985). Thus, there is a mechanism for sensing of duodenal osmotic pressure with nervous transmission to the CNS but, once glucose has been absorbed, it seems to have no effect under the conditions of the work done so far, in which food was only available for short periods each day.

Cattle

Plasma glucose concentrations in ruminants are much lower than those in simple-stomached animals and the fluctuations are smaller. However, because of the major role of glucose as a fuel in the non-ruminant and the prevalence of the glucostatic theory of control of intake, there were several investigations in the 1960s of effects on feeding of manipulation of blood glucose levels in ruminants. Glucose had no effect in cattle whether given intra-uminally, intravenously or intra-cerebroventricularly.

Sheep and goats

Short-term intravenous infusion of glucose or insulin infusion, at physiological rates, has no effect on feeding in goats, nor has intra-cerebroventricular injection of glucose in sheep. However, intravenous infusion of 275 g or 160 g glucose/day for 8–10 days depressed intake of an optimal food by 1.95 g OM/g glucose, i.e. almost exactly 100% compensation in terms of ME (Weston, 1996). The fact that prolonged infusions were necessary to show this effect suggests that it might be via a slow adaptation, such as occurs when the energy concentration of the food is changed. It seems, therefore, that glucose is not an immediate short-term feedback signal in ruminants, not surprising in view of the small amounts escaping ruminal fermentation.

While a very large dose of insulin given into the jugular vein depressed intake, lower amounts had no effect, but a relatively slow rate of infusion into the hepatic portal vein depressed intake (Deetz *et al.*, 1980). Infusion of glucose to prevent insulin-induced hypoglycaemia blocked the intake-stimulating effect of that hormone. Injection of 2DG into the cerebroventricles, together with insulin depressed intake – a paradoxical result in that 2DG inhibits glucose uptake and would be expected to stimulate intake by causing glucoprivation in hypothalamic cells. However, Houpt (1974) showed that 2DG given intravenously induced hyperphagia in sheep, even when hyperglycaemia was prevented by adrenalectomy.

From this evidence it can again be concluded that glucose is not likely to be specifically involved in the control of feeding in sheep, although energy status is of significance. VFAs do affect intake, however, and the whole subject of receptors and the role of the reticulo-rumen in the control of feeding has been covered in Chapter 3.

Liver Receptors

The liver is well placed to monitor the uptake of nutrients from the digestive tract and, given its role in smoothing out this erratic supply to maintain more stable levels in the general circulation, it must be able to detect concentrations or rates of uptake of metabolites such as glucose and amino acids. There are important nervous links between the liver and the central nervous system and it is perhaps surprising that little serious attention was paid to the role of the liver as a source of signals for controlling food intake until the early 1970s (reviewed by Anil and Forbes, 1987).

The potent effect of portal glucose infusion is reduced by liver denervation, and electrical activity is induced in some neurones in the lateral hypothalamus by portal infusion of glucose. The activity was modified by either vagotomy or splanchnotomy. Nerve endings have not been found in liver parenchyma but there are many nerve endings in the wall of the portal vein, and superfusion of the exposed inner wall of the hepatic portal vein with glucose solution decreases firing of some vagal fibres.

There is considerable evidence that the supply of oxidizable substrates to the liver is monitored in simple-stomached animals with transmission of information to the central nervous system via the nerves of the hepatic plexus, and that this plays a part in the control of feeding (Forbes, 1988a).

The liver is an important site of fat metabolism in mammals, where in the rat the intake-depressing effects of fatty acids are blocked by substances that block fatty acid oxidation. Vagal section prevents these effects, further strengthening the belief that fatty acids can play a significant role in satiation via the liver. The hypophagic effect of metabolites is linked to a particular step in their metabolism, principally in the liver (Scharer *et al.*, 1996). Whereas glycerol and malate depress intake, their oxidation products dihydroxyacetone and oxaloacetate do not, indicating that the oxidation process itself is important. Lactate and its product of metabolism, pyruvate, depress intake to an equal extent and, as lactate is metabolized to pyruvate and as pyruvate itself is oxidized to acetyl-CoA, the importance of the oxidation step is supported.

When a high-fat diet was offered, lactate and pyruvate no longer showed the intake-depressing effect, but fat is known to depress pyruvate oxidation; it is likely that such a depression occurred in this experiment because blood levels of these metabolites remained elevated for longer after injection in rats fed the high-fat diet compared with those on a high-carbohydrate diet. All of this evidence points to the oxidation step in liver metabolism being the key to effects of the liver on food intake (Forbes, 1988a).

Several studies have failed to confirm an important role for the liver in sensing nutrients and transmitting the information via the nervous system, but M.G. Tordoff and M.I. Friedman (personal communication) have noted that those experiments in which there has been no effect on feeding of increasing nutrient flow to the liver have exposed animals to different, contrasting, treatments at short intervals, thus confusing them by not allowing adequate time for them to learn the effects of different infusions (see Chapter 6). Despite the evidence presented here, there is still considerable controversy as to whether the liver is important in the control of intake under physiological conditions.

Poultry

Several experiments have investigated the glucostatic theory of intake control in birds without finding any significant depression due to glucose injections or infusions. In the first recorded infusions of glucose solutions into the coccygeomesenteric vein (leading into the liver) of chickens, Shurlock and Forbes (1981a) infused a solution of 60 g glucose/l at a rate of 1.2 ml/min into cockerels over a period of 3 h. Even though this high rate of infusion had no effect on food intake when given into the jugular vein (32 versus 28 g/3 h), it almost completely suppressed feeding when given into the liver (34 versus 2 g/3 h). Further, when a range of solutions from 1 to 60 g/l was given, there was a highly significant negative correlation between the concentration of glucose in the solution and the weight of food eaten during the infusion (see

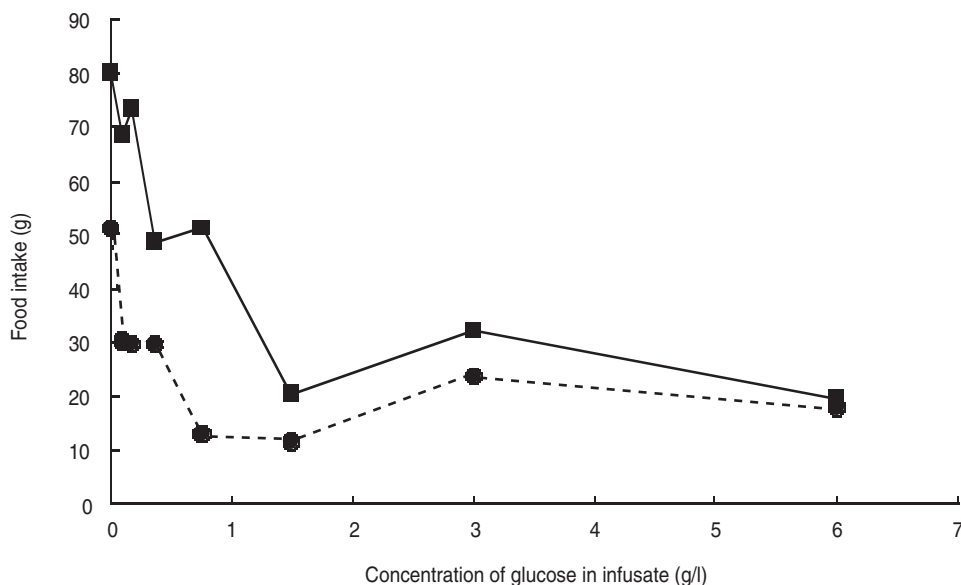


Fig. 4.1. Effect of infusing at 1.2 ml/min isotonic saline (including glucose) into the liver of cockerels on food intake over 1 h (■) and 3 h (●) (from Shurlock and Forbes, 1981a).

Fig. 4.1). The slope of the relationship is steep at lower concentrations, which is the physiological range, suggesting that liver sensitivity to glucose has the potential to exert a powerful control over feeding in the normal chicken.

The effects of overnight fasting on the response of cockerels to portal infusion of glucose were investigated by Shurlock and Forbes (1981a). Intake was depressed only by the highest dose of glucose when access to food was allowed during the infusion. When food was withheld until the end of the infusion there was a large, dose-dependent inhibition of voluntary intake. This result, together with observations made during the post-infusion period in previous experiments, showed that the effect of glucose lasted beyond the infusion period and was more likely to be a result of changes in liver glycogen or glucose content rather than simply an effect of the concentration of glucose in the blood perfusing the liver.

An amino acid mixture infused into the portal vein also depressed intake, while jugular introduction at the same rate had a much smaller effect (Shurlock and Forbes, 1984); effects of glucose and amino acids were additive and possibly affected the same system in the liver. Lysine infused at 50–150 mg/3 h caused a reduction in intake during the 3-h treatment, whereas ammonia at an equivalent rate did not and leucine had a delayed effect (Rusby and Forbes, 1987a). Vagotomy at the level of the proventriculus blocked these effects of portal infusion of glucose and lysine (Rusby *et al.*, 1987; Fig. 4.2), although doubt is cast on this conclusion by the lower intake of the vagotomized birds during the control infusion, compared with the intact chickens, suggested as being due to the changed feeding pattern of the former (see below).

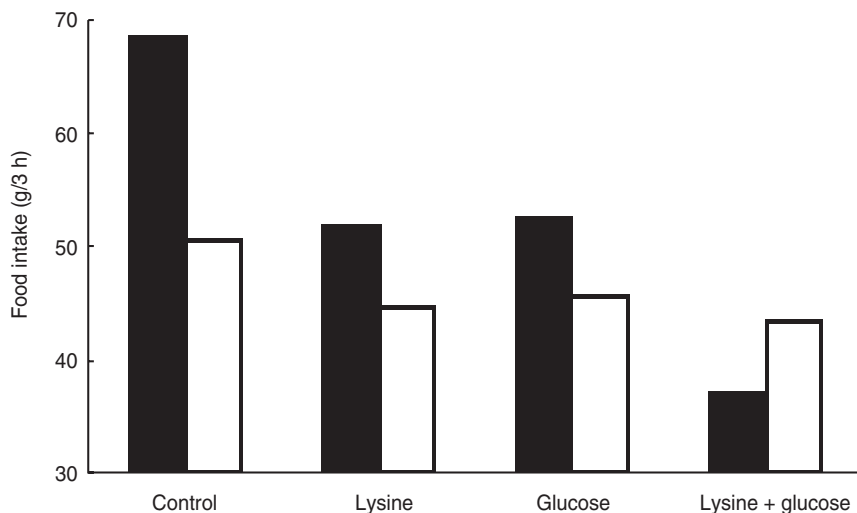


Fig. 4.2. Food intake during 3-h infusions of glucose and/or lysine solutions into the liver of intact (solid bars) or vagotomized (open bars) chickens (from Rusby *et al.*, 1987).

Adrenaline injected into the hepatic portal vein at low doses of up to 0.1 mg/kg depresses intake, an effect which is blocked by section of the hepatic branch of the vagus nerve (Howes and Forbes, 1987a). As adrenaline causes glycogenolysis, these results suggest that it is glucose concentration in or around hepatocytes that is important rather than the direction of flow of glucose through the hepatocyte membrane. In order to study the mode of action of adrenaline, an α -adrenergic blocker, phenylephrine, was given into the liver at a wide range of doses, but without effect; a β -blocker, salbutamol, depressed intake but the range of doses used (500–2000 μ g) was probably too high to achieve its effect just by a physiological blocking of endogenous adrenaline. The intake-depressing effect of injecting glucagon into the liver of chickens is also blocked by vagal section (Howes and Forbes, 1987b), but whether the dose used was physiological is open to question.

In birds, most fat synthesis occurs in the liver, and plasma levels of triglycerides are much higher than in mammals. Cockerels of an egg-laying strain were sensitive to fat infused into the hepatic portal vein, but not into the jugular vein, while in broilers there was no effect, irrespective of site of infusion (Lacy *et al.*, 1986). Has selection of meat-type chickens bred out some of the liver's sensitivity to metabolites?

If the liver is important in the control of food intake, it would be expected that liver denervation would disrupt feeding behaviour. Local denervation has not been undertaken in the chicken, but section of both vagus nerves as they cross the proventriculus (the equivalent of sub-diaphragmatic vagotomy in mammals) has been carried out, this affecting many visceral organs, not just the liver. It is perhaps surprising, therefore, that Savory and Hodgkiss (1984) found no differences in feeding behaviour between vagotomized and

sham-vagotomized chickens, although Rusby *et al.* (1987) observed significantly fewer meals, each of a larger size, but there was no effect on total daily intake. If, as suggested in Chapter 10, many feedback factors are integrated by the CNS, the loss of some of these would not necessarily result in a change in daily intake, but would be likely to result in larger meals.

Pigs

Infusion of a solution of 150 g glucose/l, or of 250 ml of a solution of 100 g amino acids/l, into the jugular vein or hepatic portal vein during feeding had no effect on the voluntary intake of pigs trained to eat in one session per day under operant conditions (Stephens, 1980). These results are in contrast to those with other mammals and birds, but there is no *a priori* reason why the pig should be different to other mammals, as its liver metabolism is similar to that of the rat. It seems likely that the feeding regime used in experiments with pigs, with only one or two periods of access to food per day, makes them reliant on different stimuli to terminate feeding compared with animals with continuous access to food. Perhaps the large amount they must eat in the short period of access emphasizes the physical aspects of gut-fill as a limit to meal size.

Ruminants

Ruminant animals absorb most of their energy from the digestive tract in the form of volatile fatty acids (VFAs), of which propionate is gluconeogenic and has been shown to depress intake in sheep (see below). The only direct study involving infusions into the hepatic portal vein of cattle was that of Elliot *et al.* (1985), who noted reduced intake during 20 out of 30 infusions of 20–50 mmol/min of sodium propionate into the portal vein of growing cattle; they ascribed the variability of their results to their method of feeding, which was restricted to 2.5% of body weight/day, given in 24 hourly meals.

It had been found in sheep that propionate depressed intake to a greater extent when infused into the ruminal vein than into other vessels, and the existence of propionate receptors at that site was proposed. Anil and Forbes (1980b) showed that a 3-h infusion of 1.2 mmol/min of sodium propionate into the hepatic portal vein almost completely prevented feeding in sheep, while the same rate of infusion into the jugular vein had little effect. It seems highly likely, therefore, that the ruminant liver is sensitive to its rate of utilization of propionate.

The route(s) taken by information from the liver to the CNS have been studied by sectioning the hepatic plexus of nerves, by sectioning or anaesthetizing the splanchnic nerves and by sectioning the hepatic branch of the vagus nerve (Anil and Forbes, 1980b, 1988). Almost complete section of the hepatic plexus, bilateral splanchnotomy (Fig. 4.3a) or temporary blockade of nervous transmission in the splanchnic nerves (Fig. 4.3b) all prevented the intake-depressing effect of 3-h infusions of sodium propionate into the hepatic portal vein at

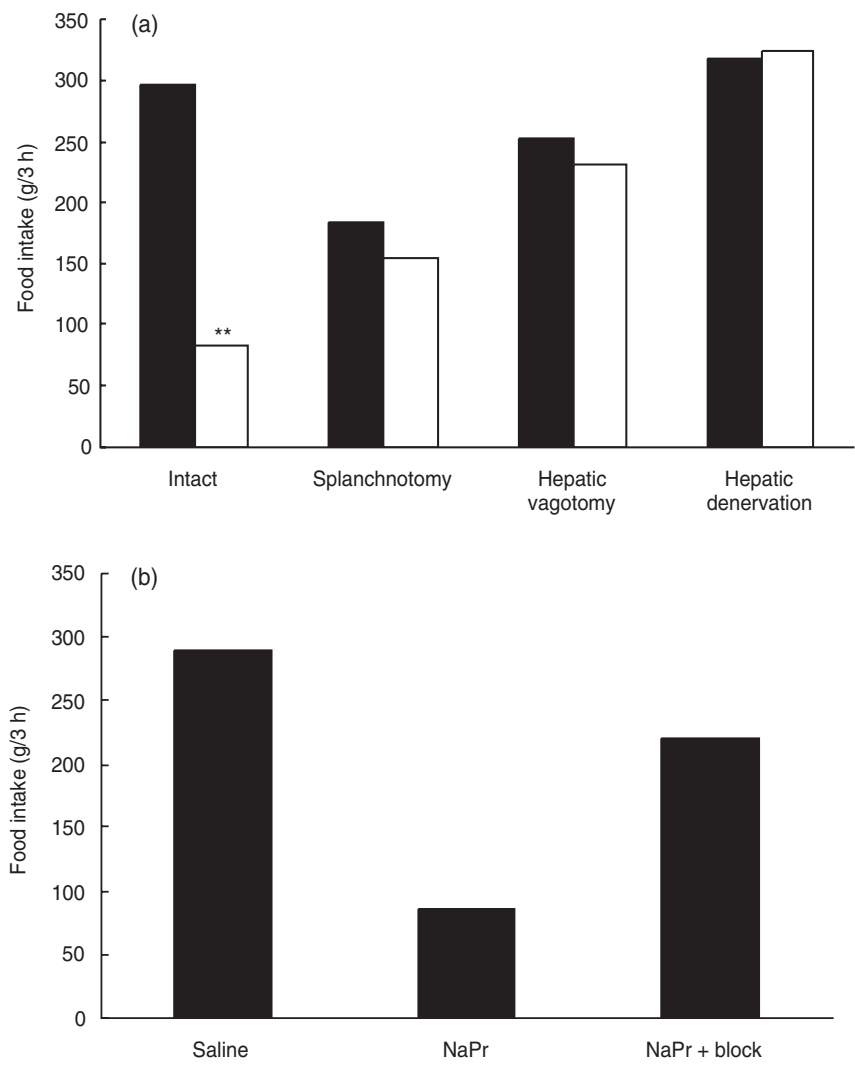


Fig.4.3. (a) The effect on food intake of saline (solid bars) and sodium propionate (NaPr) solution (open bars) infused into the hepatic portal vein of sheep subject to bilateral splanchnotomy, section of vagal innervation of the liver or total liver denervation; (b) effect on food intake of sodium propionate infused into the hepatic portal vein of sheep with and without splanchnic blockade with anaesthetic; **, highly significant effect of propionate infusion (from Anil and Forbes, 1988).

1.2 mmol/min. The paradoxical situation whereby either one of the two likely routes for transmission of afferent information from liver to CNS results in blockage of the effects of propionate given into the liver has not been resolved, but may be due to some efferent involvement with the control of blood flow or enzyme activity that is prevented by nerve section.

These clear-cut effects of propionate infusion into the portal vein on feeding by sheep have not always been seen by other workers. De Jong (1981) infused a mixture of the sodium salts of VFAs into the hepatic portal vein of goats at a rate similar to that used for sheep by Anil and Forbes (1980b), but found no change in food intake despite a doubling of plasma levels of VFAs. The protocols used by the two groups were very similar, and it seems unlikely that there is a fundamental difference between such closely related species – perhaps the tips of the cannulae in de Jong's animals were beyond the receptors in the wall of the veins entering the liver, while those of Anil and Forbes ended in the mesenteric vein into which they were introduced, i.e. short of the portal entry to the liver (see below). The effect observed in the sheep is not likely to be simply osmotic, because sodium acetate infused into the portal vein at 4 mmol/min (i.e. more than three times the osmotic load of the sodium propionate infusion) had no effect on feeding (Anil and Forbes, 1980b); acetate is not utilized by the liver in significant quantities.

Denervation of the liver does not affect daily food intake in several species, including sheep, and this has been cited as evidence that the liver does not play a role in the control of food intake. However, the meals are larger and less frequent than those of normal animals (Anil and Forbes, 1980b), as would be expected if some, but not all, of the negative feedback information from the visceral organs had been cut off.

A nervous pathway from the liver to the nucleus of the solitary tract in the *medulla oblongata* via the vagus nerve has been identified (M.H. Anil, P. Chatterjee and J.M. Forbes, unpublished observations), and it would appear that the sheep is similar to the rat in that both vagal and splanchnic afferent pathways are involved in the transmission of information from liver to brain (Anil and Forbes, 1988).

Attempts in our laboratory to study vagal discharges from chemoreceptors in the liver of the sheep have not revealed any consistent responses to propionate injected into the hepatic portal vein (M.H. Anil and J.M. Forbes, unpublished observations). Nor have we been able to find receptors in liver tissue of sheep or chickens by electron microscopy (P. Chatterjee, M.H. Anil and J.M. Forbes, unpublished results). This is in line with the failure to demonstrate receptor nerve endings in the parenchyma of the liver of several other species, including the rat (see above). Structures with the appearance of chemoreceptors have, however, been located in the hepatic portal vein of the rat, so further studies are required in farm animals. The finding that propionate depressed food intake by sheep when given for 20 min at 2 mmol/min into a mesenteric vein – but not the portal vein (where the tip of the infusion catheter would lie within the liver) – supports the idea that the receptors are in the portal vein rather than in liver parenchyma (Leuvenink *et al.*, 1997).

Ingestion by sheep of the plant *Lantana camara* leads to ruminal stasis and anorexia, which McSweeney and Pass (1983) showed to be due to liver damage rather than to direct effects of the toxin on receptors in the reticulo-rumen. Liver denervation of intoxicated animals reduced the severity of the reduction in ruminal muscular activity, and it was concluded that the effects of lantana poisoning on the rumen were indirect and that the ruminal stasis was reflex in nature, the primary lesion being in the liver.

Lipids

Fat is stored in the body in large quantities, with continuous turnover involving the release of fatty acids, glycerol and ketones such as D-3-hydroxybutyrate. There is particular interest in ways in which adipose tissue might affect feeding, in view of the practical significance of preventing or reversing over-fatness, both in humans and in farm animals (see Chapter 15).

Dietary fat is absorbed into the lymphatic system rather than into the venous drainage of the intestines in mammals, and thus bypasses the liver. However, the liver is an important site of fat metabolism in mammals and especially in birds. Intravenous infusion of fat emulsion depresses intake, an effect that is not accompanied by changes in plasma glucose or insulin concentrations. As animals fatten, there is a gradual increase in plasma insulin concentration, and the impressive evidence that this is reflected in increased concentrations of insulin in the cerebrospinal fluid that inhibit intake, thus acting as a homeostatic mechanism for body fat, has recently been reviewed (Stricker and Woods, 2004). Because of its importance in controlling fat deposition, insulin has received much attention in studies on relationships between body fatness and voluntary food intake. In particular, insulin resistance increases with increasing body fatness.

The continuous turnover of adipose tissue involves the release of fatty acids, glycerol and ketones. Glycerol levels in blood do not increase during a meal, so that any involvement in the control of intake is more likely to be as a long-term signal of adiposity, added to the immediate signals of the nutrient value of food being eaten or recently eaten. Infusion of glycerol into the portal vein of castrated male sheep at a physiological rate of 0.3 mmol/min for 3 h did not increase the peripheral concentration of glycerol and had no short-term effect on intake (P.M. Driver and J.M. Forbes, unpublished results). Glycerol does not seem to be a strong candidate for a signal mediating reduced intake in sheep, although proportionately higher doses do depress intake in rats.

Palmitate increases liver cell membrane potential (via the sodium pump driven by oxidation), and this could be a way in which fat metabolism influences feeding. Inhibition of fatty acid utilization in rats with intraperitoneal mercaptoacetate, which inhibits fatty acid oxidation, reduced the latency to eat without affecting meal size, thus implicating fatty acid oxidation in the maintenance of satiety after a meal (see review by Scharrer, 1999).

A net synthesis of lipids and deposition in adipose tissue is a drain on nutrients – particularly glucose and fatty acids – from the blood, which will cause a compensatory increase in food intake. However, there must be an upper limit to the rate and amount of fat deposition and, when either of these limits is approached, the uptake of nutrients for fat synthesis will be reduced and food intake will decline.

Poultry

The site(s) of action of fats on intake has not been adequately studied in chickens. If the situation is similar to that in mammals, then one of the effects of

fat in the diet is to slow the rate of emptying of the stomach, and this has been confirmed in hens but not in young broilers. If a reduction in rate of passage does occur it might in turn depress food intake by a stomach distension mechanism. In view of the discussion above, there is clearly a lot of scope for studies on the involvement of lipids in the mechanisms that control intake in the chicken.

The chicken seems to be particularly sensitive to the effects of parenterally infused fat on feeding, which may be related to the fact that most lipid synthesis occurs in the liver and the lipid is then transported in the bloodstream. As little as 100 mg of lipid given in suspension into the hepatic portal vein of cockerels of an egg-laying strain over a 30-min period depressed subsequent intake to one-half of control levels, while similar infusion into the jugular vein was without effect. However, a much larger amount was without effect in broiler chickens of the same weight (but younger age), and these birds were also insensitive to glucose infused into the hepatic portal vein (Lacy *et al.*, 1986). Broilers have been selected for high food intake, but whether this has involved reduced sensitivity to metabolites is not yet understood.

Cattle

Choi *et al.* (1997) have tested the hypothesis that inhibition of fatty acid oxidation by sodium mercaptoacetate blocks the decrease in food intake by dairy heifers when the fat content of their diet is increased. They observed a decrease in intake during the 4 h after injection rather than the expected increase, and suggested it might be due to the changes in hormones and metabolites induced by mercaptoacetate.

Plasma insulin is higher in obese than lean heifers and there is a bigger insulin response to glucose in the obese, especially during oestrus.

Sheep

There must be a positive relationship between intake and rate of fat deposition, other factors being equal, and Mears and Mendel (1974) concluded from an experiment with young lambs that intake was stimulated in animals with greater numbers of adipocytes, due to the faster removal of metabolites from the circulating pool: 'The amount of glucose removed from the glucose pool could be the feed-back signal which results in a high long-term food intake'. It is in older animals that the established size of the fat depots affects intake in a negative manner.

Adipose tissue is continually undergoing lipolysis and lipogenesis, and plasma free fatty acid levels are approximately proportional to body fat stores. Intravenous infusion of long-chain fatty acids depresses food intake in sheep (Vandermeersch-Doize and Paquay, 1982), but this is not likely to represent a simple feedback loop because high free fatty acid levels also occur in underfed animals which, if offered free access to food, eat more than well-fed animals.

However, a well-fed animal has high plasma insulin levels while an underfed one has a low rate of insulin secretion. Perhaps fatty acids are satiating only in the presence of high insulin concentrations in plasma.

McCann *et al.* (1992) fed adult Dorset ewes in lean condition a pelleted hay-grain food and observed a doubling of body weight over 42 weeks from 47 to 97 kg, and the lipid content of the carcass increased from 25 to 49%. From week 5 to 20, intakes were at the maximum allowed (3.0 kg/day) but then fell steadily to about 1.2 kg at 42 weeks. Once they had reached the static phase of obesity, intake per unit of body weight was the same as required for maintenance by lean sheep. Plasma insulin rose from 50 to 249 pmol/l by week 30. At around 25 weeks thyroid hormones rose significantly, plasma free fatty acid levels rose and voluntary intake started to decline, changes which might have been related to changes in morphology and/or humoral signals emanating from adipocytes. The high insulin levels coupled with high plasma glucose showed that insulin resistance had occurred.

Vandermeersch-Doize *et al.* (1982) found that plasma insulin concentration increased steadily from 10 to 300 μ U/ml over a 35-week period of ad libitum feeding of sheep; by the end of this period body weight had stabilized. Insulin concentration also increases in goats as they get fatter. This suggests that the declining intake was not simply due to a reduction in ruminal capacity with increasing volume of abdominal fat; had this been the only cause, then insulin levels would have been more likely to decrease due to a fall in plane of nutrition.

Volatile Fatty Acids

Although plasma levels of the VFAs increase in ruminants after large meals, the changes in peripheral blood during and between small spontaneous meals are not clear-cut. The available evidence indicates that acetate affects receptors in the ruminal wall (see Chapter 3) and propionate affects the liver (see above); transport in the general circulation is not considered to be very important as a negative feedback signal.

Amino Acids

Amino acids stimulate gut receptors, but whether these are osmoreceptors or whether there are specific amino-receptors is not clear. Once absorbed, amino acids reach the liver and some metabolism takes place, including deamination and oxidation of those present in excess. An imbalance in the proportions of amino acids relative to the requirements invariably leads to reduction in food intake (see Chapter 12).

The liver of the chicken is sensitive to lysine, as infusion into the portal vein causes a much greater depression of intake than infusion at the same rate into the jugular vein; the liver effect is blocked by vagotomy in the same way as the effect of portally infused glucose (Rusby *et al.*, 1987).

The evidence for a direct effect of amino acids on the brain is stronger than that for glucose. Tobin and Boorman (1979) fed chickens on a histidine-deficient diet that depressed food intake and found that infusion of histidine into the carotid artery, which goes directly to the brain, reversed the effect of the amino acid imbalance while infusion into the jugular vein had no effect. Thus, histidine appears to act directly on the brain to alleviate the intake-depressing effects of deficiency rather than more generally in the whole body.

Metabolic Hormones

Insulin

In farm animals, the effects of insulin administration have sometimes been to depress food intake and sometimes to stimulate it. In the chicken, mammalian insulin depresses intake but avian insulin is structurally different from that of mammals and any future work will need to use chicken insulin.

Exogenous insulin has been shown to stimulate voluntary intake of pigs under some circumstances (Houpt *et al.*, 1977). Similarly, some experiments with sheep have shown increased intake (e.g. Houpt, 1974) while others have not. Intravenous administration of 0.7 $\mu\text{g/kg}$ of insulin at the beginning of a meal depressed food intake during the following 30 min by 14% when given to cows deprived of food for 11 h, but not in those fed 4 h beforehand (Faverdin, 1986), so the role of insulin in short-term control of intake depends on nutritional status.

Evidence that insulin does play an important physiological role in maintaining food intake in ruminants comes from the observation that alloxan-induced diabetes causes inappetence and death in sheep (Reid *et al.*, 1963). This is due to the lack of insulin rather than to the general toxic effects of alloxan, because replacement therapy with insulin maintains intake at normal levels.

A collation of data from the literature on effects of intravenous insulin in ruminants (Dulphy and Faverdin, 1987) shows that, in the short term (15–30 min after injection), doses up to about 0.5 $\mu\text{g/kg}$ depress feeding but doses above this have less effect; higher doses (84–170 $\mu\text{g/kg}$) stimulate intake from 2–4 h after injection. Infusion of glucose to maintain plasma levels prevents the insulin-induced hypophagia in sheep, but in cows a euglycaemic clamp applied for long-term infusions (4 days) during hyperinsulinaemia generally depressed intake (Faverdin, 1999). Given the many physiological responses, both direct and indirect, to changing the concentration of insulin in the blood, it is not possible to explain these diverse results without a deeper understanding of all of the factors effecting, and affected by, changes in insulin secretion.

In summary, insulin may play a role in long-term intake and weight regulation in ruminants but it does not seem likely that it plays a role in the depressed intake in dairy cows in early lactation when the insulin concentration is low.

Glucagon

Glucagon has been found to increase in blood during feeding. The liver is the focus of attention for effects of this hormone on feeding, as injections into the portal vein are more effective in depressing feeding than those into the general circulation, and hepatic vagotomy blocks the effect of glucagon given portally.

Glucagon injected into the portal vein of cockerels at doses of 5–50 μg was found to depress food intake in a dose-related manner during the subsequent 90 min (Howes and Forbes, 1987b). This effect was prevented by vagotomy, although interpretation of the results was somewhat clouded by the fact that control levels of feeding at the time of day the experiments were carried out were lower in vagotomized birds than intact birds. The reason for this is probably that vagotomized chickens eat fewer meals and the infusion period happened to include less meals after vagotomy.

Of the few studies of glucagon and glucagon-like peptide 1 (GLP1) on food intake in ruminants, one shows that glucagon administered intravenously at physiological concentrations does reduce intake in sheep. More research is required in ruminants on the effect of glucagon and GLP1 to unravel their importance in intake regulation.

Corticotropin-releasing factor (CRF)

CRF is the hypothalamic releasing hormone that controls the output of pituitary corticotrophin and thus the adrenal output of corticosteroids. Centrally administered, CRF reduces food intake in cattle and it may be that it plays a role in the reduced intake around calving and during other stressful events (Ingvarsen and Andersen, 2000).

Growth hormone and somatostatin

In the sheep, spontaneous meals of a highly digestible food are preceded by peaks of growth hormone (GH) in plasma, as shown in Fig. 4.4 (Driver and Forbes, 1981). Unexpected withdrawal of food resulted in much greater peaks of GH secretion within 2–3 h and, within a few minutes of replacement of food, levels were low once again. The concentration of GH in lactating cows also tends to fall during spontaneous meals. Growth hormone secretion is a sensitive index of nutritional status, and this suggests that the pre-meal peak is an indication of the need to replenish body stores, rather than a direct cause of eating. Injection of GH to mimic spontaneous peaks has no effect on feeding behaviour (P.M. Driver and J.M. Forbes, unpublished results), so that the release of GH from the anterior pituitary (under the control of the hypothalamus) and the onset of feeding seem to be independent consequences of a relative shortfall in nutrient supply from the digestive tract.

Somatostatin is the hypothalamic factor that maintains inhibitory control on GH secretion. In a summary of 11 studies, it was found that growing cattle

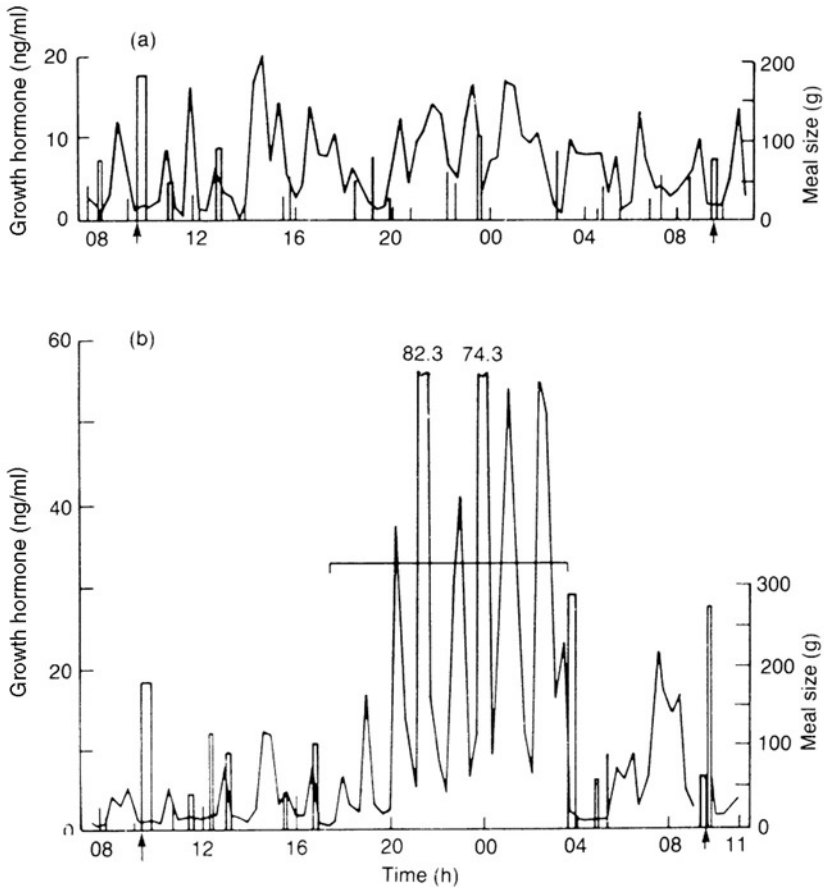


Fig. 4.4. Plasma growth hormone concentrations and meal sizes during 27-h periods in a sheep; (a) with free access to food throughout; (b) food removed from 17.30 to 03.30 h (from Driver and Forbes, 1981).

immunized against somatostatin ate an average of 4.2% more food than did controls (Ingvarsen and Andersen, 2000). This effect is likely to be via the increase in growth, and thus in nutrient requirements, caused by the immunization. It may seem paradoxical that GH should both signal a shortage of nutrients and stimulate growth. However, it should be borne in mind that insulin secretion is reduced by underfeeding so that mild underfeeding will allow fat mobilization (increased GH and reduced insulin), while encouraging deposition of non-fat tissues.

Adrenaline

Eating stimulates the sympathetic and parasympathetic branches of the autonomic nervous system, causing the release of adrenaline both from the

adrenal medulla and from sympathetic nerve endings in the liver, which might contribute to satiety via actions on the liver. Intramuscular injection of adrenaline at doses of 0.2–1.0 mg/bird caused hypophagia for several hours (Sykes, 1983). This inhibition of feeding was not overcome by prior starvation for 24 h, but pre-treatment with 1.5 mg phentolamine or 0.4 mg propranolol (α -adrenergic antagonists) completely blocked this effect. Injection of up to 2.5 mg adrenaline into the hepatic portal vein of cockerels depressed intake in a dose-related manner, but the effect of the highest dose was not attenuated by vagotomy at the level of the proventriculus (Howes and Forbes, 1987a). Phenylephrine, a pure β -blocker, given intraportally at doses of up to 3.0 mg, had no effect on food intake whereas the β -blocker salbutamol gave a dose-related depression, whether or not the vagus nerves were intact. The biological significance of these results is in doubt, however, as the doses used are likely to be well above the physiological range.

Leptin

It had long been suspected that adipose tissue secretes a substance in proportion to its mass, that acts as a feedback signal to the CNS. Leptin possesses many of the characteristics necessary for this function, as adipose tissue produces this hormone increasingly as adipocyte size increases (see review by Houseknecht and Spurlock, 2003). Leptin is taken up in the CNS where it inhibits feeding via the NPY system, with pro-opiomelanocortin, melanocortin-stimulating hormone and agouti-related peptide also likely to be involved as mediators. Leptin primarily binds to the dorso- and ventromedial nuclei of the hypothalamus and to the arcuate nucleus, areas of the brain that are involved in the control of hormone secretion (including GH) and food intake.

While much of the research on leptin has been performed with laboratory animals and humans, there is evidence that it has similar functions in farm animals (Ingvarsen and Andersen, 2000). Leptin also affects energy expenditure, glucose metabolism, insulin secretion and action, the adrenal axis and hormones of the growth hormone axis, but virtually no research in these areas has been conducted with farm animals, although it has been demonstrated that growing pigs injected intra-cerebroventricularly with 10, 50 or 100 μ g porcine leptin showed a dose-related depression in food intake over approximately the next 24 h (Barb *et al.*, 1998).

Although there have been some studies on the effects of GH on plasma leptin levels in cattle, there appears to have been no work on voluntary intake.

Leptin in the plasma of sheep shows a mean concentration of 2.9 ng/ml, but with secretory episodes at 4.8 pulses/day with a mean amplitude 0.67 ng/ml and length of 1.13 h. These parameters are not affected by pattern of feeding or light (Tokuda *et al.*, 2000b). There appears to be a seasonal influence on the effects of leptin in sheep, as ICV injection in the autumn reduces food intake by 30%, when it is already low (see Chapter 17), while the same injection in the spring has no effect (Adam and Mercer, 2004).

Administration of single injections of 200 μg of mouse leptin intra-cerebroventricularly daily for 7 days in sheep reduced intake and body weight (Tokuda *et al.*, 2000a), and continuous infusion for 3 days of recombinant human leptin at 20 $\mu\text{g}/\text{h}$ into the cerebroventricles of sheep decreased the food intake significantly (Henry *et al.*, 1999).

If we can envisage leptin as generating 'discomfort' in the CNS, then we can integrate it into our concept of MTD, whereby its effects are added to those of other feedback signals (see Chapter 10). A small but persistent effect of leptin could, when added to the short-term signals from the digestive tract and liver, result in significant long-term reduction in intake in obese animals. There is no need to consider short-term and long-term controls of intake as being different in nature, just in the rate of change of the signals involved.

While there have been hopes that our increasing knowledge of the biology of leptin would lead to advances in the treatment of obesity in humans, it is difficult to see how knowledge of the leptin system could be made use of commercially in farm animals. If leptin is contributing significantly to the control of intake, then neutralizing leptin (e.g. with specific antibodies) would allow food intake to increase but the extra nutrients would be used for fat synthesis, which is not usually required. If, on the other hand, the animal is eating insufficient to support its metabolic needs, then adipose tissue will have been depleted and its production of leptin will be low, rendering neutralization ineffective.

Not all agree that the leptin hypothesis is valid. Speakman *et al.* (2002) point out that there are very great differences in the concentrations of leptin in people of similar fatness; different fat depots produce different amounts of leptin, subcutaneous fat a great deal, omental fat hardly any; in some species leptin is produced in the liver as well as in adipose tissue. Leptin production is very sensitive to immediate food intake, so leptin should be thought of as a starvation signal, i.e. a memory of energy deficit, and body mass is then considered an output variable rather than part of a closed loop, and to be susceptible to social factors, etc. Speakman's alternative proposals to explain the maintenance of more-or-less constant body fat content are discussed in Chapter 15.

Ghrelin

This is a hormone produced by the stomach wall that stimulates feeding by acting on the hypothalamus. Plasma levels increase during fasting, and humans injected with ghrelin have reported sensations of intense hunger. In pigs, intravenous infusion of 2 $\mu\text{g}/\text{kg}/\text{day}$ of ghrelin for 5 days stimulated weight gain and insulin, GH and cortisol secretion without affecting food intake (Salfen *et al.*, 2004). This reinforces the endocrine effects of ghrelin without giving any support for an effect on intake.

Ghrelin and its cDNA-encoding precursor have been identified from the chicken proventriculus, and Kaiya *et al.* (2007) review ghrelin structure, distribution and function in birds.

In sheep, peaks of ghrelin in plasma have been noted just before scheduled feeding times, falling back to baseline 1 h after feeding (Sugino *et al.*, 2002). It was suggested that ghrelin was acting as a hunger hormone.

Another hormone, obestatin, was found in late 2005 to *decrease* appetite. It is encoded by the same gene as ghrelin, but the purpose of this mechanism remains unknown.

Cholecystokinin

The secretion of several gut hormones is increased during feeding and subsequently as digesta pass through the stomach and duodenum. Of these, cholecystokinin (CCK) is perhaps the most studied as a satiety signal, but others, such as bombesin and gastrin, are also likely to be involved; CCK is produced principally in the wall of the duodenum. Strong evidence that endogenous CCK is important in the limitation of feeding has been provided by autoimmunization of rats to CCK, which increases food intake and weight gain and by the conditioning of a flavour preference to CCK with very low doses; higher doses condition an aversion.

The receptors for CCK that are involved in the feeding response were initially assumed to be those in the brain, but it has been shown that there are also receptors in the stomach, as gastric vagotomy prevents the effects of exogenous CCK on intake. The major effect of peripheral injection is probably on the digestive tract, stimulated to contract and thereby activate mechanoreceptors whose information is relayed to the CNS via the vagus nerves. The effect of injection into the brain is direct, and the effect on feeding is probably independent of that on the gastrointestinal tract (see Chapter 5).

Poultry

Intravenous injection of CCK in chickens reduces food intake, depresses gizzard motility and stimulates muscular activity in the duodenum. It has been found that intravenous infusion of CCK had less effect in birds offered diluted food and it was suggested that CCK may induce gastrointestinal responses that lead to abdominal discomfort; these are reduced when the motivation to food is higher (Savory and Gentle, 1984). Savory (1987) used conditioning tests to demonstrate that bombesin or CCK-8 at 1–10 $\mu\text{g/kg}$ were mildly aversive, increased heart rate and induced abnormal gastrointestinal motility. Cholecystokinin is less effective when arousal is reduced with reserpine, when the birds are very hungry or when their attention is distracted, all these points being used to support the contention that CCK acts by inducing abdominal discomfort rather than normal satiety.

Covasa and Forbes (1994b) confirmed the effects of CCK in broiler chickens by intraperitoneal injection and demonstrated a learned aversion to the colour of food offered for 2 h after 14 $\mu\text{g/kg}$ CCK injections, compared with saline. Vagotomy at the level of the proventriculus (equivalent to sub-diaphragmatic vagotomy in the mammal) prevented the effect of CCK on feeding and the learned aversion to CCK-paired coloured food. A very low

dose of CCK (2 µg/kg) had no significant effect on feeding and did not elicit a preference for the colour paired with the injection.

The CCK-blocker, MK-329, given intraperitoneally at doses of ≥ 90 µg/kg, significantly increased food intake over the next 2 h while, when given intravenously, somewhat lower doses were effective (Covasa and Forbes, 1994a). Lower doses of MK-329 did not affect food intake and failed to condition a preference or aversion for the colour of food given for 2 h after the injection. Cholecystokinin (14 mg/kg) caused a reduction in feeding, but this effect was not blocked by pre-treatment with intraperitoneal injection of MK-329 (32, 90, 180 and 360 mg/kg), thus questioning the role of endogenous CCK in satiety in chickens. A logical next step would be to see whether MK-329 still stimulates intake when given intraperitoneally in vagotomized birds.

Pigs

Cholecystokinin is thought either to constrict the pylorus, reducing the rate of stomach emptying, or to increase the sensitivity of vagal afferent receptors. CCK given into the jugular vein of pigs at a rate sufficient to depress food intake by 25% did not affect gastric emptying, however, suggesting that an effect on stomach motility is not necessary for CCK to exert at least some of its effect on feeding. This is confirmed by the observation that MK-329 reverses the depression of intake caused by fat infusion, but does not reverse the effect on gastric emptying. MK-329 increases intake in operant-fed pigs and also in pigs given a single meal after an overnight fast (Rayner *et al.*, 1991). Another CCK antagonist (L-364,718) blocked the inhibition of food intake induced by jugular or abdominal aortic infusion of CCK or duodenal infusion of emulsified fat or monoglyceride, while the responses to duodenal glucose, glycerol or oleic acid were not blocked.

Feeding in the pig is depressed by infusion of CCK into the general circulation but not by that into the hepatic portal vein or gastric artery. Probably CCK is most active in the upper intestine, as it is most effective when given into the branch of the mesenteric circulation going to this part of the intestine. The site of action is concluded to be in the intestines, but it is not yet known whether this is dependent on vagal innervation. The fact that duodenal infusion of phenylalanine or tryptophan in pigs increased plasma concentrations of CCK, but did not affect feeding (Rayner and Gregory, 1985), casts further doubt on the role of CCK as a true hormone of satiety. However, pigs immunized against CCK increased their intake by 8.2% and their growth by 10.6% (Pekas, 1983), strong support for a physiological role for CCK in the control of food intake.

Baldwin *et al.* (1983) have suggested that exogenous CCK causes a general malaise in the pig. They trained pigs by operant conditioning to respond for food, water, sucrose solution or heat. Doses of 20 or 40 units of CCK octapeptide given intravenously transiently reduced responding for food, water or sucrose but had no effect on responses for heat. These results show that CCK affects several types of behaviour and is thus unlikely to be a specific food satiety factor. However, the CCK receptor antagonist MK-329 caused a dose-related increase in food intake during 2 h following intravenous injection,

and MK-329 also abolished the intake depression caused by CCK (Ebenezer *et al.*, 1990). This suggests that endogenous CCK does play a role as a negative feedback inhibitor of food intake.

It is likely that the doses of exogenous CCK used have mostly been above the physiological and have caused malaise, but the recent work with low doses of exogenous CCK, with antagonistic drugs and with immunization against CCK, provides very strong evidence for a role for CCK in normal satiety.

Ruminants

In ruminants there are delays between eating and the arrival of food at the duodenal CCK-producing sites. Thus, CCK might be less important in these types of animal than in those such as the pig in which the simple stomach releases digesta into the duodenum as soon as a meal starts. However, a dose-dependent increase in plasma CCK concentrations to feeding different amounts of fat to cows has been observed 3 h post-feeding (Choi and Palmquist, 1996), giving some support to a role for CCK in controlling food intake in ruminants.

Grovmum (1981) infused CCK into several blood vessels in sheep and found that there was no greater effect on food intake when infusion was into the carotid artery or portal vein than when it was given into the jugular vein. He concluded that neither the brain nor the liver were involved in the reduction of food intake in response to CCK. The main effect is probably on the digestive tract. However, the flow of digesta through the duodenum is relatively constant in free-feeding ruminants, and Furuse *et al.* (1991) found no significant fluctuations in plasma levels of CCK in cows either with concentrate or roughage feeding. Without such meal-related fluctuations it is difficult to see how CCK can be involved in the control of feeding.

Other gut hormones

Pentagastrin depressed food intake of sheep whether given into the jugular vein or portal vein (Anil and Forbes, 1980a), while secretin had no effect by either route. Two other gut peptides, somatostatin and bombesin, also depress food intake and the former has many properties that make it a possible satiety hormone. The effect of somatostatin administered peripherally is blocked by gastric vagotomy, but that of bombesin is not and the route whereby the latter influences the CNS is unknown.

Other Hormones

Vasopressin

0.75–3.00 µg/kg of vasopressin given by intraperitoneal injection reduced food intake by goats in a dose-dependent manner (Meyer *et al.*, 1989). This effect was reversed by a V_1 -receptor antagonist or an α -adrenergic antagonist. The

vasopressin concentrations achieved in plasma as a result of the injections were similar to those seen during stress, and it was suggested that this hormone might be involved in stress-induced anorexia.

Hormones involved in growth and reproduction are covered in Chapters 15 and 16, respectively.

Conclusions

This chapter cannot claim to do justice to the complex subject of the roles of metabolites and hormones in the control of voluntary food intake. Although the glucostatic theory in the form originally proposed is no longer tenable, it is clear that animals can monitor the availability of energy-yielding materials and use this information to control their food intake. Because glucose is the major energy-yielding substrate in most non-ruminants, its infusion causes a reduction in food intake, especially when given into the liver. The liver is sensitive to oxidizable nutrients including glucose (propionate in the ruminant).

The effects of infusion of glucose or propionate into the liver can be blocked by local section of the vagus and/or splanchnic nerves, showing that the information to the brain is transmitted via the autonomic nervous system. A major role of the liver is to prevent the uneven flow of nutrients from the digestive tract causing undue fluctuations in the energy supply to the rest of the body, especially the CNS, so it is well placed to play a major role in the control of feeding.

Fats and proteins can also yield energy and therefore affect the energostatic control of intake in situations where they are oxidized. This utilization is influenced by metabolic hormones, and the effect of metabolites is modified according to the insulin and glucagon status of the animal. The role of insulin in the control of food intake is complex and dependent on the nutritional status of the animal as well as on other hormones and metabolites.

Most hormones affect food intake when given in large amounts, but it is often difficult to decide whether they are acting directly on the CNS or peripherally and whether they are important under normal, physiological conditions. This is true for the gut peptides such as CCK, which act at both sites and whose natural sites and rates of secretion are difficult to mimic experimentally.

5

Central Nervous System and the Special Senses

The central nervous system is clearly the integrator of most of the actions of the animal and, as such, plays a vital role in the control of voluntary food intake as well as in growth, fattening and reproduction. It is axiomatic that information from receptors in other parts of the body, including the special senses, is relayed to the brain, which integrates this with what it has previously learned about the consequences of feeding and makes decisions whether or not to seek and eat food.

The centres in the brain that are involved in feeding control were originally thought to be in the hypothalamus, a region with a volume of about 0.5 cm^3 in the sheep, lying just above the pituitary gland and optic chiasma at the base of the brain. These centres have been associated with the glucostatic, thermostatic and lipostatic theories of control of feeding (see Chapter 1). The ventromedial hypothalamus (VMH) is important in the control of anterior pituitary function as well as in food intake, while the lateral hypothalamic area (LHA), being a part of the medial forebrain bundle, receives information both from the visceral receptors and from higher centres of the brain.

Early studies used lesioning techniques to destroy small parts of the brain, followed by observation of changes in behaviour following recovery from the anaesthetic. Subsequently the effects of electrical stimulation were studied, while more recently effort has been concentrated on the neurochemistry of intake control using techniques such as injection of drugs that mimic or block the effects of the naturally occurring brain chemicals.

It is now accepted that feeding is organized by circuits and networks of neurones rather than by discrete 'centres', but the full picture is far from being complete. The involvement of the brain in the control of food intake with particular respect to poultry has been reviewed by Denbow (1985), while Forbes and Blundell (1989) have covered the subject for pigs and Baile and McLaughlin (1987) for ruminants. None of these reviews is recent and, while subsequent research is covered in this chapter, studies with farm animals

have decreased in the last two decades. Research using laboratory animals is presumably of relevance to farm animals, but there is evidence of significant differences between species. Reference in this chapter to species other than farm animals is minimal, and the reader is referred to the book edited by Stricker and Woods (2004).

Lesioning Studies

The first evidence of a particular locus for feeding within the brain was based on hypothalamic tumours found in obese humans in the late 19th century. Then, in the early 1940s, it was found that abnormalities of feeding and/or body weight occurred when discrete electrolytic lesions were made in the medial and lateral hypothalamus of the cat. Further studies in the 1940s and 1950s confirmed that lesions of the ventromedial hypothalamus (VMH) led to obesity and hyperphagia in the rat, and this area became known as the 'satiety centre'.

Lesions of the lateral area of the hypothalamus (LHA), on the other hand, caused aphagia and death, although rats kept alive by force-feeding did eventually resume spontaneous feeding and survived, albeit at a lower body weight than normal; this area became known as the 'hunger centre'.

Poultry

The VMH appears to be important in birds, and lesions in this area induce overeating and obesity in chickens, ducks and geese. However, the increased fatness of VMH-lesioned chickens (probably by depression of the secretion of growth hormone) was not always accompanied by hyperphagia. An increase of lipoprotein lipase activity precedes any increase in intake, suggesting that when hyperphagia occurred it was a response to altered fat metabolism rather than a primary effect of the lesions (Snapir and Robinson, 1989).

In a detailed review of nerve tracts involved in food intake control in birds, Kuenzel (1989) describes mechanoreceptors in the bill/beak that are innervated by the trigeminal nerve. However, lesions of the quinfrofrontal tract (the destination of the trigeminal nerve) in chicks affect feeding for only a few days, in contrast to the pigeon, which cannot recognize food for several weeks. Lesions involving the optic system cause severe feeding problems, while removal of the olfactory bulbs causes an increase in food intake, but without obesity as metabolic rate is also increased. Further evidence that obesity and hyperphagia are not always linked came from the observations in which septal-lesioned cockerels overate but did not become obese.

Lesions placed in the mid-lateral hypothalamic region (equivalent to the 'hunger centre' of mammals) induced hypophagia and loss of weight in only a small proportion of individuals, but careful work by Kuenzel, involving bilateral lesions in the LHA of the chick, showed hypophagia for only a few days; more posterior lesions gave more persistent effects.

Gold thioglucose, which causes hypothalamic lesions and hyperphagia in mice, had no effect in chickens whether given systemically or implanted directly into the hypothalamus.

Removal of the pineal gland from the brain of day-old chicks stimulates subsequent voluntary intake and weight gains (see Chapter 17), but no effect of pinealectomy on subsequent food consumption was found when the operation was carried out at 9 days of age.

Pigs

VMH lesions in pigs cause hyperphagia while LHA lesions induce aphagia, with no signs of recovery when the animals were kept alive by force-feeding. Lesions in the VMH of young pigs (5–6 weeks old) did not immediately induce hyperphagia, although other metabolic effects were seen (Baldwin, 1985). This is similar to young rats, where hyperphagia and fatness occur only after the infantile stage has been passed, both in VMH-lesioned and genetically obese animals.

Sheep and goats

Small VMH lesions in sheep did not change food intake, but they may not have involved destruction of a large enough portion of the critical area because Baile *et al.* (1969), making larger lesions that destroyed the whole ventromedial part of the hypothalamus of goats, did observe overeating and excessive fatness. Electrolytic lesions in the LHA of goats and sheep caused hypophagia, but not aphagia or death.

Electrical Stimulation

Lesioning is obviously a clumsy technique, and more sophisticated methods of studying brain function have been used since the original lesioning studies. Information is transmitted along nerve fibres electrically and between nerves by chemical transmitters, and both electrical and chemical stimulation have been used experimentally.

Although several species of bird have been tested for feeding responses to electrical stimulation, very few such responses have been obtained, even when the site of stimulation was the lateral hypothalamus (chicken, Tweeton *et al.*, 1973).

The only electrical stimulation which appears to have been performed in the pig has been self-stimulation in which animals, aged 10–16 weeks, were trained to press a panel to stimulate the hypothalamus in addition to panels to obtain food and water (Baldwin and Parrott, 1979). After a 22-h fast, there was a high rate of self-stimulation compared with the rate after eating to satiation in two out of four pigs, both of which had the electrodes in the lateral hypothalamus. Of six

other animals tested on 5 consecutive days, four decreased their food and water intake when self-stimulation was available, suggesting that the intake of food and/or water is pleasurable; these four had electrodes in the lateral hypothalamus while the other two had them implanted in other regions of the brain. The pigs did not starve themselves in favour of self-stimulation, however, indicating that there are more inputs to feeding control than simply the pleasure of eating.

Stimulation of the lateral hypothalamus causes satiated sheep and goats to start eating again and to continue eating voraciously as long as the stimulus is applied. Stimulation of the ventromedial nucleus of goats reduces feeding activity.

Brain Activity during Feeding

Studies have been made of changes in single unit activity in the lateral hypothalamic area of goats during scheduled feeding (Nagamine *et al.*, 2003) in order to clarify the location of feeding centres. Of 31 units studied in seven goats, only five altered their firing rates in response to feeding. Firing rate slowed or stopped as rate of eating slowed and the animals reached satiety. It was subsequently found that all the active units were located in the dorsolateral hypothalamic area close to the fornix. As these animals were fed only twice daily, they would have been quite hungry at the time these recordings were made; the relevance of the findings to spontaneous meals in animals fed ad libitum is therefore uncertain.

Kendrick (1992) recorded electrical activity of single neurones in regions of the sheep brain thought to be involved in feeding control. Cells in the lateral hypothalamus and *zona incerta* responded to the sight, but not to the smell, of food, mostly only when food was moved towards the mouth. Sheep can also be trained to associate coloured non-food objects with food, and cells in the *zona incerta* then respond to the sight of those objects. It takes seven to 13 trials for the association to be established and only a couple of hours for it to be forgotten, but it is well known that sheep retain preferences for certain foods for much longer than this. When the conditioned stimulus is a less artificial object, i.e. a novel food, learning is much quicker (one to two trials) and retention is much longer (months, see Chapter 6).

The cells that respond to the sight of food respond only to palatable food, not to foods that the sheep will not eat. Probably these sites in the brain are associated with rewarding aspects of stimuli but not with their negative aspects. Oats, which are highly palatable, cause stomach upsets when eaten in too great a quantity. Two sheep that had eaten too much rolled oats no longer responded as well in terms of increased firing rate of neurones as they had before this overeating. Cells that respond to food will respond to salt instead when the animal is rendered sodium deficient (see Fig. 5.1). Cells that respond to the sight of food also respond to its ingestion, but if an animal is not allowed to eat the food, its continued presence does not result in continued firing of these cells. Cells that respond to food in solid form do not do so when the same food is liquefied.

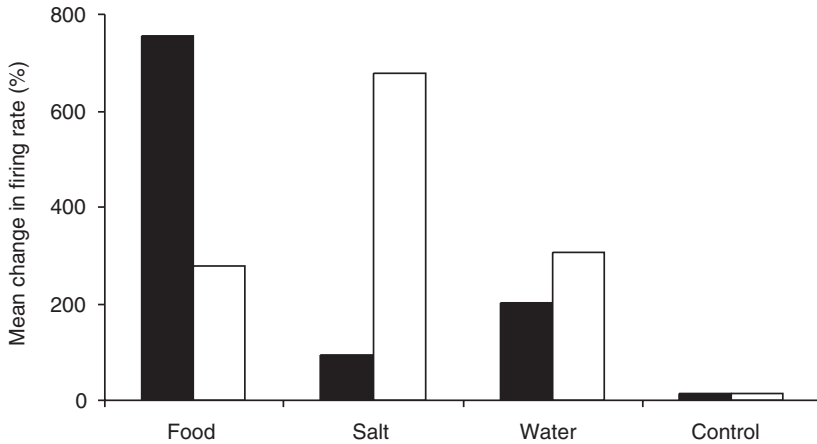


Fig. 5.1. Response in firing rate of neurones in the *zona incerta* of sheep to the sight of food, water and salt when the animals were food-deprived for 12 h (solid bars) or sodium-deprived for 4–6 days (open bars) (from Kendrick, 1992).

Before parturition, firing rate increases most in response to foods, and no cells respond to fetal fluid odours. After parturition, however, there is very little response to food odours but large responses to lamb odours, whether from the ewe's own lamb or from an alien lamb. Cells responsive to food sometimes fire in the absence of food; is this when the sheep is thinking about that food, i.e. when it is hungry?

Chemical Stimulation

Although transmission of signals along nerves is primarily electrical, interneuronal communication is mainly chemical. Neurotransmitters, such as noradrenaline and acetyl choline, are released by the terminals of one nerve and stimulate the receptors on one or several other neurones, which respond by an increase or decrease of firing rate. There is more scope for both physiological and pharmacological mechanisms to work at the synapse than along the nerve fibre and, in recent years, chemical stimulation of the brain has been used as the major experimental technique. The development of pharmacological antagonists to neural transmitters has also provided useful tools for the investigation of brain function.

Methods of introducing drugs into the brain include injection via cannulae implanted in the lateral ventricle, micro-injection via fine cannulae implanted or advanced through guides into brain tissue and by electrophoretic introduction. Invariably, drugs must be injected in amounts greater than the amount normally present in brain tissue in order to cause a significant response, and the question arises as to whether results can be considered to be 'physiological'. Despite such methodological problems, it seems likely that substances in the extracellular fluid

of the brain are involved with the physiological control of feeding. Martin *et al.* (1973) transferred 1 ml of cerebrospinal fluid (CSF) from fasted sheep into the lateral ventricle of recipients and found a fivefold increase in food intake during the following 15 min; CSF from satiated sheep had no effect.

Anaesthetics

By preventing neural transmission through affected parts of the brain, local anaesthetics are expected to have similar effects on feeding to lesions in the same areas. In general, this has proved to be the case.

Pentobarbital (a local anaesthetic) injected into the third ventricle or basomedial hypothalamus of chickens caused intake to increase from 14 to 32 g during the 1 h after injection, even though the birds were almost asleep; there was no effect when the injections were made into the posterior lateral hypothalamus (Snapir *et al.*, 1973). A dose of 6.5 mg of sodium pentobarbital given into the LHA depresses intake in hungry pigs, while in the VMH or cerebroventricles it stimulates intake in satiated animals.

Cerebroventricular injections of pentobarbital stimulate feeding in calves, goats and sheep. Detailed studies with sheep, in which a range of barbiturates with different durations of action were compared, showed that long-acting ones were more effective than those with a short action in inducing feeding when injected into the third ventricle (Seoane *et al.*, 1973). The effects of barbiturates were similar in a hot environment and at normal temperatures, and with high roughage and high concentrate rations. Micro-injection of barbiturates into the medial hypothalamus also stimulates feeding in sheep.

Adrenergic agents

Substances such as anaesthetics are, of course, unnatural, and manipulation of the concentrations of substances found naturally in the brain, and their analogues and antagonists, have formed the basis of most recent work.

Since the original work with rats there has been ample confirmation of a major place for adrenergic transmitters in the control of intake, and numerous experiments have demonstrated that noradrenaline given into the medial hypothalamus stimulates intake in several species, including farm animals. This effect can be prevented by prior injection of the appropriate blocker, but blockers given alone do not stimulate feeding. Work originally concentrated on the VMH and LHA and the paraventricular nucleus (PVN) as being the most sensitive sites mediating the actions of adrenergic agonists on eating. It seems likely that the PVN and its α -adrenergic receptors are important in the control of eating in response to deprivation and, possibly, to post-ingestional satiety signals.

Brain turnover of noradrenaline is increased by glucoprivation, a situation that can be reversed by providing substrates, either by ingestion or infusion, which could be used by the brain. This is evidence for a physiological role for noradrenaline in the control of feeding.

Poultry

Cerebroventricular injections of adrenaline or noradrenaline increase food intake in broiler-type chickens, while dopamine has no effect. However, the injection of adrenaline had no effect in birds of a layer strain. A differential response was also noted to cerebroventricular injections of 5-HT which, in broilers, depressed food intake in fully fed birds but not in 24-h fasted birds, while in layers 5-HT decreased food intake in both fully fed and 24-h fasted birds.

Further studies (Denbow *et al.*, 1986), with lines of broilers selected for fast and slow growth, showed that methoxamine (an α -adrenergic agonist) increased feeding in the fast- but not in the slow-growing strain, while 5-HT had no effect in fully fed birds but did depress intake in 24-h fasted birds of both lines. Genetic selection for growth has been demonstrated to alter the meal pattern as well as to alter the feeding response to intubations of amino acids and cerebroventricular injections of biogenic amines. Further studies are required to explore the mechanisms of these differences between breeds and strains.

Injection of 6-hydroxy-dopamine, which depletes noradrenaline, into the cerebroventricles or hypothalamus not only increases food intake but also causes obesity and testicular atrophy in geese.

Fenfluramine is a well-known appetite suppressant in mammals and, when incorporated in food, it induced a dose-dependent reduction in food intake by broiler chickens (Hocking and Bernard, 1993).

Pigs

In the pig, noradrenaline injected into the hypothalamus stimulates feeding while isoproterenol (a synthetic β -adrenergic agonist) causes temporary anorexia, blocked by propranolol (a synthetic β -adrenergic antagonist). The volume injected was large, however, so these results tell us little about the exact site of action.

Cattle

Lateral ventricular injection of noradrenaline in cattle stimulated voluntary intake over a very narrow range of doses (50–200 nmol), whereas isoproterenol was effective over a broad range (500–2000 nmol).

Sheep

Baile and his colleagues were, for several years, particularly active in this field (see Baile, 1975). They found that intraventricular injection of noradrenaline at doses of 542 nmol induced hyperphagia for some 30 min after injection. The effect was blocked by prior injection of α -adrenergic blockers, and it was later confirmed that intrahypothalamic injections had similar effects. At very low doses (4–16 nmol), the β -adrenergic agonist isoproterenol stimulated intake for about 1 h and this was blocked by β - but not by α -adrenergic antagonists. This

suggests the existence of two classes of adrenergic receptors and adrenaline, which has both α - and β -adrenergic activity, stimulated intake at two dose ranges, presumably corresponding to optimum stimulation of the two types of receptor.

One major drawback to ventricular injection is that the site of action cannot be determined because CSF secreted in the lateral ventricles transports the injected material through several parts of the brain. More precise targeting can be achieved by implanting guides through the cranium, which are directed towards certain loci in the brain. Using sheep prepared in this way it was shown that noradrenaline (240 nmol) and isoproterenol (8 nmol) had similar effects on feeding when given into hypothalamic tissue as they did when given intraventricularly. Again, effects of each were blocked by the appropriate blocking agent and the dose-response curve showed an optimum range with depression at high doses.

A brain locus sensitive to noradrenaline was not usually responsive to isoproterenol, and prostaglandins (PG) injected at loci sensitive to noradrenaline had different effects on feeding than at loci sensitive to isoproterenol. Doses of 14 or 28 nmol of PGE1 depressed food intake when injected at loci that showed feeding in response to noradrenaline. A PG antagonist, polyphloretin phosphate, not only blocked the effects of subsequent PG injection but by itself significantly increased intake. Whether this means that PGE1 normally inhibits feeding is not clear. At sites that responded to isoproterenol, PGE1 significantly stimulated intake. This subject is complex and will not be properly understood until the full range of the pharmacological and metabolic effects of these substances is known.

Serotonin (5-hydroxytryptamine, 5-HT)

In the mammalian central nervous system, 5-HT systems occupy a strategic anatomical location, projecting to, and passing through, the hypothalamus. Experimental manipulations of 5-HT metabolism can, under certain conditions, produce marked changes in food intake, food preferences and body weight, most obviously the suppression of food intake by experimental treatments that directly or indirectly activate 5-HT receptors. More controversial is the role of 5-HT in diet selection (see Chapter 7). Serotonin binds to several distinct receptor types in peripheral tissues but, while the significance of these receptor types in the CNS is uncertain, there is evidence linking them with effects on eating (see Forbes and Blundell, 1989).

In chickens of an egg-laying strain, 33–100 μ g 5-HT injected intraventricularly depressed intake, while in broilers it had this effect only if the birds were relatively satiated.

Intravenous injection of the serotonin agonist 8-OH-DPAT significantly increased food intake in the 45 min following injection in non-deprived pigs, while after 4 h of deprivation it had no effect on food intake (Baldwin *et al.*, 1995). After deprivation, pigs are likely to eat so quickly that it will be difficult to demonstrate effects of experimental treatments unless they are severe.

In sheep, 5-HT has smaller effects on feeding than noradrenaline and at fewer sites, the responsive ones being concentrated in the area of the anterior commissure.

Cholinergic agents

Acetyl choline is a neural transmitter found in significant amounts in the hypothalamus. In the rat, ventricular or hypothalamic injection of carbachol, a slowly metabolized cholinergic agonist, causes an increase in water intake but a consistent and large depression in food intake.

Carbachol injected into the hypothalamus of sheep at doses as low as 7 nmol stimulated feeding for 30–60 min and when atropine, a cholinergic antagonist, was injected a few minutes before a 28 nmol dose of carbachol, the hyperphagia was prevented (Forbes and Baile, 1974; Fig. 5.2). The adrenergic antagonists phentolamine and LB46 did not attenuate the carbachol effect, showing that it was acting on cholinergic receptors in the hypothalamus rather than causing non-specific stimulation. However, atropine alone had no effect on intake, which implies that endogenous acetyl choline is not involved in feeding control.

It had been shown that significantly increased feeding followed the injection of 50 nmol of carbachol into the lateral ventricle. However, larger amounts of carbachol (56–436 nmol) given into the lateral ventricle of sheep almost totally

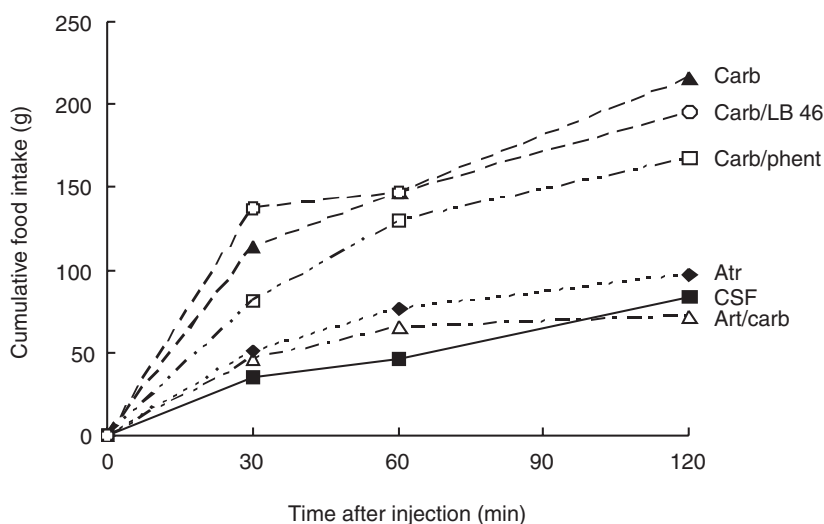


Fig. 5.2. Food intake by sheep 30, 60 and 120 min after intrahypothalamic injection of: (i) synthetic cerebrospinal fluid (control, CSF); (ii) carbachol (28 nmol, Carb); (iii) atropine (28 nmol, Atr); (iv) carbachol preceded by atropine (Atr/carb); (v) carbachol preceded by phentolamine (120 nmol, Carb/phent); or (vi) carbachol preceded by LB46 (120 nmol, Carb/LB46) (Forbes and Baile, 1974).

prevented feeding for 1 h, accompanied by significantly elevated plasma levels of growth hormone (Driver *et al.*, 1979). Experimental differences that might be responsible for this discrepancy between the two sets of results have not been identified.

It is unlikely that the carbachol-induced stimulation of growth hormone secretion directly caused the reduction in food intake because intrajugular growth hormone infusion to mimic peaks of this type had no effect on feeding behaviour in sheep (P.M. Driver and J.M. Forbes, unpublished results). It is equally unlikely that the low food intake following carbachol injection would give such a rapid response in growth hormone secretion; feeding and growth hormone were probably affected independently by carbachol.

Gamma-amino butyric acid (GABA)

Intracerebroventricular (ICV) injection of several GABA agents induced hyperphagia in layer-type chicks (Bungo *et al.*, 2003). However, in broiler chicks two of the agents (muscimol and nipecotic acid) had similar effects while baclofen depressed feeding. These results suggest that there are some differences in central GABAergic systems between these strains of chicks, but that GABAergic systems have an important role in the regulation of food intake in neonatal chicks.

Muscimol, the GABA-A receptor agonist, increased operant responding for food in pigs after injection into the lateral ventricles, an effect that was completely abolished by simultaneous administration of bicuculine, a GABA antagonist (Baldwin *et al.*, 1990b). GABA itself at 800 and 1600 nmol increased intake, and this was also abolished by bicuculine.

It has also been found that muscimol given intraventricularly stimulated feeding in sheep, and this was prevented by the GABA antagonist, γ -vinyl GABA; GABA itself had little effect on feeding, however (Seoane *et al.*, 1988).

Cholecystokinin (CCK)

CCK was first implicated in the control of feeding following experiments involving peripheral injections (see Chapter 4). CCK is found in the brain and reduces food intake when injected intraventricularly. The possibility that CCK is a neurotransmitter involved in a physiological control is discussed by Baile *et al.* (1986).

Poultry

ICV injection of chickens with 0.1 or 0.4 μ g CCK-8/kg (CCK octapeptide, CCK-8, is the active moiety of CCK) had no effect on gizzard or duodenal motility but caused drowsiness in some birds and reduced intakes by 20 and 31%, respectively, during the following 30 min (Savory and Gentle, 1984). Dibutyryl

cyclic GMP, a CCK receptor blocker, stimulated intake, supporting a physiological role for CCK. The mean concentrations of CCK-8 in different parts of the brain did not differ between fed birds and those fasted for 24 h, however, but no measurements of turnover have been reported.

Four-week-old broilers injected intracerebroventricularly with 100 and 150 ng of CCK-8 reduced intake, respectively, for 60 and 105 min. The fact that smaller amounts of CCK are required to depress intake by a given amount when injected into the brain, compared with peripheral injection, has been used to support the concept that brain CCK receptors are more important than gut CCK receptors in the control of food intake. However, brain injections are made into a much smaller volume than peripheral injections, making comparisons of efficacy very difficult.

Pigs

Doses of CCK-8 thought to be within the physiological range based on concentrations of CCK found in human CSF were injected into the lateral ventricles of prepubertal pigs. There was a dose-dependent reduction in food intake, cessation of feeding appearing to be similar to normal satiety, with no effect on drinking (Parrott and Baldwin, 1981). Greater doses injected intravenously were without effect, strongly suggesting that the effect on feeding was on central mechanisms. However it has been suggested that exogenous CCK (given intravenously) causes a general malaise in the pig and thus depresses food intake non-specifically (see Chapter 4).

Sheep

Infusions of CCK-8 into the lateral ventricles of sheep at 0.01 pmol/min significantly depressed intake and ruminal motility during a 3-h period and were much more effective than a single injection (Della-Fera and Baile, 1980). There was no effect on water intake or body temperature, and increasing the time of fasting before the infusion reduced the magnitude of the effect. This experiment offers no proof of a physiological role for CCK in the central nervous control of feeding. However, continuous ventricular infusion of dibutyryl cyclic GMP (a CCK antagonist) led to a large increase in food intake in the sheep (Della-Fera *et al.*, 1981) suggesting that endogenous CCK in the brain is a natural satiety factor.

Bombesin

This brain peptide is as effective as CCK in inhibiting feeding when given into the lateral ventricle of sheep, but in rats there is considerable evidence that it induces abnormal behaviour. Injected intracerebroventricularly at doses of 1.25–5.00 µg, bombesin depressed food intake in the 17-h food-deprived young pig (Parrott and Baldwin, 1982), but the behaviour induced was not

typical of normal satiety as the pigs appeared uncomfortable and occasionally vomited. In water-deprived pigs, bombesin also inhibited drinking showing that it, like intravenously administered CCK, was non-specific in its behavioural effects.

Opioid peptides

Many peptides of the opiate family are synthesized in the brain and the existence of brain receptors for these peptides suggests that they have a physiological role. Amongst other effects the opiates have been found to stimulate feeding in rats and sheep after cerebroventricular injection. Endogenous opioids might play a role in the regulation of food intake as the opioid antagonist naloxone decreases feeding in rats and in a variety of other species ranging from the slug to the wolf. It is likely that more than one opioid receptor and more than one brain site are involved in the opioid modulation of feeding.

Resistance to the inhibitory effects of naloxone on feeding occurs when animals are eating large amounts of food per kg of body mass and/or have a high basal blood glucose concentration. This strongly suggests that, although opioids play an important role in initiating food-seeking behaviours, they are not the only food drive system. Much evidence has accumulated suggesting that stress-induced eating is driven by activation of the opioid system. Similarly, the hyperphagia associated with diabetes mellitus appears to have an opioid component.

Poultry

A stable analogue of met-enkephalin, D-ala²-methionine enkephalinamide, stimulated food intake by pullets for 30 min after 2 and 8 µg/kg were given into the cerebroventricles, but had no effect when given intravenously at 15 and 60 µg/kg (Savory *et al.*, 1989). Naloxone had no effect after either cerebroventricular (50 and 200 µg/kg) or intravenous (1 and 4 mg/kg) injection. Nalmefene, a more potent and long-lasting opioid antagonist than naloxone, inhibited feeding in a dose-related manner at doses from 0.2 to 1.6 mg. It appears that central release of endogenous opioids may reinforce feeding in birds. Further evidence of opioid release during feeding in the chicken comes from the observation that the reduction in tonic pain during feeding is reversed by naloxone (Wylie and Gentle, 1998).

Pigs

There was no effect on feeding of naloxone injected into the lateral ventricles at doses of 0.4 or 0.8 mg, 10 min after access to food was given following an overnight fast. This was attributed to the fact that the pigs were young and had been subjected to a fast, and were therefore very highly motivated to feed.

An injection of 200 μg of dynorphin (a natural endorphin) given into the lateral ventricles resulted in a meal within a few minutes (Baldwin *et al.*, 1990a). Leumorphin and α -neo-endorphin also elicited feeding but α -neo-endorphin did not. Administration after the start of a meal taken after 4 h of deprivation increased the size of that meal; 400 μg of naloxone significantly reduced intake after 4 h of deprivation and abolished the effects of dynorphin. It appears that dynorphin and related endogenous opioids might be involved in the regulation of food intake in pigs.

Feeding seems to induce an opioid-based analgesia, as the latency of tail-flick to a painful stimulus was longer after feeding than before, and this was abolished by naloxone. However, sows with marked behavioural stereotypies had shorter tail-flick latencies after feeding.

Sheep

Opioid levels are elevated in the brain of sheep after a 4-h fast, at which time the animal would be expected to be hungry, and intracerebroventricular injections of several opioids stimulate feeding. Baile *et al.* (1987), reviewing their work on involvement of opioids in feeding control in sheep, concluded that more specific agonists are needed before a full elucidation is possible.

Naloxone given intravenously prevents the feeding stimulated by cerebro-ventricular injection of enkephalamide (Bueno *et al.*, 1983). Many times more analogue were required to generate a similar effect on feeding when it was given intravenously compared with injection into the lateral ventricles, implying that the major site of action is the CNS.

Neuropeptide Y and peptide YY

The pancreatic polypeptide family consists of pancreatic polypeptide, neuropeptide Y (NPY) and peptide YY (PYY). Very low doses increase feeding in rats when injected directly into the paraventricular nucleus (PVN), the magnitude of the increased food intake following NPY injections being much greater than that seen following central administration of opioid peptides or of noradrenaline. PYY has been shown to be an even more potent stimulator of feeding in rats than is NPY, and when PYY is administered every 6 h for 48 h it causes massive hyperphagia (80.5 g/day compared with 31.1 g in the control group) and stomach distension, attesting to the fact that central factors can override the physiological satiety signals from the periphery.

Poultry

Central (lateral ventricle) administration of NPY or PYY significantly stimulates feeding in chicks, possibly as a result of stimulation of insulin secretion, and NPY immunoreactivity has been found around the area of the PVN in chickens (Keunzel and McMurtry, 1988).

Pigs

NPY has been injected into the brain of prepubertal pigs trained on an operant schedule with a fixed ratio of 5 to obtain reinforcements of 12 g of food (Parrott *et al.*, 1986). Amounts of 25–100 μ g of NPY injected into the lateral ventricles stimulated responding for food in a dose-related manner, the highest dose causing a 12-fold increase in the number of reinforcements obtained in the 30 min following injection, and reducing the latency to feed from 17.0 to 1.5 min. Both meal size and duration were increased and there were no aversive effects nor any influence on drinking.

Sheep

A 10 μ g bolus of NPY into the cerebral ventricles immediately stimulated feeding in sheep while continuous infusion slowly increased feeding, but the cumulative effect was the same as that of the bolus injection. A 3 nmol injection of NPY given intracerebroventricularly increased food intake by up to 150% over the following 30 min. This was not blocked by an α -adrenoceptor antagonist, which demonstrates that NPY does not work via an α -adrenergic pathway. NPY overcomes the intake-reducing effects of ruminal distension and VFA infusion (Miner, 1992).

Growth hormone-releasing factor (GRF; somatoliberin)

A dose of 100 ng/kg GRF given intraventricularly stimulated intake of a concentrate food by about 25% only in the first hour after injection in sheep, while with hay the stimulation of intake occurred later, from the 2nd to the 8th hours (Riviere and Bueno, 1987). With both foods this was by increased rate of eating rather than by a change in number of meals. When ten times this dose was given intravenously (the minimum dose required to stimulate feeding), cerebroventricular administration of insulin (40 mU/kg) blocked the effect. The fact that GRF is effective at a much lower dose when given into the brain rather than peripherally suggests that it is acting centrally, and the fact that its effects are blocked by insulin suggests it might be acting via growth hormone secretion, some of the metabolic effects of which are blocked by insulin.

Leptin

Leptin is a feedback factor from adipose tissue to CNS, i.e. a hormone, dealt with alongside other hormones in the previous chapter. Rather than describe here the effects of leptin administration directly into the CNS and thereby dividing the subject in two, it has been discussed in Chapter 4.

Orexins

These are a group of peptides involved in the regulation of food intake. Orexin-B stimulates food intake in pigs after intramuscular injection. ICV injection of porcine orexin-B ($0.3 \mu\text{g/kg BW}$) stimulated food intake (Sartin *et al.*, 2001). There was no effect of orexin injection on plasma free fatty acids, glucose, growth hormone or insulin concentrations, suggesting that its action was directly on the CNS centres controlling intake rather than via metabolic routes.

When this treatment was compared to or combined with NPY ($0.3 \mu\text{g/kg BW}$), they had similar effects (0.07 kg/2 h after injection for control, 0.23 kg for orexin and 0.2 kg for NPY), while the combination of NPY and orexin had a greater effect on food intake (to 0.34 kg) (see Fig. 5.3). Thus, the sum of the two separate effects was 0.29 kg , versus 0.27 kg for the combined injection, i.e. an additive effect.

Melanocortin

The recently discovered brain melanocortin receptors reduce food intake when stimulated and increase feeding when exposed to antagonists. ICV administration of a melanocortin receptor agonist suppressed food intake compared with controls for up to 72 h in growing pigs (Barb *et al.*, 2004), but an antagonist failed to stimulate intake. The authors stated that these results did not support a role for endogenous melanocortin in regulating food intake in the pig.

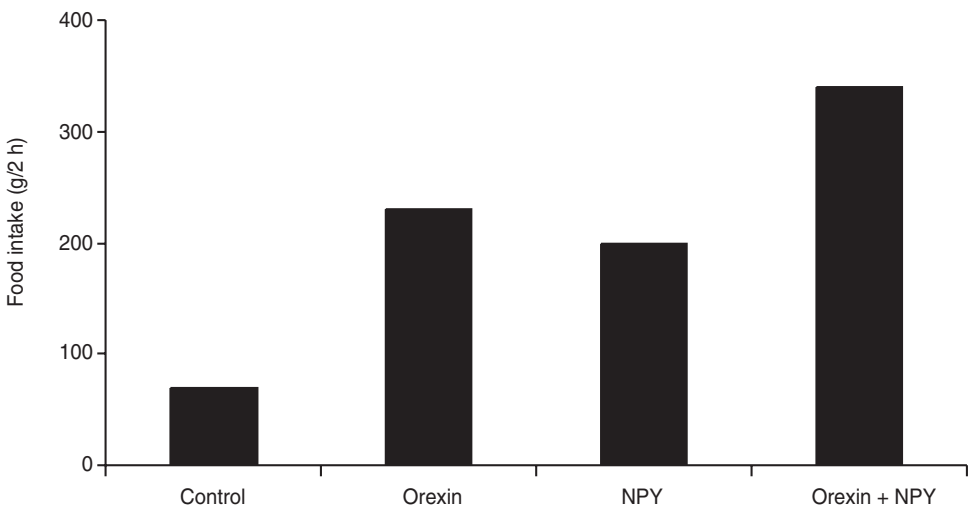


Fig. 5.3. Food intake by sheep during 2 h following ICV injection of orexin, NPY (each at $3 \mu\text{g/kg}$ body weight) or both (from Sartin *et al.*, 2001).

Steroid Hormones

Oestrogen treatment, except at very low levels, depresses food intake (see Chapter 16), and oestrogen receptors have been demonstrated in the hypothalamus. Following the demonstration that oestradiol infused intravenously into sheep and goats depresses intake, small amounts were injected into the lateral ventricles of sheep (Forbes, 1974). A low dose (10 μg) led to a 60% increase in intake of a complete pelleted food during the 2-h period after injection, with little effect on daily intake; intake was progressively lower than this maximum as the dose increased and, above 60 μg , was lower than control. The stimulating effect of 10 or 20 μg was blocked by simultaneous intraventricular injection of 1.25 or 1.88 mg progesterone.

Ionic Changes

The concentrations of several ions in the extracellular fluid are very important in controlling neural function. In laboratory animals, ionized calcium salts injected into the cerebroventricles or hypothalamus stimulate feeding, suggesting that the calcium:sodium ratio controls body weight. Plasma levels of many minerals are regulated and the fluctuations in concentration in the CSF are normally small. It is uncertain whether any of the effects of perturbing concentrations of salts in the CSF, outlined below, represent real effects that could be induced by excessive or deficient dietary intakes of minerals.

Pigs

Baldwin *et al.* (1975) injected 12.5–50.0 μmol of calcium or magnesium ions into the lateral ventricles and found that food intake was increased by both, in a dose-related manner. The maximum stimulation followed the injection of 25 μmol of calcium plus 25 μmol of magnesium, whereby food intake increased from a control level of 60 g to a staggering 950 g during the 30 min following injection.

Sheep and goats

Sheep seem to be especially sensitive to ionic changes in the CSF but, even so, changes large enough to affect feeding are probably beyond the normal range.

Solutions of calcium salts injected into the third ventricle of sheep in order to change the composition of the CSF in the region of the hypothalamus increased voluntary intake during the 30 min following injection in a dose-related manner. Magnesium had a similar effect, while both were blocked by increasing concentrations of sodium or potassium (see Fig. 5.4). Calcium or magnesium (1 μmol in 1 μl) injected into the hypothalamus also stimulated intake (Seoane *et al.*, 1975); magnesium stimulation was not blocked by pre-injection with several pharmacological blockers, whereas the calcium effect was

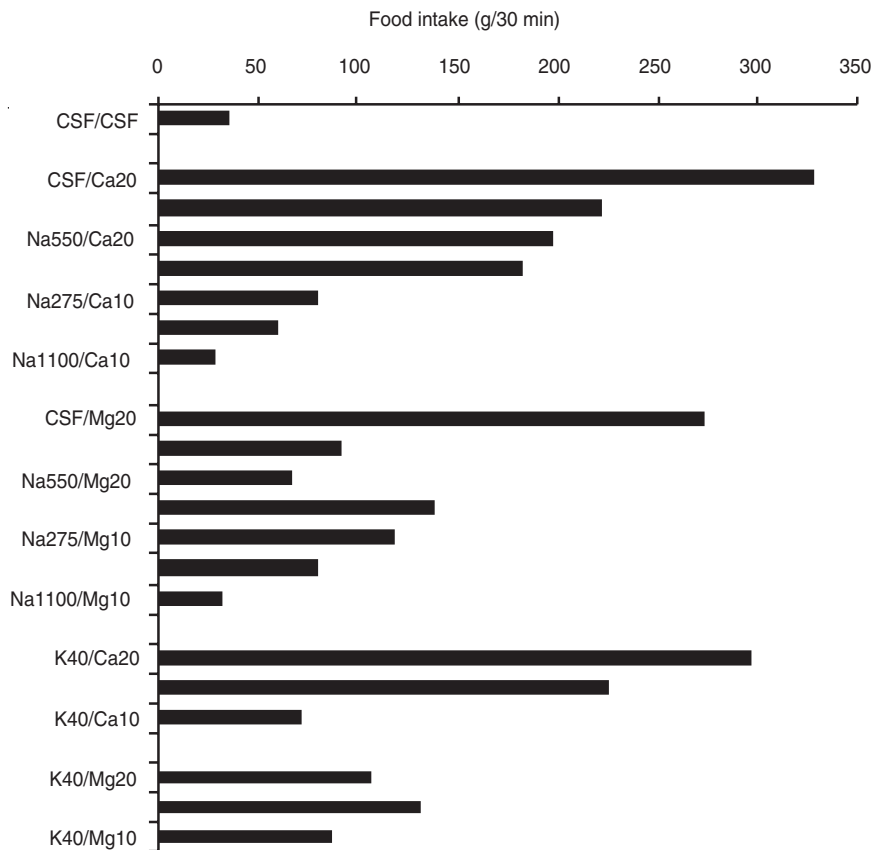


Fig. 5.4. Effects on food intake by sheep of solutions of different ionic composition injected into the third ventricle. Ca20, for example, is calcium salt at a dose of 20 mmol (from Seoane *et al.*, 1975).

blocked by atropine. The intake-stimulating effect of pentobarbital injected into the ventricles was reduced by sodium chloride (Seoane *et al.*, 1988).

ICV injections of sodium or potassium into goats suppressed feeding, whereas slow infusion of similar amounts over 30 min actually elicited feeding (Olsson, 1969). Given that CSF is produced at around 0.5 ml/min, a slow infusion would result in a very much lower concentration being achieved than would a single injection of the same amount, and it may be that very low concentrations of these ions are stimulatory.

Thermostatic Control

Brobeck (1948) said that ‘Animals eat to keep warm and quit eating to prevent hyperthermia’ and, as the anterior hypothalamus is the most important temperature sensor in the body, it would be expected that heating or cooling this part of

the brain would affect heat loss and/or production, which might then indirectly influence food intake through change in energy and nutrient requirements.

Local cooling of the preoptic area and anterior hypothalamus stimulated feeding in satiated goats (Andersson and Larsson, 1961). Even if the animal was dehydrated to the point of aphagia, or heated until rectal temperature had risen by 1°C, hypothalamic cooling induced feeding, demonstrating a direct effect. Warming the same area inhibited feeding and induced drinking; in one goat with lesions in the preoptic area food intake was normal even at supraphysiological body temperatures above 41°C.

Although these observations support the thermostatic theory as far as the goat is concerned, heating or cooling of the hypothalamus of the pig had no effect on voluntary intake (Carlisle and Ingram, 1973). In addition, hypothalamic temperature showed no increase during feeding in the goat, whether during the very large meal occurring after a 20-h fast or during force-feeding (Baile and Mayer, 1968). Infusion of acetate into the rumen, which suppressed feeding, also caused a 0.25°C reduction in hypothalamic temperature, so the acetate clearly does not act via a hyperthermic mechanism. Although pentobarbital depressed hypothalamic temperature, this occurred after the increase in feeding (see above) and was unlikely to be the mediator.

The thermostatic theory of the control of food intake is true in the sense that mammals and birds maintain a relatively constant body temperature and that heat production is proportional to the weight of food eaten; too little food will, eventually, result in a shortfall in heat production, although body reserves will normally be mobilized to prevent undue hypothermia. Overeating, on the other hand, will increase heat production, and heat loss mechanisms are activated to prevent hyperthermia. It is only under conditions where heat loss cannot increase further that voluntary intake falls to prevent hyperthermia.

Thus, intake is controlled to supply energy for heat production in addition to energy for other purposes. If further evidence of the fallibility of the thermostatic theory is needed, it can be found in the observation that the lactating animal produces more heat than the non-lactating animal and has a higher body temperature, but also eats more food.

CNS Sensitivity to Metabolites and Hormones

A question of considerable significance in the control of intake and metabolism is how the brain, which is well insulated from marked short-term fluctuations in nutrient flow, is informed of the energy status of the body. The evidence for direct effects of blood metabolites on the brain is sparse, but new hope of finding the missing link came from the observation that infusion of insulin into the lateral ventricles of baboons at physiological rates over many days causes lower food intake and body weight. Central implants of insulin-secreting cells into the base of the third ventricle (i.e. hypothalamus) depress intake. Insulin in the CSF has a much longer half-life than it does in plasma, but reflects plasma insulin in the long term. As insulin is secreted in increasing amounts with increasing fat deposition, this might be how the brain is made aware of fatness as well as nutrient status.

Parts of the brain are sensitive to the direct effects of glucose and/or insulin. Glucose-sensitive neurones in the lateral hypothalamus decrease their firing rate in the presence, locally, of glucose. These same neurones appear to be linked with glucose-sensitive receptors in the liver, as most of these neurones in the lateral hypothalamus decreased their rate of firing when glucose was infused into the hepatic portal vein.

So far as feeding is concerned, the important receptors in the brain are probably not glucose-specific, as intracerebroventricular infusions of mannose and 3-D-hydroxybutyrate (both of which can be utilized by the brain) – as well as glucose – depressed food intake in hypoglycaemic rats. Whether their effect is exerted through oxidation, as is the case in the liver (see Chapter 4), is the subject of speculation. It is not fully understood whether the brain's sensitivity to lack of glucose is called into play under normal circumstances or whether the peripheral mechanisms that normally protect the brain from fluctuations in glucose supply mean that the central mechanism for detecting glucose is called upon only in emergencies.

Although there is incontrovertible evidence that the hypothalamus is intimately involved in the control of feeding, studies of the hindbrain demonstrate that the *area postrema* and the nucleus of the solitary tract are sensitive to glucose and capable of exerting an influence on diet selection. Reciprocal connections exist between the hypothalamus and the caudal hindbrain, which presumably form part of the neural circuitry that controls feeding.

Baby rats with forebrain–hindbrain transection still suck at a normal frequency when tube-fed into the mouth. Sucrose given into the stomach of such animals depresses the amount of sucrose accepted into the mouth and CCK also suppresses intake as normal. Therefore, the caudal brainstem integrates metabolic stimuli and can perform the important function of modifying feeding behaviour according to nutrient demands.

Lack of glucose causes activation of the sympathetic nervous system, leading to release of catecholamines, glucocorticoids, growth hormone and glucagon, as well as to inhibition of insulin secretion, all of which mobilize glucose and protect the brain. Injection of insulin to increase glucose uptake by peripheral tissues, or 2-deoxy-D-glucose (2DG) to block glucose entry into cells, activates a cerebral response that results in feeding; for example, a dose of 2DG too small to have any effect when given into the general circulation causes a marked feeding response in rats when given into the cerebroventricles. Glucose-sensitive neurones have been identified in the brain, but little is known about their characteristics other than that they are probably activated by lack of glucose within the cell rather than on its surface. It might be more appropriate to talk of 'energoprivation' rather than 'glucoprivation', because D-3-hydroxybutyrate, which is used by brain cells when glucose is unavailable, prevents the feeding induced by 2DG.

Poultry

The voluntary intake of chickens was depressed by the intraventricular injection of glucose, but this was found to be true only when the birds were satiated. Implantation of gold thioglucose¹ at several sites in the brain of chickens had no effect on feeding behaviour, and it was concluded from this that there is no central nervous glucostatic control of food intake in birds (Smith and Szper, 1976).

Pigs

Parrott and Baldwin (1978) trained pigs aged 3–4 months to operant conditioning for 8 g reinforcements of food on a fixed schedule ratio of 5 and then injected 4 mmol of glucose, xylose or 2DG into the lateral ventricles. All three compounds stimulated drinking, presumably because of osmotic effects on the brain. Food intake was only stimulated by 2DG which blocks the uptake of glucose into cells, and this supports the concept of glucoprivation outlined above.

Sheep and goats

Infusion of glucose or acetate into the lateral ventricles of goats has no effect on feeding. 2DG stimulated sheep to eat more when infused into the third ventricle, but so did xylose and the results suggested an osmotic effect rather than a specific response to the 2DG (Seoane and Baile, 1972). The absence of a direct negative effect on feeding of metabolites in the brain of ruminants suggests that the various types of visceral receptors referred to in Chapter 3 are of greater importance in the control of food intake.

There is strong evidence for an effect of insulin on the CNS which is part of the system for controlling body fat content (Chapter 15). Six-day intracerebroventricular infusions of insulin at what was thought to be a physiological rate for sheep (123 ng/kg body weight/day) depressed food intake by 40% and plasma insulin to about half that of controls (Foster *et al.*, 1991). However, this treatment increased the concentration of insulin in CSF by 10 to 100-fold which suggested a supra-physiological rate of infusion. It is still not known, therefore, whether insulin transferred from the plasma to the CSF is involved in the normal control of food intake.

The Special Senses: Identification of Foods

It has become abundantly clear in recent years that animals learn to associate the sensory properties of foods with the metabolic consequences of eating those

¹ A substance taken up by, and toxic to, the VMH (at least in some strains of mouse).

foods (see Chapter 6). Nowhere is this more obvious than in the field of diet selection, to be discussed in Chapter 7. In this section we consider how foods are perceived by animals in order that they can learn about their nutritional value.

Without visual or taste cues, animals cannot identify an appropriate diet. The dominant sense differs between species but most animals can use any of their senses to identify food. Thus, although Wilcoxon *et al.* (1971) demonstrated that rats use taste more than vision as a cue for aversion to nauseating effects while quail use vision more than taste, either species is capable of using either sense.

Vision

Most domesticated animals have good visual acuity and this is used both by carnivores in hunting and herbivores in gathering herbage. Visual perception in farm animals has been reviewed by Piggins (1992).

Poultry

Newly hatched chicks initially peck at small, round (seed-like) objects but become more selective as they learn the specific visual characteristics of seeds.

Chicks possess colour vision and sometimes show a weak innate preference for food of a particular colour; we have usually observed that green food is preferred over red in naïve chicks. Preferences for other colours can be induced simply by prior exposure to them or, more specifically, by pairing them with a more balanced food given in choice with an imbalanced food of another colour (e.g. Kutlu and Forbes, 1993c), while strong colour aversions can be induced in birds by association with toxic substances (e.g. Martin *et al.*, 1977).

Sheep

Sheep are thought to be colour-blind, although their eyes do possess cones. Temporary covering of the eyes does not interfere with the preference for herbage species by grazing sheep, suggesting that they use smell, taste and tactile stimuli to a great extent to discriminate between different plant species.

Objects of different hue can be discriminated by sheep, but this may be due to brightness rather than colour; there is uncertainty as to whether they can discriminate colour. Bazely and Ensor (1989) found that none of their sheep learned to discriminate between green and yellow of the same brightness, but could differentiate between different brightnesses (41 or 77% reflectance). This does not discount the possibility that sheep have colour vision, but brightness might be important for grass as it is proportional to protein content of perennial ryegrass.

Sheep have all-round vision (290°), although acuity is only good in the 40° field where the two eyes overlap, i.e. they can see food in front of them very clearly. Sheep, like cattle, goats and chickens, can make quite complex discrimination between shapes.

Taste

Perry (1992) discusses olfaction and taste, with particular respect to farm animals, while Houpt and Wolski (1982) review studies of taste thresholds and preferences in domestic animals. The taste of food is a more proximate guide to food quality than is vision or olfaction, and is used as a powerful cue with which to associate the nutritional properties of food, especially in mammals.

A bitter taste is often associated with toxins in the food, so it is understandable that such tastes are innately disliked by many species. Sweetness, on the other hand, signals sugars, a rich source of energy, and is innately preferred by the young of most species of mammal.

Poultry

The chicken has a good sense of taste but flavours as such, although initially able to influence intake and preference, soon lose this ability if the birds learn that there is no nutritional implication of the different flavours. A line of broiler chickens selected for high lean weight had lower preference at any given concentration for dextrose, and lower aversion for quinine, compared with a low growth line (Barbato *et al.*, 1982), but it is not clear whether these differences are due to changed sensory abilities or to changed nutrient requirements.

Removing the sense of taste by cutting nerves of the mouth in the pigeon leads to loss of interest in food, although drinking and grooming are unaffected (Zeigler and Karten, 1975); clearly, in this species the taste and texture of food in the mouth is an important reinforcer of feeding.

The taste of saccharin is accepted as similar to sucrose by mammals, whereas chickens will not drink saccharin solutions but take readily to sucrose or glucose (Injidi, 1981).

Pigs

Baldwin (1976) has reviewed studies on taste preference in pigs. Young pigs are quite sensitive to taste, and their preference for glucose or sucrose solutions increases with the logarithm of concentration in aqueous solution up to 0.1 molar. The preference for saccharin solutions was not as marked and in other work was found to be very variable. Aversion can develop to tastes associated with a feeling of illness.

McLaughlin *et al.* (1983) studied weanling piglets put in a T-maze to assess preference for flavoured versus unflavoured foods. Five flavours that were well-preferred in these short tests (they did not belong to any one category as assessed by human taste) were used in sustained preference tests over 5 days, and two of these were then tested for 5 weeks after weaning and resulted in significant improvement in performance in the first week after weaning. In a large-scale growth trial with over 1200 pigs, one flavour (cheesy) increased body weight gain, but only in first week. It was concluded that some flavours might be useful in overcoming the stress of weaning.

There are other examples of intake of food by weaned pigs being stimulated by flavours, but also cases where no significant effects have been observed.

Sugar and other flavouring ingredients are widely used in weaning foods for young pigs to attract their interest in solid food and encourage high levels of intake. The fact that young pigs are aware of the flavour of the food, and that the flavour is apparently preferred when given in choice with foods of other flavours, does not necessarily mean that they will eat more when the preferred food is given alone.

Nofre *et al.* (2002) carried out two-bottle preference tests with pigs on 60 compounds, all of them perceived as sweet by humans, and related the responses to a sweet-taste receptor model at the molecular level. Of the compounds tested, 35 gave preferences, against plain water, but at concentrations many times the minimum that can be sensed by humans. From a comparison of human and pig taste responses it was concluded that there are eight differences in the amino acid composition of the sweet-taste receptors of the two species, and these are detailed by these authors.

Cattle

Cattle are sensitive to bitter, sour, salty and sweet solutions (Goatcher and Church, 1971) and are able to detect tastes with greater sensitivity than sheep.

Calves preferred a food that included 2 ppm of monosodium glutamate (MSG, a flavour enhancer) over a similar food without MSG, but it is not known whether offering only the MSG-flavoured food would result in higher intake and growth than a similar food without MSG. Preferences or aversions to bitter, sour, salty and sweet tastes can be blocked by including 5–50 ppm of MSG in the solution.

Nombekela (1994) tested the effects of various additives on the preference ranking by lactating cows of a silage:concentrate food mixture fed twice daily beginning 8 days post-partum. Taste preference ranking was: sweet (1.5% sucrose in DM) > control > bitter (1% urea) > salt (4% NaCl) > sour (1.25% HCl), and cows consumed 12.8% more DM for sweet than for the second-place (control) diet; however, the length of time for which this increase was sustained is not reported and caution is required in extrapolating from short-term preference tests to long-term voluntary intakes. In a further study, MSG was preferred equally to a control diet > molasses > dehydrated lucerne > anise.

Sheep and goats

Goats are more sensitive to bitter, sour, salty and sweet solutions than are sheep, but less than cattle, in general (Goatcher and Church, 1971).

The normal type of two-choice preference test confounds the sensory impressions of the foods or liquids offered with post-ingestive factors. Whereas Goatcher and Church (1971) found aversion to a 22 g/l solution of salt in water, by using sheep with oesophageal fistulae that could be opened when required to prevent the entry of swallowed food or drink into the digestive tract, Chapman and Grovum (1982) found a preference for hay containing up to 200 g/kg of sodium chloride, due presumably to post-absorptive effects of sodium ions in the

former case. Care must be taken in the interpretation of results from oesophageal fistulated sheep, however, as they lose much saliva through the fistula, become sodium deficient and might therefore prefer a higher concentration of sodium chloride than intact sheep. Urea was discriminated against at all levels of inclusion, from 10 to 80 g/kg.

Because of regurgitation of digesta from the rumen, it is possible that the taste of the major products of fermentation, the VFAs, might affect food preferences, as it has been demonstrated on several occasions that sheep prefer the taste of butyrate over several other compounds (e.g. Gherardi and Black, 1991). When a food containing 25 ml of 2M acetic acid/kg was offered *ad libitum* to sheep, intake was less than the intake of untreated food; addition of carbocaine, a local anaesthetic, at 500 mg/kg returned intake to control levels.

Olfaction

Olfactory ability varies widely between species, some carnivores detecting prey by smell over very long distances while other animals have a very poor sense of smell. Herbivores are often surrounded by food, in which case an ability to smell is of little use in seeking food.

Poultry

It is often said that poultry have no sense of smell because they are willing to eat grain contaminated with wild onion bulbs that other stock reject. Chickens, whether in the wild or in captivity, usually search close-by for food and identify it by sight – smell is a long-distance cue and may be of little importance to them.

Pigs

The lack of apparent effect of olfactory bulbectomy on food intake in pigs suggests that olfaction plays little part in food intake control, although it was difficult to confirm that the sense of smell had been removed, because pigs learn very quickly to locate hidden food by exploration. Presumably, however, smell is used when selecting from a range of available foods.

Cattle

Remarkably, sodium-deficient cattle can detect sodium bicarbonate at up to 20 m if assisted by wind direction, as anosmic cattle took longer than controls to identify a salt solution from amongst an array of buckets of water (Bell and Sly, 1983). It can thus be deduced that cattle can smell salt solutions, but no explanation was offered as to how non-volatile salts can have a smell. Anosmic cattle can still taste salt, clearly demonstrating that the senses of smell and taste are separate.

Sheep

There are some odours, e.g. that of carnivore faeces, that are so innately aversive to sheep that they never habituate to them and avoid them at a distance.

The internal state of an animal can influence its response to odours: Kendrick (1994) found that in pregnant ewes the firing rate of neurones in the olfactory bulb increased in response to odours of foods but not to fetal fluid odours. After parturition, however, there is very little response to food odours but large responses to lamb odours, whether from the ewe's own lamb or from an alien lamb.

Physical properties of food in the mouth

Changes in texture, temperature and taste during a meal, or even a single swallow, have been proposed as having a big impact on a food's palatability, accepting that 'palatability' depends on context, including metabolic context. Memorable foods are more easily learned with regard to their eventual metabolic properties, compared with bland foods. The concept of 'dynamic contrast' has been proposed, which refers to the manner in which foods give changing sensations during chewing and swallowing. We should consider texture, in its various manifestations, as an additional cue in characterizing a food, in conjunction with its sight, smell and taste. Memories of chewing pressures and number of chews/swallows may even help to recall how much food to eat for satiety.

Conclusions

Although lesioning studies helped to identify possible important control sites within the brain, they have been largely superseded by less invasive techniques. Finding that lesions of the ventromedial hypothalamus increase food intake and deducing that this part of the brain is the 'satiety centre' is akin to hammering a nail into a radio, observing that this causes it to emit a loud whistle, and concluding that the nail had penetrated the 'anti-whistling centre' of the radio. The organization of the brain is not in discrete centres, but in circuits, each involving millions of neurones and interacting with other circuits and with other parts of the body.

While other techniques for studying brain function in relation to feeding are less crude than lesioning, it is often difficult to decide whether what they are showing are artefacts due to the type of chemical injected, its dose or leakage into other parts of the brain. Le Magnen (1992) warned: 'It is interesting to observe that almost all compounds, intraventricularly or locally infused in either deprived or satiated animals, augmented or inhibited food intake'. Just because a substance affects feeding when injected into the brain does not mean that it plays a significant role in normal circumstances.

The variety of substances found in the brain and the diversity of sites at which exposure to these substances, their analogues and antagonists affects feeding, means that this chapter is something of a catalogue. If any conclusion can be drawn it is that the PVN seems to be of paramount importance and that NPY is of particular importance as far as transmitters are concerned.

The results of experiments involving electrical and chemical stimulation give only glimpses into what might eventually become a well-described system of connections within the brain. Up to the present time there has been little work in farm animals on the changes taking place in the brain that might be correlated with feeding behaviour. Changes have been seen in the firing rate of neurones in the lateral hypothalamus of rats in response to the carbohydrate status of their environment, and Maddison and Baldwin (1983), recording from single neurones in the brain of the conscious sheep, found responses in the lateral hypothalamus to the sight of food and in the ventrobasal thalamus to tactile stimulation of the mouth and face.

Many of the responses made by animals to food are learned (see Chapter 6), and the plasticity of the brain in the young animal means that it is possible for different neurones using different transmitter substances to be used for the same purpose in different individuals. We may be as likely to make progress in understanding the development and functioning of the CNS involvement in feeding by neural network modelling as by injecting yet more chemicals into the brain.

Tranquillizer drugs, given in the food or by injection, stimulate food intake and have been studied for their possible use as commercial intake stimulants. It is unlikely, however, that the use of such drugs will be allowed for anything other than short-term treatment under veterinary supervision.

The relative roles of the special senses in detecting food and determining whether it is safe to eat or not vary between the species under consideration. As will become clearer in Chapter 6, the important principle is that animals learn to associate one or more sensory properties of foods with pleasant or unpleasant metabolic consequences when foods with these same or similar sensory properties have been eaten previously.

6

Learning about Food: Conditioned Preferences and Aversions

There can be no doubt that learning to associate the sensory properties of a food with the metabolic consequences of eating that food is central to animals' ability to make sensible choices between foods. It will become obvious that there is no clear demarcation between the contents of this chapter and those of the subsequent one on diet selection (Chapter 7). In principle, the evidence presented in the current chapter is based on learned preferences for foods demonstrated in short-term tests, whereas in the subsequent discussion of diet selection, the extent to which animals show consistent choices over more than a few days is covered. We will discuss in Chapter 10 the likelihood that this learning also underlies the control of intake of a single food.

Animals are born with innate preferences and aversions to particular foods, but these cannot be relied on for the rest of their life. For example, a food that has been tasted once or twice in the spring and has been found to be bitter might, by the summer, have become sweet; it might have changed from toxic to nutritious or vice versa. Therefore, an animal ought to be able to benefit from prior experience to be able to best exploit its environment, and evolution has seen the development of this ability – indeed, it might be said that such capability accompanied the origin of the chemical and visual senses – but also to be flexible and to be able to relearn the associations when necessary.

The previous chapter has shown that animals can identify foods by means of all the special senses. Because of the taste acuity of mammals and the ease of adding flavours to most types of food, much of the research in this area has been done using flavoured foods. For poultry, however, where vision seems to be more important as a means of identifying food, much of the research has used food colour as a cue.

There are other important methodological considerations in conducting research on how and when animals learn about food. In particular, it is necessary to separate the unconditioned stimulus (US) from the conditioning

stimulus (CS) (food and bell, respectively, in the case of Pavlov's dogs) if the interpretation of the results is to be unequivocal. While there is not space, nor is it necessary to go into experimental detail in every case given, the methods of Arsenos and Kyriazakis (1999) are given in detail below in the section on 'Continuum from Preference to Aversion' as an example of good methodology.

Motivation

Eating is continuous in very simple animals and the drive to eat is very primitive and powerful. It seems likely that higher animals have inherited this drive but that satiating factors have developed to temporarily override it. Sham feeding, in which the ingested food leaves the digestive tract via an oesophageal fistula before any gastric, intestinal or metabolic effects have occurred, is continuous in rats that have always been fed by gastric tube and have not learnt to associate the act of eating with eventual satiety. This is in contrast to the results of other studies in which animals with gastric fistulae were sometimes fed with the fistula closed so that they learned to stop eating after a certain amount of food had been eaten.

Motivation is a reversible brain state induced by internal and external signals, which results in an increased tendency to perform a specific behaviour. The tendency to seek food can be of similar intensity whether due to high level of hunger in the absence of food or low hunger in the presence of food. As an animal can normally perform only one behaviour at a time, there must be a decision-making process to determine which activity the animal does at any given time. Models based simply on motivation to eat, declining as ingestion takes place, result in dithering output as the animal switches from one activity to another and back again. If a positive feedback is introduced, then some semblance of real behaviour is seen. That is, feeding, once started, tends to reinforce itself until such time as satiating factors become dominant.

Learning can modulate the expression of motivational state. Animals are sensitive to a number of nutrients and can make appropriate choices, according to how they feel. Therefore, if a food is deficient or imbalanced in one or more essential nutrients, the animal is malnourished and feels ill, which influences how much it eats. No animal offered a single food is likely to have its requirements met exactly by the food for more than a very short part of its life, so an imbalanced diet is the norm for animals provided with a single food.

Non-primate species should not have their intelligence judged on the basis of their ability to form artificial associations between objects and rewards. Work on imprinting in chicks shows that natural stimuli are more effective than artificial ones. In general, farm animals do not perform well on complex learning tasks involving the making of artificial associations, but have no difficulty learning complex information about the natural environment.

There are connections between the hypothalamus and the caudal hindbrain that form part of the neural circuitry that controls feeding. The medial forebrain bundle, coursing between the fore- and hindbrain through the lateral hypothalamus, carries largely subconscious information that contributes

to the animal's knowledge, but not necessarily awareness, of the consequences of eating particular foods. This information is integrated with awareness of foods gained by the special senses and committed to memory to serve the animal when it next has to make decisions about how much, or what, food to eat. Of particular importance in the hindbrain is the *area postrema* (AP), which possesses chemoreceptors. Destruction of the AP prevents the development of conditioned taste aversions (CTA) to a variety of toxic agents.

Awareness of digestive and metabolic sensations

Once a bite of food has been swallowed there are few conscious sensations of food passing through the digestive tract and being processed, unless the food contains toxins or induces excessive distension. Nevertheless, information concerning both physical and chemical changes in various parts of the digestive tract is transmitted to the central nervous system (CNS) via the autonomic nervous system and in the circulating blood. There is no compelling reason why learning or cognitive abilities require awareness (Nicol, 1996).

For example, ruminant animals have mechano- and chemoreceptors in the rumen and reticulum with afferent pathways in the vagus nerve (see Chapter 3). There is a clear relationship between the degree of stimulation of a family of receptors by inflation of a balloon, or infusion of salts of volatile fatty acids into the rumen, and the increase in firing rate in vagal fibres leading to the hindbrain, particularly the nucleus of the solitary tract. This, in turn, is correlated with the depression in food intake. Thus, the CNS is informed, normally subconsciously, of the consequences of eating in terms of physical and chemical effects on the digestive tract, and uses this information in how it responds when it again becomes aware of the food, i.e. what food it chooses to eat and how much it eats.

The liver is the first organ to have a reasonably complete picture of the results of eating a particular food, in terms of supply of metabolites. Evidence for neural transmission of metabolic information from liver to CNS is extensive, and it is clear that the brain uses the degree to which substrates are being oxidized as part of the complex control of food choice and intake (see Chapter 4). A major function of the liver is to stabilize the fluctuating supply of nutrients arriving from the digestive tract as a result of eating discrete meals into a more even supply of nutrients to the rest of the body, particularly the CNS. Thus, the brain is informed by the liver of the balance between the supply of nutrients from the gut and the demand for nutrients by the rest of the body.

Measuring motivation – operant conditioning

Rewards of food are powerful, unconditioned stimuli in an operant-conditioning situation, i.e. one in which the animal has to respond (e.g. by pressing a button) in order to elicit a reward (technically known as a reinforcement, e.g. the

delivery of a portion of food). Animals quickly learn to respond, and the bigger the reinforcement the more quickly is the association learned.

When animals are trained to press a bar to obtain food and the number of presses required to initiate a meal is varied, increasing the effort required to start a meal causes a reduction in the number of meals, but an increased meal size so as to maintain total intake and body weight (see Chapter 2). This shows that feeding is not dependent simply on short-term changes in the supply of metabolites and must involve the interaction of numerous factors.

Once animals are accustomed to working for their food they like to do so; ostriches trained to respond for food prefer to peck at a button for food than to obtain it 'free'. When a bag was accidentally dropped in the pen, they ate only a little of the spilled food and then returned to the operant dispenser.

Poultry

In laying hens, daily food intake stayed the same up to a fixed ratio of reinforcements:responses of 160 (FR160) (Fig. 2.6), but the total time spent feeding and meal frequency were negatively related to FR, while inter-meal interval, meal size and rate of eating within meals were positively related to FR. It appeared that randomness in meal taking declined at higher FRs, and FR20 seems the most appropriate to use in experiments in which it is desired to get birds to eat only when they feel hungry.

Pre- and postprandial correlations are generally higher when animals have to expend some energy to get food. As the cost rose from 1 to 5000 pecks to gain access, so the number of meals fell from about 20 to 1/day, and meal size rose from being very small to > 200 g (Kaufman and Collier, 1983). Daily food intake remained approximately constant up to about 500 pecks/meal, but rate of eating increased more or less continuously with FR. Unfortunately, there was confounding between the FR imposed and the age/weight of birds, so the observed reduction in daily intake at higher ratios might just have been due to a slowing of growth as birds were about 3 kg at this stage, at which point they were growing only slowly.

When hens trained to push a weighted door to get food were deprived of food for 12 h, they took significantly longer to gain access to food by applying the required force \times time than when deprived for 43 h, due to longer pauses between attempts to open the door. It is not necessary to construct special equipment in order to quantify animals' motivation to eat. For example, Petherick *et al.* (1992) trained hens to run down a 14.4 m alley for food. The speed with which they ran was significantly increased by deprivation of ≥ 6 h (0.29, 0.62, 0.65, 0.57 m/sec for deprivation periods of 0, 6, 12 or 18 h, respectively).

The speed with which chicks approached food was also used by Hannah (2001) in studies of motivation to eat foods made moderately (M) or highly (H) imbalanced by dilution with wheat, colouring and quinine being added as cues and compared with unadulterated food (C) given a different colour (but no quinine). During the first phase of the experiment, from 17–32 days of age, they were fasted for 1 h and given the test food for 2 h daily; for the rest of the time untreated food was available *ad libitum*. On days 26 and 33 each bird's

motivation was tested individually by recording the time taken to attack the test food to which it had been trained.

During the second period of the experiment, the training and testing procedures continued but the test food was either kept the same or changed to a moderately toxic food, as shown in Fig. 6.1, in order to study the duration and extent of the adjustment in motivation. The results show very clearly the reduction in motivation (increase in 'attack' time) of the chicks given toxic test food compared with those given the control food. By 4 days after the test food having been changed there were clear changes in motivation, which had stabilized some 10 days after the change. This demonstrates very clearly the learning and relearning involved, the latter taking only a few days in these young chicks.

In this and many other similar studies, including operant conditioning, birds have been fasted for short periods in order to increase their motivation to eat. This creates an abnormal situation, mildly stressful, and adds significantly to the time taken to perform the experiments. It has been shown that maggots are highly attractive to hens, who show great motivation to eat them even without prior fasting, and it has been suggested that they could be used as test foods for poultry (Bruce *et al.*, 2003).

Pigs

Sows, fed at a commercial level of 2.3 kg/day, were trained to lift a lever to obtain reinforcements of 2.7 g of food on a 10:1 FR. After 1 h of responding, the FR was raised to 20, and so on. Extinction (failure to respond sufficiently to obtain a reinforcement) occurred at ratios which varied from 70:1 to 430:1 for different

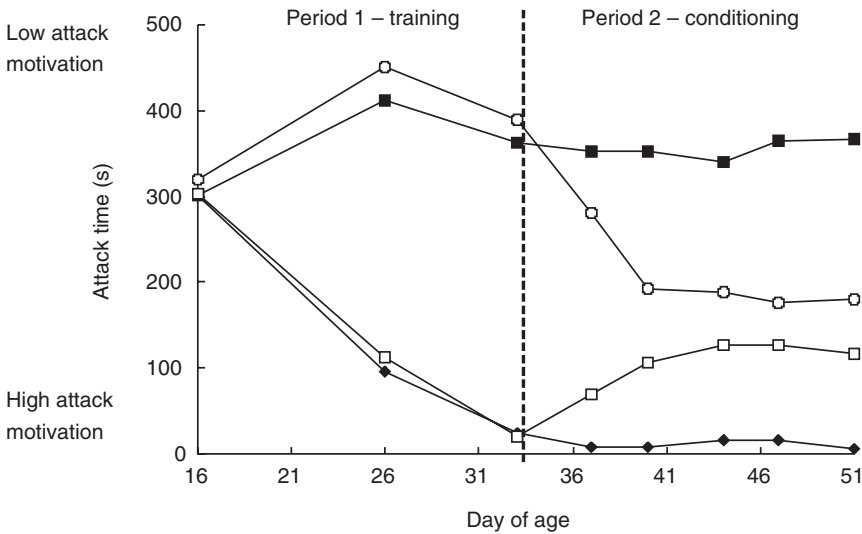


Fig. 6.1. Attack times for each treatment group: ■ HH, ◆ CC, ○ HM, □ CM. C, control test food; M, moderately; H, highly toxic test food. Vertical dotted line shows where the foods were changed (see text for details) (from Hannah, 2001).

sows. For high FRs, it was estimated that the energy cost of responding was greater than the benefit gained from the food. Sows trained to lift a lever to obtain straw, twigs, nothing or a portion of food responded for food, most frequently (Hutson, 1992).

Specific nutritional deficits or general nutrient restriction will increase hunger and the motivation of the animal to ingest food (Lawrence *et al.*, 1993). Jensen *et al.* (1993) found that individually housed, protein-deficient, growing pigs increased their general activity relative to those animals offered a diet excessive in protein or to those offered a choice between the two foods. Food-restricted (ad libitum – 20%) pigs spend less time lying than pigs fed ad libitum. They also rooted the straw substrate significantly more.

In group-housed situations, pigs may redirect their behaviour towards penmates as alternative foraging stimuli and hence increase the chance of injuries through excessive abnormal behaviour. Pigs with an inadequate dietary protein supply tend to have an enhanced attraction for blood. It is not known whether the inadequate protein nutrition predisposed the animal's attraction specifically for blood or would have been similar for other protein-rich substances. Thus it is proposed that, if animals are allowed a choice of balanced foods such that they can select a diet to meet their requirements, they can satisfy their motivation to ingest food.

Sheep

Sheep can quite easily be trained to respond for food (Kilgour *et al.*, 1990).

Learning

Selection of a food may be euphagic, i.e. implying nutritional wisdom or hedonistic, i.e. selection for pleasurable flavour. Because there will be some food items that have an innately pleasant appearance or flavour but are nutritionally inadequate or even toxic, animals should not rely solely on inborn preferences to determine their food choice. Rather, they should sample a range of foods and, when they have learned which ones are nutritious, eat predominantly from those while sampling other foods occasionally to take advantage of any nutritious foods that may become newly available – a food that is toxic now might not continue to be so in the future.

With a few notable exceptions, there is no reason to believe that nutritional wisdom occurs because animals can directly taste or smell either nutrients or toxins in foods. There is, rather, compelling evidence that animals learn to associate taste, smell and/or visual appearance with the consequences of food ingestion, and this affects food selection and intake. Animals acquire preferences for foods that cause satiety and aversions to foods that cause malaise. Increasing excess or deficiency of a toxin or nutrient will lead to an increasing tendency for the animal to correct the imbalance.

There are toxin receptors in the hindbrain, and consciousness is not necessary for toxins to affect the animal's response to the taste of a food.

Neophobia

When a new food is available, the animal has only its instincts to guide it; as we have already seen, this might not give it a good prediction of what will happen when the food has been ingested. Animals are initially cautious on being offered a food with a novel flavour, e.g. 'bait-shyness' in wild rats. This is advantageous in evolutionary terms, even if the nutritive value of the food has not changed, as it is mainly by taste and smell that the animal recognizes the food. When, by taking small amounts of the food, the animal learns that it is safe, then normal rates of intake can be resumed. Abrupt weaning, such as usually carried out in intensive animal husbandry, challenges the young animal by removing the familiar food and forcing it to assess novel food and to drink water for the first time. The weanling is clearly *aware* of its changed circumstances, conscious of its hunger, but innately cautious in its acceptance of novel foods.

Learned Aversions

It is known that when an unpleasant metabolic experience occurs around the time a novel food has been eaten, this food becomes aversive. For example, injections of lithium chloride, known to induce nauseous feelings, when paired with red food, induce aversion for that colour by chickens.

There are several unusual features concerning the conditioned aversion to food paired with abdominal discomfort: (i) the aversion can develop after a single trial; (ii) it can occur even though there may be a long delay (several hours) between the unconditioned stimulus (US) and conditioned stimulus (CS), making this learning different in character from Pavlovian association, in which US and CS must be presented almost simultaneously; and (iii) tastes are much more effective than visual or aural cues, at least in mammals. Even animals under the influence of an anaesthetic when a painful stimulus (US) is given learn to associate it with the food available when they are regaining consciousness (CS). It is important for food to be novel, with a strong taste and/or odour, and these characteristics are often associated with high-protein foods.

As an example of the methodology used in studies of the development of conditioned aversions, research with CCK and coloured foods for chicks is presented. CCK, produced in the duodenum and proposed as a satiety hormone (see Chapter 4), has been shown to condition an aversion to coloured food. CCK given intraperitoneally (i.p.) is known to depress food intake, and the aim of studies by Covasa and Forbes (1994b) was to determine whether this reduction was due to a pleasantly satiating effect or an unpleasantly nauseating effect of CCK.

On days 1, 4 and 7, one-half of the birds were injected with 100 µg CCK i.p., sufficient to depress intake by about 20% over the next 2 h; for 2 h after the injection the normal food was replaced with food of the same composition, but coloured green for one-quarter of the birds and red for the other quarter.

The other half were injected with saline and, again, one-quarter given green food and one-quarter red for the next 2 h. On days 2, 5 and 8, each bird was given the alternate injection with the alternate colour and on days 3, 6 and 9 were made mildly hungry by fasting for 1 h and then individually given a choice between green and red food.

The colour approached was noted and, as shown in Fig. 6.2, they became progressively averse to the colour of food associated with CCK – it is clear that the effects of the hormone are unpleasant and that the birds had become conditioned to believe that their discomfort was due to food of a particular colour – the identity of the colour is not important. For the next 11 days, no injections were made but the preference test was repeated from time to time – the aversion was lost within a few days. Then, from day 26, injections were paired with the opposite colours to those used in the first phase of the experiment and aversion rapidly developed, again followed by return to no preference within a few days of stopping the injections. Thus, colour preference can be easily manipulated and the same is true for the association between food flavour and the consequences of eating, which is more readily evident in mammals.

It is known that the intake depression caused by giving CCK i.p. can be prevented by section of the vagal nerves (i.e. CCK stimulates abdominal receptors that transmit information to the CNS via the vagal pathway, Chapter 4) and, when the above experiment was repeated with chickens vagotomized at the level of the proventriculus, no significant colour preferences or aversions became established.

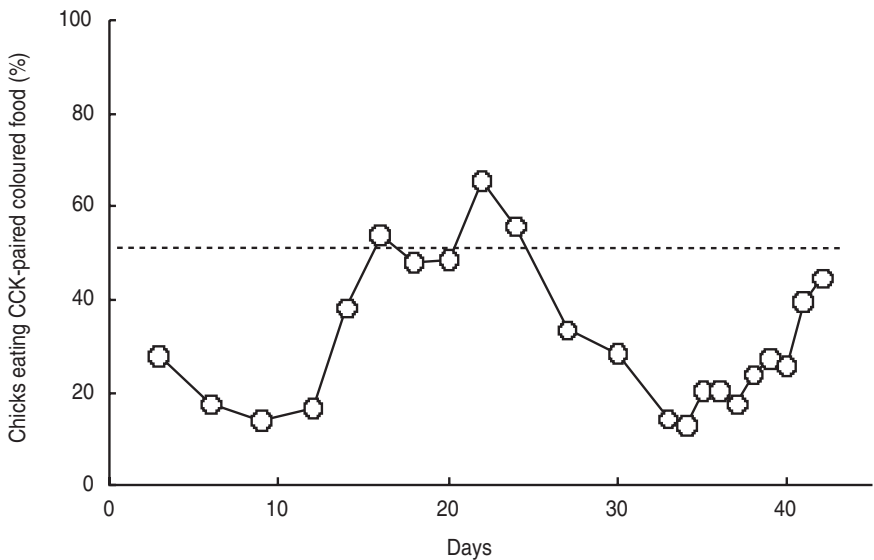


Fig. 6.2. Percentage of chicks favouring the colour of food associated with CCK injection; dotted line, 50% (see text for explanation) (from Covasa and Forbes, 1994b).

Unnatural toxins

Lithium chloride (LiCl) has been widely used as US in studies of conditioned aversions. It has approximately the same effects in various species on a per-body weight basis and is effective when given either enterally or parenterally.

Poultry

Hayne *et al.* (1996) studied aversion learning and retention in chicks whose drinking water was coloured blue and adulterated with LiCl for a period of 24 h. The chicks self-administered large and often lethal doses of the LiCl solution but subsequently avoided blue water during two-bottle preference tests administered 3–7 days, but not 14 days, after exposure. Surprisingly, neophobia alone was insufficient to prevent non-deprived chicks from ingesting large quantities of a toxin during their initial encounter with it. On the other hand, those that survived had learned to avoid the colour associated with toxic consequences although this had been forgotten 1–2 weeks later.

Pigs

It appears that no studies with LiCl have been made in pigs!

Cattle

Pfister (2000) used LiCl to induce aversion to toxic pine needles, and the work of Cibils *et al.* (2004) is another example in which the ability to associate stimulation of the external skin-defence system with the internal gut-defence system was tested. Young cattle made averse to high-quality foods by means of electric shocks were not put off from eating these foods when they were in 'safe' locations, whereas they avoided foods rendered aversive by means of LiCl irrespective of location. It can be concluded that non-food features of the environment are not used as CS for food aversions, a conclusion also reached by J. Catterall and J.M. Forbes (unpublished observations), who paired solid floor (preferred) or wire mesh (avoided) with different coloured foods and found no aversion to the mesh-paired colour of food.

Sheep

The rumen, by storing food for several hours, may act as a buffer between eating a meal and experiencing its metabolic consequences and thereby reduce the chance of a toxin being associated with its originating food. Alternatively, the rumen may assist learning by prolonging the time over which a toxin from a particular meal is available to the host animal. Presumably because of their large size and high cost of carrying out research with cattle, most of the studies on ruminants have been carried out with sheep.

Sheep find LiCl, injected or in the food, to be unpleasant and the degree of learned taste aversion varies closely with the dose. Strong aversion was shown with injection of 150 mg/kg, similar to the dose causing strong aversion in rats.

Feeding neophobia was also increased in proportion to the last dose of LiCl used. When sheep and goats were given 2% LiCl in food, they ate a maximum of around 39 mg/kg body weight for sheep and 27 mg/kg for goats, levels not much higher than those causing mild discomfort in humans.

Lambs made averse to a novel food by means of LiCl persisted in avoiding this novel food, even when not adulterated, but gradually this aversion wore off (Burritt and Provenza, 1996). However, when at a later date they were given the novel food together with another novel food adulterated with LiCl, they subsequently avoided the original novel food at first, demonstrating a memory for the effects of LiCl. In a second experiment, lambs were offered a novel food for either 28, 14, 7 or 1 day, followed by a single exposure to LiCl. The longer the lambs had experienced this food, and become convinced that it was safe, the less persistent the aversion.

Sheep can clearly detect different concentrations of a flavour and prefer a lower concentration of a flavour associated with the unpleasant consequences of LiCl administration. Lambs offered food with a medium concentration of LiCl after being offered a high-LiCl food increased their intake, while those previously on a low-LiCl food decreased their intake when given the medium-LiCl food; the influence of either US (LiCl) or CS (flavour) on preferences and intake is, therefore, relative rather than absolute.

Naturally occurring toxins

Oxalic acid is a mild toxin found in some materials used as animal feed, such as the leaves of many root crops. Conditioned taste aversions have been induced in sheep that persisted for up to 60 days after the last dose of oxalic acid (Kyriazakis *et al.*, 1997). The rate of development and severity of the aversion were dependent on the rate of administration of oxalic acid, developing after as little as one exposure to a very high dose but requiring many exposures to low doses (Kyriazakis *et al.*, 1998). These findings show that it is not only powerful unnatural toxins that aversions are developed, but to substances that are found in the diet and are only mildly toxic at natural concentrations.

Excess of nutrients

Not only do substances that are overtly toxic act as US in conditioned aversion, but even essential nutrients can depress intake and preference when their supply to the animal exceeds the animal's needs. Sheep prefer a straw of a flavour associated with the provision of NaCl until their requirements are met, then they find this same flavour aversive; a similar situation applies to sulphur. These and other appetites are described and discussed in Chapters 8 and 13.

There is a large and significant literature on learned preferences and aversions to the protein:energy ratio of foods, and this is discussed below in the section on 'Continuum from Preference to Aversion' and in Chapters 7 and 8.

Distension of the digestive tract

We have seen above that animals prefer foods, or flavours associated with foods, that provide adequate amounts of nutrients. Foods high in fibre and therefore occupying a lot of space in the stomach might be expected to generate aversion, as it has been shown that gut distension in rats conditions an aversion to the paired taste (Bardos, 2001). In pigs, feeding motivation is inversely proportional to the bulkiness (measured as water-holding capacity) of iso-energetic meals (Day *et al.*, 1996b).

In the only relevant study in ruminants, non-lactating cows had a balloon in the rumen inflated with 12 l of water for 2 h, immediately after which each was given 500 g of either unflavoured or citrus-flavoured concentrate food (Klaiss and Forbes, 1999). This was repeated on the following 2 days and for a further 3 days when the treatments (\pm balloon, \pm flavour) were reversed. The following day, a preference test was administered in which 500 g of flavoured and 500 g of unflavoured concentrate were given at different ends of the food trough and the times at which each animal changed from one food to the other were noted. For the next 6 days, the training was continued by alternating the treatments (\pm balloon), still associated with the same flavour as before, on alternate days, followed by another preference test.

No significant preferences were observed, for which the authors gave three possible reasons: (i) the cows could not differentiate between the flavoured and unflavoured foods. This is highly unlikely, as the citrus flavour was easily recognized by humans and the concentration used was greater than that of a similar citrus flavour that was clearly distinguished by cows; and (ii) the distension of the rumen caused neither pleasant nor unpleasant sensations. This seems unlikely because such distension depresses intake of forage and the balloon was added to a rumen that was already fairly full; or (iii) filling the balloon just before, rather than just after, giving the flavoured/unflavoured concentrate. While animals associate unpleasant stimuli applied from a few seconds to several hours *after* eating a distinctively flavoured food, application of the CS (in this case balloon inflation) *before* exposure to the US (in this case the flavoured food) might not condition the association. The reason for inflating the balloon before the concentrate meal was to avoid the disturbance associated with inflation coinciding with the critical time just after exposure to the US – the eating of flavoured or unflavoured food.

Conditioned Preferences

Sources of energy

Infusions of starch into the rumen, to provide 2.5–9.4% of daily DE intake, causes preference for the flavour of food given at the time of the infusions, which lasts up to 8 weeks after infusions have stopped (Villalba and Provenza, 1997c). The fermentation of starch in the rumen is predominantly to propionate, and this VFA is required for the synthesis of glucose, which is often

in short supply in the forage-fed ruminant. Infusion of propionate into the rumen also induced a preference for the flavour of food given with the infusion, even though the propionate supplied was equivalent to no more than 1.4% of the daily ME intake (Villalba and Provenza, 1996). This preference was induced by the propionate rather than by the sodium or osmolality of the infusions.

Other conditioned preferences have been demonstrated but, as these are included in the following section, they will not be referred to here.

Continuum from Preference to Aversion

Examples of aversions and preferences to stimuli paired with administration of nutrients have been given in the preceding sections. In some cases the difference between preference and aversion is one of dose – small amounts of a nutrient given to an animal deficient in that nutrient are likely to generate a learned preference for the paired stimulus (e.g. flavour of novel food), while amounts given in excess of requirements will generally cause an aversion. It can be envisaged, therefore, that given the opportunity, an animal will eat increasing amounts of a food that supplies a needed material until its need is met (or even exceeded), at which point it will limit its intake of that food in order to obtain an amount of the material that meets its requirements – there is a continuum of effect as the dose provided is increased, from preference through aversion. We now provide examples of such continua.

The first example is given in some detail as an illustration of the methodology of this type of research. Arsenos and Kyriazakis (1999) have demonstrated a continuum between conditioned preferences and aversions in sheep to flavoured foods associated with doses of casein from 9, 17, 35 and 53 g given by gavage. Growing sheep were maintained on a protein-deficient basal diet containing 9.5 g CP/kg. A test food containing 393 g CP/kg was prepared, with either orange or aniseed flavouring. Twice a day on days 1, 2, 5 and 6 of an 8-day period, each lamb was given a particular dose of casein by stomach tube and offered one of the flavoured test foods, or the other flavour of test food with water given into the stomach. Flavour order and association with dose of casein were completely randomized within each casein dose. On the 8th day, both flavoured test foods were offered simultaneously for 40 min to monitor the degree of preference. This procedure was repeated three times after which, without further conditioning, preference tests were performed 7, 21 and 35 days later to investigate the persistence of preferences or aversions in the absence of reinforcement. The results are given in Fig. 6.3.

No preferences or aversions were apparent after the first conditioning period (preference ratios (PR) not different from 0.5), but subsequently the lower two doses led to conditioned flavour preferences ($PR \geq 0.7$), presumably because they alleviated a deficiency of N, while the higher two doses led to conditioned flavour aversions ($PR < 0.4$ and much less with the highest dose of casein), presumably being sensed as toxic overdoses.

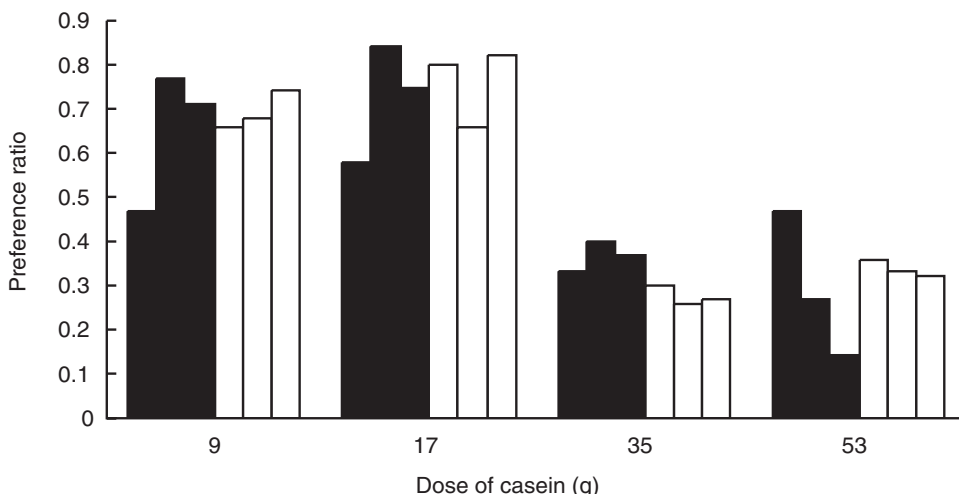


Fig. 6.3. Preference for flavour associated with administration of casein into the rumen on first, second and third test during conditioning (solid bars), for doses of casein from 9 to 53 g, and 7, 21 and 35 days post-conditioning (open bars) (from Arsenos and Kyriazakis, 1999).

The preference tests carried out after cessation of conditioning showed no significant diminution in the preferences or aversions observed immediately after conditioning, demonstrating strong persistence. The authors observe that the existence of a continuum of flavour preferences and aversions created by different amounts of the same nutrient source could be the basis of how ruminants select a diet that meets their nutrient requirement at a particular point in time. The concept of an optimum rate of intake of a nutrient for a particular animal is utilized in the MTD hypothesis described in Chapter 10.

In a similar experiment in which different doses of urea were paired with different food flavours, a low dose (0.12 g N/day) led to preferences, while a higher dose (0.23 g) produced aversion; in a second experiment, doses of 0.23 and 0.46 g N gave preferences for the paired flavour of food while the highest dose of 0.92 g N led to aversion (Villalba and Provenza, 1997b). The difference between the thresholds in the two experiments is probably related to the different basal diets between the experiments.

Energy-yielding nutrients have also been shown to cause flavour-associated aversions or preferences, depending on the dose of US administered. Propionate given at 4% of daily DE intake engendered a preference, while at 12% it produced an aversion to the flavours paired with the administration of propionate (Villalba and Provenza, 1997a).

Thus a food that the animal is conditioned to believe alleviates a deficiency becomes preferred over other foods, while one thought to be excessive in the same nutrient becomes aversive. Under natural conditions such responses would lead to 'nutritional wisdom', i.e. eating a mixture of foods that most closely meets the animal's nutrient requirements.

Trade-offs and Interactions

Whenever a food contains a toxin, an animal offered this food alone has to trade off the consequences of reducing its daily intake, thereby escaping the full effects of the toxin and suffering a lack of nutrients (bearing in mind that, in general, the only difference between a toxin and a nutrient is the concentration of the substance in the diet).

Interactions between nutrients

The ratio of VFAs administered can influence the degree of preference or aversion generated. The preference by straw-fed lambs for the associated flavoured food was greater when the ratio of acetate:propionate in the infusate was 55:45 than when it was 75:25 (Villalba and Provenza, 1997a). It is likely that sheep on the straw diet would be deficient in glucose due to low rates of production of propionate in the rumen, and this would be alleviated more effectively by the mixture with the higher proportion of propionate.

Lambs prefer a poorly nutritious flavoured food eaten during, and shortly after, an intra-ruminal infusion of energy or protein. Preloads of casein decrease preferences for flavours previously paired with casein and increase preferences for flavours paired with starch, while preloads of energy have the opposite effect. These animals can, therefore, discriminate between the post-ingestive effects of energy and protein and associate the effects with food flavours in order to regulate macronutrient ingestion.

It has been proposed that certain types of diet provide imbalances between energy and protein supply at different times of day, even though they may be balanced overall. Kyriazakis and Oldham (1997) set out to test whether such asynchrony of nutrient supply would influence diet selection, relative to a food designed to provide the same nutrient supply in a synchronous manner. Foods were formulated to provide rapidly or slowly fermentable energy with high or low ruminal degradable protein (RDP) – all foods had the same calculated contents of metabolizable energy and metabolizable protein. When choices were offered, the proportion of the low-RDP food in the selected diet was lower when the carbohydrate source was rapidly rather than slowly fermentable, which is consistent with the hypothesis that ruminants learn to select a mixture of foods that minimize metabolic imbalance.

There is thus accumulating evidence that ruminants prefer to avoid a food with an adequate nutrient balance overall that delivers different nutrients at different rates and results in temporary imbalances.

Interactions of nutrients with toxins

Animals on a high plane of nutrition are better able to withstand toxins than underfed animals. Sheep are able to eat more LiCl when on a diet high in energy and more of several toxins when on a diet high in energy and protein

(Villalba and Provenza, 2005). Presumably the higher rate of metabolism on a higher level of nutrient intake enables a faster rate of detoxification.

Conversely, dosing with toxins (terpenes, nitrates, tannins or LiCl) has caused sheep to select a diet with a higher protein:energy ratio, while treatment with cyanide causes a decrease in the protein:energy of the diet selected. Thus, there is no common response to different toxins; rather, they vary on a toxin-by-toxin basis depending on physiological state.

It sometimes happens that the plants with the highest yield of digestible nutrients are those containing toxins, and grazing animals must trade nutrients off against toxins. Deer offered pairs of foods with different ratios of phenolic toxin to digestible energy eat high-energy foods when these are low in phenolics, but low-energy foods when the high-energy ones are high in phenolics. Similarly, goats eat more low-digestibility blackbrush twigs when the high-digestibility twigs are high in toxin, and lambs prefer foods lower in readily available carbohydrate when a high-energy food has tannin added to it (Titus *et al.*, 2000). Given PEG, which neutralizes tannin, these lambs moved their preferences to lower-energy foods to a significantly lesser extent after tannin levels were increased than those which did not receive the PEG supplement.

In most studies of conditioned preferences and aversions, access to test foods has been given one at a time, giving plenty of opportunity for animals to learn the association between each US and its attendant CS. In nature, animals are confronted with many different plants at the same time, and Duncan and Young (2002) studied the ability of goats to learn about foods when multiple foods were available simultaneously. Different conifer species were offered on separate days and animals were dosed with LiCl (20 mg/g DM foliage consumed) as a negative stimulus, sodium propionate (90 mg/g DM foliage consumed) as a positive stimulus or sodium chloride (54 mg/g DM foliage consumed) as a neutral stimulus. The goats were able to learn the associations and adjusted their diet selection accordingly (see Fig. 6.4a). However, when a different set of animals was given all three test foods and all three associated US simultaneously during the learning phase of the experiment, the animals took a mixed diet (see Fig. 6.4b), thereby reducing their chances of learning the associations. The authors state that: '... caution is required in extrapolating results of artificial conditioning experiments to free-ranging herbivores'.

Lambs given two foods containing different toxins (tannins, terpenes or oxalates) ate more food in total than when given only one of the foods; those offered three foods, one containing each toxin, ate even more as the intake of each individual toxin was lower than when only one of the foods was on offer (Villalba *et al.*, 2004). This improvement is likely to arise only when the different toxins are detoxified by different mechanisms. The experience of eating these foods enhances total intake when such choices are given up to 8 months later, and emphasizes the importance of carrying out research with more than one toxin at a time and of considering the long-term as well as the short-term responses to such choices.

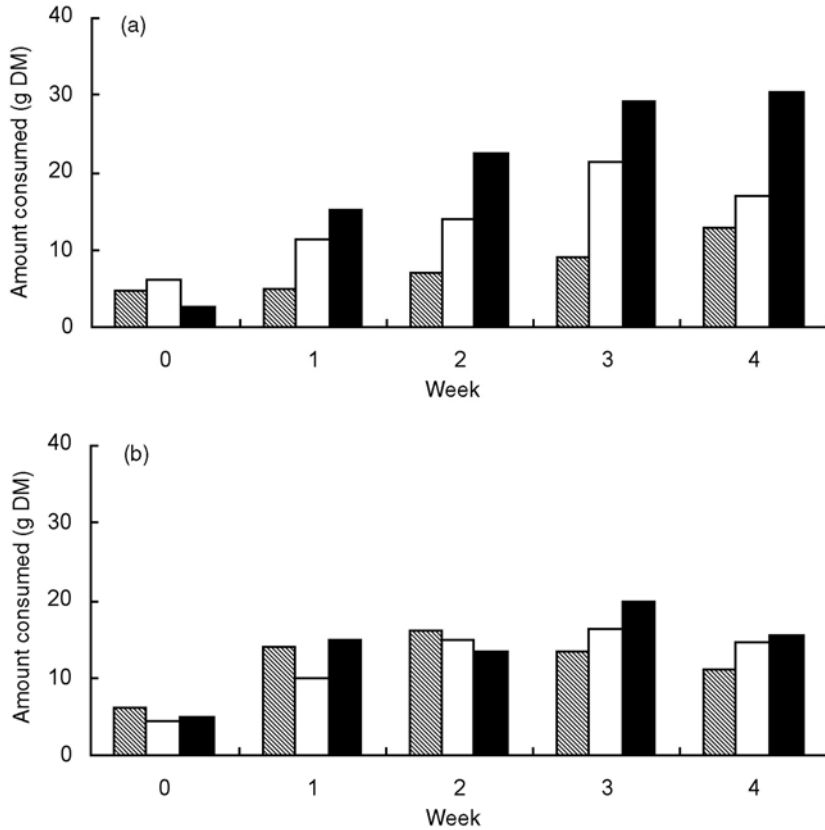


Fig. 6.4. Influence of post-ingestive stimulus (lithium chloride, shaded bars; sodium chloride, open bars; sodium propionate, solid bars) on intake of associated conifer species in three-way preference tests when individual conifer species were offered; (a) on separate days during conditioning weeks in the temporal separation experiment; (b) simultaneously during conditioning weeks in the simultaneous experiment (from Duncan and Young, 2002).

Interactions between ‘working’ and nutritive value

The quality of food frequently differs in different parts of the animal’s environment, and they must choose whether to stay eating a poor food or expend effort in moving to a food of better quality. In order to study this type of trade-off, Ginane *et al.* (2002) offered heifers a poor hay ad libitum and a limited amount of a better-quality hay on the other side of the test arena. As they depleted the limited quantity of the better food, the animals spent more time eating the poorer one; also, they were prepared to walk less to obtain the better hay when the difference in quality between the two was small, compared with when it was large. Although these heifers tended to behave in a manner likely to maximize their energy intake, their choices were sometimes suboptimal and the authors speculated that the animals desired to diversify their diet, not simply to maximize energy intake.

Relearning Following a Change of Food, Animal or Environment

Change of diet

Animals must relearn when the food to which they have been accustomed is suddenly changed to another with different sensory and nutritional properties. In most practical and experimental situations, sudden changes are avoided by a slow change of diet; in changeover experiments it is usual to wait for animals to stabilize on a new diet before recommencing recording of feeding behaviour. There are few data in the literature, therefore, with which to illustrate the time-course of adaptation. Figure 6.5 shows what happened when 32 individual sheep accustomed to oaten chaff were suddenly changed to a diet of barley straw; the mean daily intakes are shown, together with intakes of two individuals, selected at random (J. Hills, 1998, unpublished results).

The intake of oaten chaff was fairly stable at around 1200 g/day, but on the first day after the change to barley straw the sheep ate very little, which suggests that they were not familiar with the new food and were showing neophobia – a wariness of new food in which only small amounts are taken in order to assess whether there are unpleasant consequences to eating it. Then intake increased (but with a minor decrease on days 4 and 5 after the change, perhaps due to ruminal disturbance if the microflora has not adapted to the new food) to reach a plateau of around 800 g/day some 10 days after the change. The two individuals shown in the figure conform quite well to the mean for all 32 animals, but with greater day-to-day fluctuations than the mean.

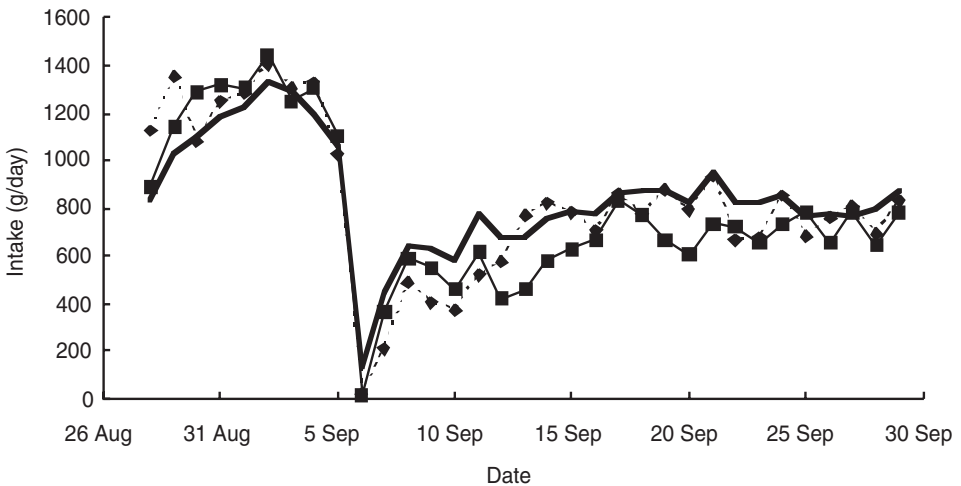


Fig. 6.5. Mean daily intakes for 32 sheep (solid line) and two individual sheep (lines with symbols) selected at random; on 6th September the oaten chaff was replaced with barley straw (from J. Hills, unpublished results).

Changes in the animal

As the animal grows and develops so its optimum diet changes. These changes occur slowly and there is plenty of time for animals to learn whether small increases or decreases in intake are necessary to conserve minimal discomfort.

On the other hand, as a cow progresses from late pregnancy into early lactation, there are much more rapid physical and metabolic changes, including: (i) a reduction in the competition for abdominal space; (ii) changes in amounts and ratios of nutrients required; (iii) oestrogens increasing in late pregnancy and then falling at parturition; and (iv) the distraction of parturition itself. Thus, there is a whole new balance of factors required in order to achieve optimal metabolic comfort, which takes the animal a long time to get right, hence the slow increase in early lactation (see Chapter 16).

Timescale of Aversions and Preferences

Provenza (1995) has proposed that there are three kinds of memory involved in the association between sensory and metabolic properties of foods. The first is that provided by evolution through the special and general senses, whereby some food-related stimuli are innately aversive (e.g. odour of faeces) or preferred (e.g. sweet taste). The second kind of memory is provided by the mother, who is a source of 'transgenerational knowledge', reducing the risk involved in learning about foods and environments. The third kind of memory is that of the individual itself, involving post-ingestive feedback from nutrients and toxins and associations with sensory properties of foods. Thus, each animal has its own genetic and behavioural history, making it difficult to predict how it will react in a particular choice situation.

CS-US interval

For most associations to be learned, the CS (the ringing of a bell in the case of Pavlov's dog) must be presented a few seconds before the US (the presentation of food in order to elicit salivation). However, with learned preferences and aversions to foods, the presentation of the conditioning stimulus (CS, the flavour/appearance of the food that the animal has learned to be associated with its metabolic properties) and of the unconditioned stimulus (US, the effects of the metabolites absorbed from the food) can be many minutes, or even hours, apart.

In some cases animals find a food aversive only when discomfort is felt soon after ingesting that food. For example, giving sheep 150 mg/kg LiCl (US) either at the time of offering oat chaff (CS) or 1 or 2 h later resulted only in the development of an aversion for that food in those given LiCl at the time of offering the chaff. In other cases, however, longer intervals can elapse between CS and US, such as at least 8 h in sheep (Arsenos *et al.*, 2000). Preferences are stronger, however, when the interval is short (Villalba *et al.*, 1999), and this

may well be why a stronger preference is induced by starch (rapidly digested) than a fibrous material when introduced into the rumen, and why sheep actively seek plant parts high in soluble carbohydrates.

It is not even necessary for animals to be conscious during the time they are exposed to the nauseating effects of a toxin: when sheep were given a novel food and then anaesthetized while a nauseating dose of LiCl was administered, and maintained unconscious until its effects had dissipated, they still found that food aversive when offered it subsequently (Provenza *et al.*, 1994a, b). Thus, animals need not be consciously aware that some foods are mildly toxic and are inducing a learned aversion; the whole process is automatic unless, of course, the toxin concerned is powerful, in which case the discomfort is obvious.

Speed of learning

It is to be expected that the speed of learning will depend on the degree to which the animal has been moved from its normal state, e.g. by previous feeding of a deficient diet, as the reinforcing properties of feeding can be very rapid indeed.

The speed with which chicks learned new associations between the protein content of a food and its colour was investigated by training them to associate one colour with a high protein content of 248 g/kg and another colour with a low protein content of 103 g/kg (Hannah, 2001). Then they were fasted for 1 h, offered both foods and the time taken to start eating from each was monitored. In Fig. 6.6, the area to the left of the dashed vertical lines shows that they ‘attacked’ the high-protein food significantly more quickly than the low-protein food, whether the high- or the low-protein food was coloured green. On day 48, the colours were reversed and there was a rapid reversal of the attack times so that within 3 days the high-protein food was once again

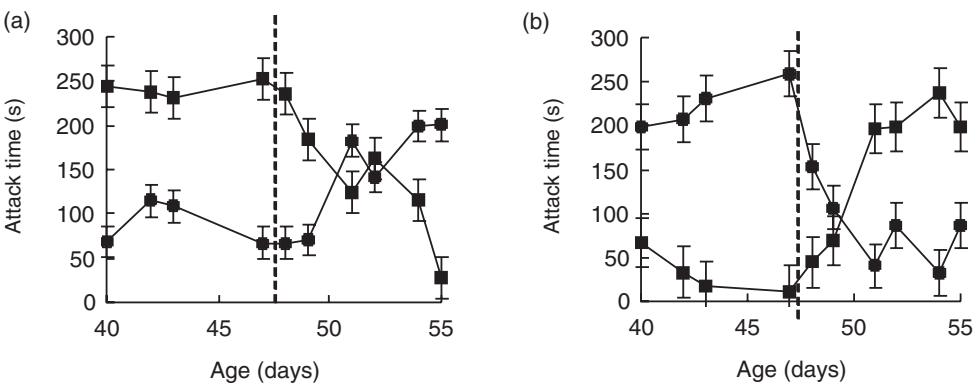


Fig. 6.6. Mean times to attack foods with different protein contents and colours. (a) treatment 2 (red, HP, green, LP and reversed at day 48); (b) treatment 4 (red, LP, green, HP and reversed at day 48). ■, red food; ●, green food; the vertical dashed line shows the time that the food colours were reversed (from Hannah, 2001).

being attacked far more quickly than the low-protein food. This relearning time is similar to those noted in other experiments with chicks.

Jones and Forbes (1984) found that sheep which obviously discriminated against quinine-treated hay in a preliminary period ate equal amounts of treated and untreated hay in subsequent 5-day choice periods, thereby demonstrating adaptation as they learned that there were no harmful consequences to eating the quinine-flavoured food. Following a change in flavour, even without changes in the nutritive value of food, sheep sample the food cautiously.

Speed of forgetting

There is a difference between a situation in which the UC–CS association is changed, as in the examples above, and one in which an association is no longer reinforced. In other words, once learned, for how long is the memory of the nutritive value of a food retained? The answer seems to vary with the circumstances. This makes sense because it is necessary, on the one hand, for conditioned taste aversions to persist (otherwise they have no function), but also to be flexible (otherwise an animal might be saddled with an unnecessary aversion for the rest of its life). The stronger the aversion the longer it persists.

Growing broilers seem to forget the aversive properties of a coloured food paired with an i.p. injection of cholecystokinin within a few days (see Fig. 6.2) and it might be thought, therefore, that this aversion is a mild one. However, it needs to be remembered that the younger an animal, the faster it is likely to learn and forget. Once sheep have eaten > 10 g of supplement/day they will subsequently eat it readily even if they have not seen it for 3 years. Sheep moved from native pastures to high-quality pasture select a food with significantly lower nitrogen content than sheep reared from birth on that pasture. This is true even after the introduced sheep have been on the good pasture for 3 months.

There are many examples to show that experience of eating a particular food is helpful. Sheep reared on grass are more dextrous and have a higher biting rate for grass than those experienced in harvesting shrubs. Conversely, those used to eating shrubs do so more efficiently than those with only grass experience. Goats with experience of browsing blackbrush eat faster and more by breaking twigs off than do inexperienced goats. Lambs with experience of grazing the serviceberry shrub later grazed it more efficiently when it was sparse than did naïve lambs, while there was no such difference in the rate of eating of other foods. Lambs or ewes recognized foods to which LiCl had previously been added, after 2 months without exposure.

If an animal learns that a food item is unpalatable and avoids it, does it forget the unpalatability by it not being reinforced? Do unreinforced encounters have a memory-jogging effect? Usually animals sample from time to time foods to which they are averse, presumably so that they can be made aware of any change in their properties.

Social Components

While the general framework whereby aversions and preferences for foods can be learned has evolved over the generations, and indeed some are innate (preference for sweet taste; aversion to bitter taste), cues as to how to behave when selecting a diet can be given by other animals, usually of the same species and often the parents.

Poultry

The sight and sound of the hen pecking and giving a low call stimulates newly hatched chicks to peck at food. Those brooded with their mothers perform more locomotion and more sustained feeding activities than non-brooded chicks, as well as having different preferences from non-brooded chicks, and very clearly followed their mother's preferences (Wauters *et al.*, 2002).

Chicks can learn from each other but don't learn so well to get food if the demonstrator doesn't receive a reinforcement. To what extent is the demonstrator aware that it is teaching and does it modify its behaviour, e.g. by accentuation, when it realizes that it is a teacher? Sherwin *et al.* (2002) showed that 9-week-old chickens consumed a greater proportion of food of a colour that they had seen demonstrators pecking at more actively (but only when the food was green and not red). Their choice was not, however, affected by having observed a disgust reaction to bitter food eaten by demonstrators.

Adult birds tend to feed in groups and visual, but not auditory, cues are important in the synchronization of feeding in individually caged birds, although it has been said that feeding can be synchronized in the short term by sound alone.

Pigs

Farm animals are all gregarious species and, even when penned separately but with sight and sound of each other, tend to eat in synchrony. Weaned piglets penned close to suckling sows go to their feeder when they hear younger piglets sucking. There is synchrony of sucking within a litter of piglets, and different litters in the same house tend to suck at the same time. Tape recordings of the sounds associated with nursing have been used with some success to increase the frequency of nursing and to improve weight gains. Young pigs also accept a food more readily if it has the flavour of their mother's milk – in some studies, but not in others.

Although young piglets did not appear to observe precisely the feeding behaviour of trained siblings, some combinations of cues resulted in a significant bias of food-searching behaviour towards a site where the demonstrator had previously eaten (Nicol and Pope, 1994). Thus, observing an experienced animal does not necessarily cause acquisition of a feeding behaviour, but may direct investigation towards stimuli involved in the task, which could facilitate learning.

Other senses may be integral to the social transmission of information related to feeding, although Nicol and Pope (1994) suggested that previous visual cues were more relevant to pigs than olfactory signs in their learning about operant panel pressing. Pigs tended to press panels of a similar colour to the one they had observed the demonstrator using to obtain food.

Social facilitation of feeding is known to occur in pigs, but any attempt to investigate whether or not this might affect daily food intake would be fraught with difficulties of interpretation as it would involve keeping some pigs in isolation, which might be stressful and depress intake. Effects of group and pen size on food intake are discussed in Chapter 17. The relative importance of social transmission of feeding behaviour to pigs is relatively unknown. The importance of individual determinants is likely to vary, depending on the environment and on other current circumstances.

Morgan *et al.* (2001) investigated the extent to which pairing newly weaned piglets with others that had been weaned a week earlier would increase the acceptance of food. Each pair had visual contact and either no physical contact, contact through mesh or penned together, with pairs of inexperienced piglets housed together as controls. The two ages housed together had the highest weight gain and the inexperienced pairs ate less food than the other pairs. Pairs with no experience ate simultaneously on fewer occasions than the pairs in which one piglet was experienced. It was concluded that food intake is stimulated when an inexperienced piglet is housed with an experienced piglet, and it was suggested that this might be exploited to alleviate the post-weaning check in growth.

Cattle

Calves are social drinkers. If one calf is allowed to drink to completion and then another calf in the next pen allowed to drink, the first one starts to consume again. Even when the second calf is muzzled and put in the same pen, it tries to drink and stimulates the first to drink more. Thus it is sensible to provide plenty of teats so that all calves can drink together, in order to achieve maximum intake.

Social facilitation of feeding also occurs in adult cattle, and cows fed in groups have been noted to eat 7% more of a complete food containing 0.6 silage than individually stanchioned cows. In three herds in which first-lactation cows were either mixed with or separated from older cows, the heifers spent more time eating when they were mixed with older cows (263 versus 240 min/day), had more eating periods (6.7 versus 5.3 periods/day) and, in the one herd in which silage intake was recorded, ate more food (9.3 versus 7.7 kg DM/day) (Konggaard and Krohn, 1978). Social interactions do not necessarily facilitate feeding, however, especially if there is insufficient feeding space for all animals in a group to eat at the same time. Trough space can be a limiting factor, and less than 0.2 m/cow is likely to reduce intake.

Heifers can be conditioned with LiCl to avoid eating larkspur, but they lose this conditioning more quickly when kept with unconditioned heifers than when not kept with such untrained animals.

Sheep

Lambs quickly learn to differentiate between their mother and other ewes, the former offering herself for sucking (positive reinforcement), the latter butting and moving away to generate aversion. Lambs show preference for a food with a flavour they experienced in their mother's milk or even *in utero* (Nolte and Provenza, 1992).

Provided they are at least 7 weeks old, lambs can learn as well from either their mothers or from other adults. On two commercial farms, ewes and lambs were given grain on three consecutive days. Eighteen months later, 140 of these lambs and 140 naïve lambs were offered grain; all of the experienced ones ate by end of day 3, while less than 10% of the others had eaten by this time (Lynch and Bell, 1987). Thus, the simple strategy of giving ewes grain for a few days just before their lambs are weaned will have a very big beneficial effect if and when these lambs have to be given grain.

One limitation is that the same grain must be given; sheep trained to one grain behave naïvely when offered another. Those which had no previous experience of wheat ate very little of any grain (wheat, barley, oats, maize) in the first 3 weeks of offering, while those which had already had some wheat experience ate wheat from the first day of offering but did not take the other grains as readily, even though they eventually ate more of them than did the totally untrained animals.

Even when sight, hearing and smell are removed, learning is rapid. Sheep introduced to wheat in the presence of experienced sheep start to eat much more quickly than those penned with other inexperienced sheep. When sheep had their sight, hearing or olfaction – or a combination – temporarily impaired, only impairment of all three senses resulted in slower learning, so there is no overriding role for any one sense in the learning process.

When supplementary food is offered in drought conditions in Australia, sometimes sheep fail to eat it and suffer undernutrition or even die. In order to see the extent to which prior experience would alleviate the problem, lambs were offered wheat with their mothers for 5 days for a few minutes each day in one of weeks 1 to 7 of age (Chapple and Lynch, 1986). When, at a much later date they were offered wheat, those which had been given it when 3 weeks or older ate more than those without prior exposure or those exposed in the first 2 weeks of life. Other work showed that lambs given wheat for 5 days subsequently ate much more than those given it for only 2 days. Weaner sheep which had never seen wheat ate almost none for the first 11 days, after which their intake increased rapidly. There is also a fear of unfamiliar troughs, with a reduction in the time taken to eat wheat if it was fed in troughs from which the sheep had previously obtained hay. Sheep must overcome the fear of the trough, the fear of the food and then learn how toprehend, chew and swallow grains.

Provenza *et al.* (1993) offered ewes a novel food (elm leaves) followed by LiCl or saline, and some of their lambs were conditioned similarly. When lambs were offered a choice, those which were averse themselves, or whose mother was averse, took fewer bites of elm than controls, while there was no difference due to treatment on the number of bites of poplar, which had not been paired

with a toxin and which they had previously eaten readily. It was concluded that the toxin was more effective than the mother in determining preferences, as those lambs that received LiCl themselves avoided elm whether their mother had eaten it or not.

In a further demonstration of the power of observing adults eat, it was found that pre-weaning exposure to molasses-urea blocks had a greater influence on subsequent acceptance than post-weaning exposure.

Position of Food Cues

In most natural situations there is no fixed association between the exact position of a food item and its nutritive value, in contrast to food factors such as appearance or taste. However, in the absence of any direct sensory cues, many animals can use spatial memory to locate sources of food, or to choose between foods. In addition to the colour, shape and brightness, animals can learn the position of the food if that is consistent between exposures.

Steinruck *et al.* (1990) offered methionine-deficient broilers complete and methionine-deficient foods either in the same position every day for 36 days, or else the positions of the foods were reversed every 3, 6 or 9 days. Where the positions were unchanged there was a 68% choice of the complete food (i.e. selection for methionine, Chapter 8) but, as the changes became more rapid, so selection was less appropriate, being 65, 62 and 58% for the 9-, 6- and 3-day change-over birds, respectively.

These results are not surprising given the lack of cues, other than position, to the content of methionine, which is colourless and has little taste; moving the position confused the birds and forced them to relearn the relationship between position and methionine content. The detailed results presented by Steinruck and colleagues clearly demonstrate this relearning process, with a temporary decrease in the proportion of complete food eaten following each change-over.

Heifers learned more quickly than cows in which of two hoppers to find food after two 10-min tests/day for 5 days (92% of heifers, 23% of primiparous cows and 54% of cows after their second calving) (Kovalcik and Kovalcik, 1986). Six weeks later, tests were resumed and 77% of cows – but only 46% of heifers – went straight to the correct feeder. Thus, the process of learning was quicker in heifers but they forgot sooner than did cows, which is in general agreement with learning at different ages in other species. When cows have to push open a Calan door to obtain food, they learn within about 24 h of 'their' door being changed.

To determine whether cattle use visual cues to track food locations, steers were trained to associate traffic barricades and traffic cones with high- and low-quality foods, respectively, in either fixed or variable locations (Howery *et al.*, 2000). When the two foods were placed in different locations in different tests, and no visual cue was offered, animals succeeded in finding the food significantly less often than when cues were given and/or the foods were in the same locations in successive tests. This is a clear indication that cattle can learn to associate visual cues with different qualities of food and thereby forage more efficiently.

Sheep and goats were given a high-quality food in one arm of a T-maze, and animals of both species tended to return to the food-providing arm on a second occasion (Hosoi *et al.*, 1995). As this could be attributed to a strong lateral preference, in further studies a low-quality food was placed in the other arm. Goats, but not sheep, responded by increasing the frequency of shifting on the second free choice, particularly when the first choice was a losing one. The authors concluded that foraging behaviour may be more strongly influenced by negative experiences than by winning ones, and that this should be incorporated into foraging theory.

Thus, even though not directly aware of the presence of food or able to differentiate between two foods on the basis of their sensory properties, animals can remember the likely spatial position of appropriate foods, based on previous experience. It is not helpful to deliberately confuse animals by swapping the position of the two foods daily in choice-feeding experiments, a point apparently missed by some researchers!

‘Palatability’

The features of a food material that are sensed before it is swallowed, of which an animal is consciously aware, are often collectively called the ‘palatability’ of that food. Palatability is often confused with acceptability or preference, but it cannot be considered to be simply a quality of the food because it depends so heavily on the experience and metabolic status of the animals in question. A good definition is: ‘a response measure which is based on the outcome of the central nervous system’s integration of taste and internal-state signals combined with cues arising from previous associations’ (Grill and Berridge, 1985).

There is no single way to measure palatability, but several methods have been used: (i) intake tests, which often give very different results depending on whether the two foods are offered simultaneously or sequentially; (ii) brief exposure tests with minimal ingestion; (iii) initial rate of eating on first exposure (lick analysis); (iv) oesophagostomy or stomach fistula tests; and (v) taste reactivity observations.

It might be thought that a palatable food will be eaten in greater quantities than an unpalatable food. When a flavour is added to the single food on offer, there is sometimes a short-term increase or decrease in intake but rarely a prolonged change. It is not realistic to expect to be able to stimulate voluntary food intake in the long term simply by changing the flavour of the food.

For example, the addition of Bitrex (the most bitter substance according to the human palate) to the food being offered to growing pigs immediately caused the animals to stop eating (Blair and Fitzsimons, 1970). However, after a few hours they became hungry, sampled the food again but finding it still very ‘unpalatable’ avoided it for a while longer; eventually their hunger got the better of them and, as there had been no adverse consequences of nibbling it earlier, they increased their intake, returning to normal within 3 days of the start of addition of Bitrex.

Thus, a completely ‘unpalatable’ food had become ‘palatable’ within a few days. Although not tried in the reported experiment we can be confident that,

were the same animals to be confronted with Bitrex-adulterated food at some later date, they would recognize it as safe and eat it readily.

Greenhalgh and Reid (1967) developed an ingenious method of separating how much of the difference between intakes of different diets is due to post-ingestional differences rather than to differences in palatability. Two foods of very different sensory and chemical properties were offered to sheep without involving any differences in the composition of the digesta. This was done by matching the weight of food eaten voluntarily with an equal weight given through the ruminal fistula. When straw was given both by mouth and by fistula, the total intake was $13.8 \text{ g/kg}^{0.73}/\text{day}$ and the digestibility of organic matter (OMD) was 0.41; when dried grass was given by both routes, intake was $59.4 \text{ g/kg}^{0.73}$ and OMD was 0.74. When equal amounts of the two foods were given, one by mouth and the other by fistula, the digestibility was intermediate (0.55–0.57) but the voluntary intakes were very different: 23.5 when straw was given by mouth and $48.8 \text{ g/kg}^{0.73}$ when dried grass was given by mouth. This was said to demonstrate a powerful influence of palatability on voluntary intake.

However, given the discussion above, it is quite possible that these sheep were eating according to learned rather than to innate preferences, as they had experienced eating straw before the experiment started. As the experiment progressed they ate less straw – they learned that it provided less nutrients than the dried grass once they had had a chance to experience the effects of eating both.

An example of the lack of correlation between intake when a choice of foods is on offer and when they are given singly is the work in which pregnant ewes were offered one of three silages or else free choice of the three silages (Forbes *et al.*, 1967). Silage B was of poor quality but was eaten in quantities only slightly less than silages A or C by ewes which had access to only one food. However, the group that had access to all three ate equal amounts of silages A and C but very little of silage B.

Gherardi *et al.* (1991), studying the short- and long-term responses in intake of sheep to additions of chemicals thought to influence palatability, concluded that palatability effects are not important in determining the level at which a single forage is eaten, but can have marked effects on the relative intakes when two forages are on offer. Addition of butyrate plus monosodium glutamate increased preference for a forage by sheep, while magnesium oxide had the opposite effect.

Adding a pleasant flavour can increase the preference for a particular food, and there is sometimes a short-term increase in intake or rate of eating. Unusually, a prolonged 10% increase in silage intake was obtained with the addition of Simax 100 (a mixture of several flavours with a predominantly orange taste) (Weller and Phipps, 1989) but, more commonly, animals revert to their former level of intake once they learn that there has been no change in the nutritive value of the food.

Sudden changes in the formulation of concentrate feeds, even though the nutrient composition is unchanged, make cows hesitant in eating the new food and suspicion falls on the manufacturer. If the same flavour is included in all

batches of food then changes in the underlying formulation go unnoticed, rate of eating is not affected and the farm staff are kept happy. For example, when rapeseed meal was included in a dairy supplement there was a reluctance to eat on the first few occasions, but this was largely prevented by inclusion of a constant flavour (Frederick *et al.*, 1988).

Drinking water can be used to carry nutrients to cows; ammonium acetate would provide both non-protein nitrogen and an energy source, but it is not readily accepted by some cows. Jackson *et al.* (1968) found that addition of molasses, sodium cyclamate or ethyl acetate caused cows to drink more whereas saccharin, vanilla or aniseed gave little or no improvement.

Thus, in summary, the extent to which an animal finds a particular food 'palatable' depends on innate factors (e.g. bitter/sweet) and on the previous history, if any, of interactions between the animal and that food, or foods with similar sensory properties.

Conclusions

Animals are highly motivated to eat and drink, and this motivation is increased as metabolic demands increase. All the senses are used in the identification of food and the absence of one sense does not, therefore, result in a loss of selective or ingestive ability. However, while mammals rely primarily on taste to identify foods, birds use vision, and quickly learn to associate the sensory properties of a food with the metabolic consequences of eating that food.

Thus, the term 'palatability' is difficult to define as it depends not only on the taste and appearance of the food, but also on the nutrient requirements and history of the animal. For example, a food that is initially preferred becomes aversive when its ingestion is coupled with injections of a toxic substance. Such learned aversions and preferences are long-lived and are likely to influence animals' behaviour for many years.

In addition to innate preferences/aversions and those learned by the animal from its own experience, it can also learn from conspecifics without ever having itself ingested the food in question. Thus, a mother can pass on to her offspring some information about food before the young have themselves started to eat solid food.

As will be made clear in Chapter 13, these learned associations form the basis of the ability of animals to make appropriate selections when a choice of foods is offered, and may also play an important part in determining how much of a single food an animal eats, i.e. its voluntary food intake (see Chapter 10).

7

Diet Selection: Principles

In the previous chapter we have seen the overwhelming evidence that animals can learn to associate the taste, smell or colour of a food with the feelings they experience after they have eaten that food. It was hinted that this is a powerful ability, which allows animals to select from a range of foods to best meet their nutrient requirements, and it will be proposed later that learning is also of importance in determining how much they eat if only one food is available.

This chapter reviews the evidence for diet selection, defines the prerequisites for animals to demonstrate its occurrence and discusses the possible mechanisms whereby animals can make nutritionally wise food choices. The following chapter deals with effects of differences between animals, between foods and in different environments on food choice and shows how diet selection might be exploited in farming practice, while Chapter 13 deals with appetites for specific nutrients.

In modern farming systems, animals are typically presented with a single food. This is not a situation in which most species of birds and mammals have evolved and must be considered unnatural. The ancestors of our farm animals had the opportunity to select from a range of available foods and obviously were able to select a mixture that allowed them to grow and reproduce. It is possible that by eating at random from a variety of foods they obtained sufficient nutrients to survive, but this would not be enough in some situations, e.g. when toxic food sources make up a significant part of what is available. It should be recognized that some species of animal have evolved to eat only a single food, i.e. they have an innate inflexible diet selection. However, many species eat a variety of foods and they need to learn the properties of these foods.

Because animals do not always select from between two or more foods on offer to produce what the observer considers to be an optimum mixture, there has been considerable scepticism as to whether the ability to select is widespread, either across a wide range of species or between food and physiological situations. Sih and Christensen (2001) have collated information

on what they call optimal diet theory (ODT) from across the animal kingdom and concluded that:

Contrary to our predictions, forager types (invertebrate versus vertebrate ectotherms versus vertebrate endotherms) did not differ significantly in their fit to ODT. Apparently, even organisms with relatively low energy demands or with simple information gathering and processing abilities (e.g. insects, snails or even protozoa) are capable of adaptive foraging.

It is justifiable, therefore, to start from the assumption that farm animals have the characteristics necessary to enable them to select wisely between different foods. Sometimes it is the observer's prejudices that hinder the correct interpretation of observations made in experiments or in the wild (Forbes and Kyriazakis, 1995).

There are currently new opportunities in diet selection, both from scientific and commercial points of view. The realization that it is necessary for animals to be able to differentiate between foods with different nutrient compositions by colour, taste and/or position, and that they need to be able to learn to associate the sensory properties of foods with the metabolic consequences of eating them, has made it possible to envisage a learned appetite for each of the essential nutrients. Thus, there is now more certainty that if animals can be taught an appetite then this can be used in a choice-feeding situation to improve the balance between their nutrient requirements and their nutrient intake.

Most of the raw materials used in animal foods have concentrations of available energy within a fairly narrow range, 9–13 MJ/kg DM, whereas the content of nutrients such as protein, minerals and vitamins varies over a much wider range. An animal can control its energy intake by varying the amount of DM it consumes but can then only control its intake of nutrients independently of energy if it has access to two or more foods that differ in the content of the nutrient in question. Because of its quantitative importance, high cost and the polluting nature of its excretory products, protein has been widely studied in terms of diet selection and is used as evidence for diet selection in this chapter. An appetite for protein seems to be very primitive in evolutionary terms, as trained locusts eat more of a high-protein food after preloading of carbohydrate, and vice versa.

Some species of animal rely on a narrow range of foods for their sustenance, and the recognition of these food sources is genetically predetermined. Other species will sample a wide range of potential foods and must learn by experience those that are palatable and nutritious. Whereas deficiency in an animal of a nutrient for which there is a specific appetite will induce increased preference for a food that contains that nutrient, the reverse is not necessarily the case: that is, intake of a modestly greater amount of that nutrient than is necessary is not detrimental and may not induce a reduction in selection for a food containing it in high concentrations.

Taste and smell are the most important senses in feeding situations; visual and auditory cues are not normally part of the food experience and so are not conditioned as well in mammals, while the reverse is true for birds (see Chapter 6).

Theory of Diet Selection

The principles of diet selection have been outlined by Emmans (1991) and illustrated by Fig. 7.1. When two nutrient properties of foods are considered, the proportions of two foods necessary to meet an animal's requirements for both nutrients can be shown by a straight line (Fig. 7.1a). The two dimensions could be energy and protein. Foods A and B are both within the subspace representing adequacy, and any mixture of the two would satisfy the animal's requirements; choice between these two foods could therefore be random or according to the hedonic properties of the foods interacting with innate or learned preferences for colour, taste or other non-nutritional characteristics. Food C has too much protein and foods D and E too little protein. Offered a choice between (C and D) or (C and E) the animal could choose proportions of the two to make a balanced diet. Offered only D and E it could not avoid under-eating protein.

In Fig. 7.1b, the three dimensions are protein, energy and minerals. Foods C, D and E lie outside the adequate subspace, but a line between C and D passes through this area so that an appropriate mixture of the two would be adequate; the line between C and E does not pass through the area so there is no mixture of these two that would be adequate. A choice between (A or B) and (C, D or E) requires that A or B are predominantly eaten if requirements are to be met. Thus, to test the hypothesis that animals make selections from two or more foods according to their nutrient requirements, it is necessary for at least one of the foods to have a composition outside the adequate subspace.

Four nutrients are represented by the tetrahedron in Fig. 7.1c, in which the four vertices represent energy, protein, calcium and phosphorus. There may be a few foodstuffs, such as A and B, that contain the right ratios of all four, but it is more likely that two, three or four raw materials will be required to satisfy an animal's requirements.

This theory of what animals should eat is realistic only if we know the requirements of the animal(s) in question. We can obtain an estimate of energy and protein requirements, for example, from results of experiments in other environments, i.e. standard textbooks or tables of nutrient requirements. However, to define the responses to nutrients under the conditions under which choice-feeding experiments are to be carried out, it is preferable to conduct adequate experiments with single foods of a range of compositions, but this is not often done. Furthermore, conclusions that animals are selecting foods with a nutritional purpose are strengthened if their requirements change with time, and this change is reflected in appropriate adjustments to the proportions of different foods chosen. The change with time could be that naturally occurring during growth or an imposed change, such as one of temperature or hormonal manipulation of metabolism (see below).

One of the difficulties in studying individual variation in food choice is the complexity of graphs with many animals' results. The 'diet selection pathway' method of plotting food choice data (Kyriazakis *et al.*, 1990) is a way of clearly showing the behaviour of individuals in a compact manner. The cumulative difference between the intakes of two foods (food A – food B) is plotted against

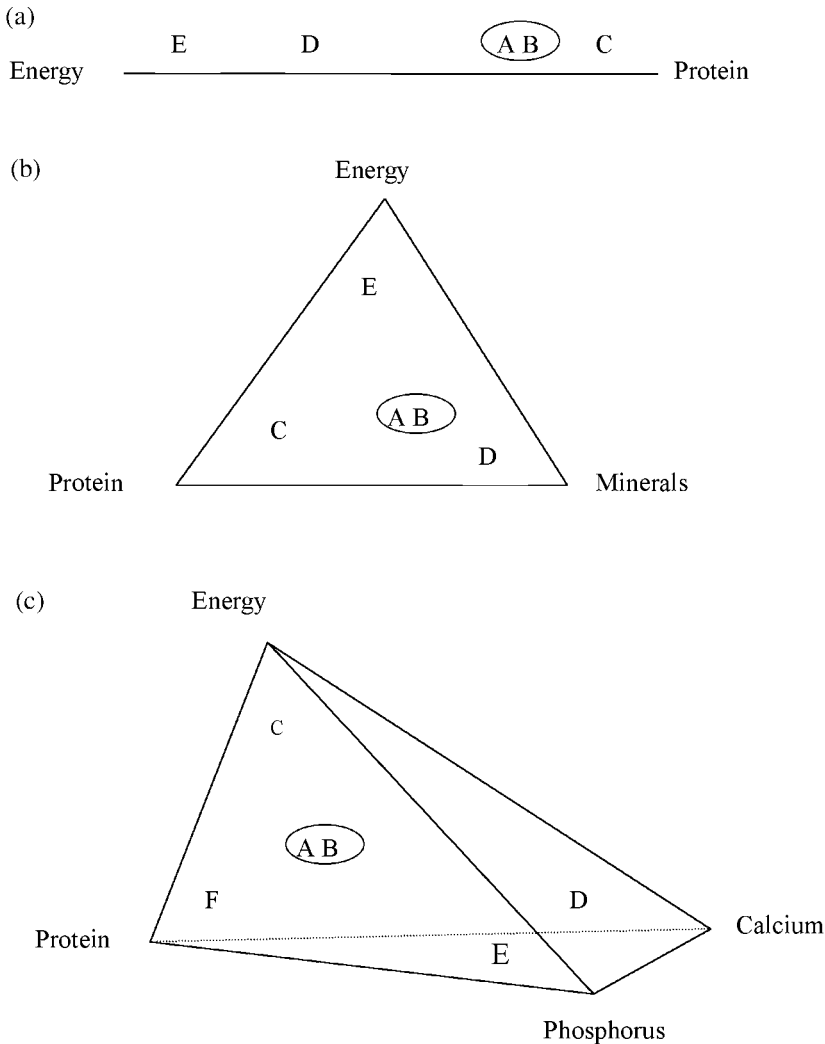


Fig. 7.1. Diagrammatic representation of mixtures of foods required to satisfy an animal's demands for nutrients; (a) two nutrients; (b) three nutrients; (c) four nutrients. The circled area is that in which the animal's requirements are satisfied. A–F are foods in positions which represent their content of the two, three or four nutrients. See text for details (from Emmans, 1991).

the cumulative total intake of the foods, i.e. a horizontal line represents equal intakes of the two foods; a line that increases shows the animal eating more of food A, while one declining shows a greater intake of food B. It needs to be emphasized that this method of presentation of daily diet choice provides a broad picture of each animal's choices, but does not draw particular attention to daily variations in the proportions selected. Figure 7.2 shows an example of diet selection pathways for eight piglets offered two foods containing 291 (HP) and 155 (LP) g CP/kg fresh matter for 3 weeks from weaning (Dalby *et al.*, 1995).

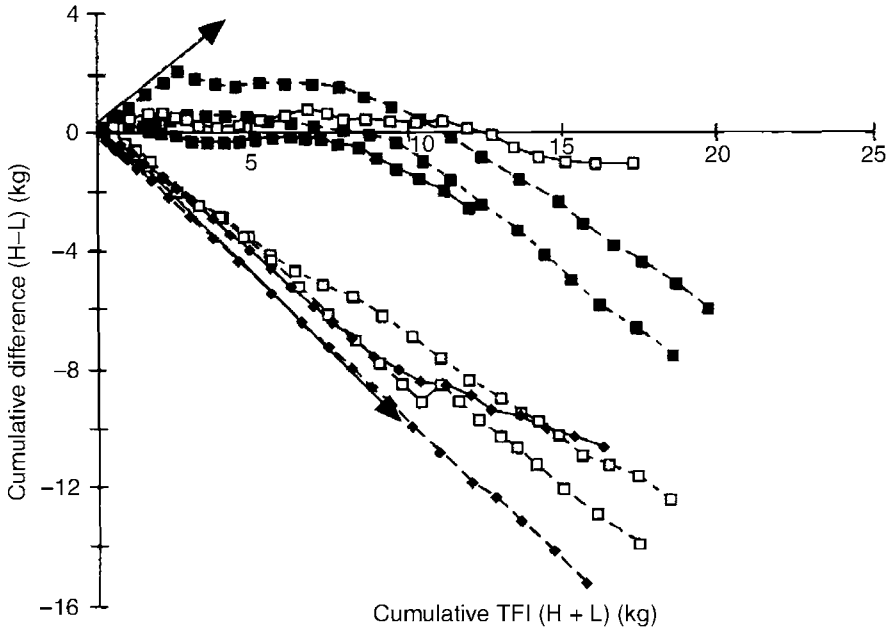


Fig. 7.2. Diet selection pathways for eight piglets with access to high- (H) and low- (L) protein foods for 25 days starting 4 days after weaning (from Dalby *et al.*, 1995).

The first point to be noted is the increased horizontal distance between points marking daily intakes from left to right. This shows the increase in total daily intake as the piglets grow; in the first few days after weaning (4 days before the first point on this graph) intake increases rapidly as the pigs become accustomed to their surroundings, including food and water. A second important point is the variation in total intake between animals (the position of the 25th day's intake on the horizontal axis varies from 12 to 20 kg). Also, there are large differences in the shapes of the selection pathways. Initially, one animal starts by eating almost all HP (pathway close to $+45^\circ$), three eat approximately equal amounts of the HP and LP (pathway close to horizontal) and four eat mainly LP (pathway close to -45°).

The first-mentioned animal, after 6 days, changes from mostly HP to approximately equal intakes of HP and LP; after about 14 days into the observation period it changes to eating predominantly LP, as do two of the three that started by eating roughly 50:50. The downward trajectories eventually achieved by all but one animal are approximately parallel, showing a similar, low, proportion of HP eaten by these animals. We can suggest that each pig learned that its needs were best met by taking a low proportion of HP, but different individuals learned this at different rates. At 10 days, when choice had stabilized, the mean proportion of HP eaten was 0.25 of total (giving a diet containing 189 g CP/kg), and this declined to 0.20 (182 g/kg) by day 25.

Additional discussion of diet selection theory is provided in Chapter 10.

Evidence for Diet Selection: Protein as an Example

Considerable evidence has accumulated for the ability of laboratory animals to make directed selection from a choice of foods and, in recent years, such evidence has also become available for farm animals. Probably the best-known example is the choice made by animals offered two foods with different ratios of protein:energy content, and this will be used to introduce the subject in the next section.

Poultry

There were numerous reports from the first half of the 20th century that hens, given a choice between foods, could select a balanced diet from amongst several imbalanced foods, and free-choice feeding has received attention ever since. Laying hens, pullets, growing broilers and growing turkeys all show the ability to select an adequate diet from a choice of two or three foods that are individually imbalanced (Forbes and Shariatmadari, 1994). In most cases, the choice has been between one food that is clearly higher in protein content than required and another lower in protein (these will be called HP and LP, respectively), but Ahmed (quoted by Rose and Kyriazakis, 1991) showed that broilers selected a diet from a range of nine different foodstuffs that provided nutrients in similar proportions to those normally recommended.

On a commercial scale, choice feeding has given mixed results in layers, though it has proved to be successful in broilers (see Chapter 8). The opinion has been expressed, however, that layers might choose better than broilers because the broilers have so little time to learn how to make the appropriate choices.

As an example of diet selection for protein by broiler chickens, the experiment of Shariatmadari and Forbes (1993) is presented. Pairs of foods differing in protein content were offered to broilers from 4–9 weeks of age. The results, shown in Fig. 7.3, show that, where possible, the birds chose proportions of the two to give themselves a diet containing 195–228 g protein/kg, i.e. the protein content known to be optimal for growth (see Chapter 12). When both foods had protein contents below this range, the birds ate predominantly from the higher one and, when both foods had protein contents higher than this range, they ate mostly from the lower, thereby selecting a diet close to the optimum.

Note that even when the bird has learned that one food provides sufficient protein (the last two treatments in Fig. 7.3), it still samples the other food, which provides a gross excess of protein. This is presumably to ensure that a change in the quality of an extreme food does not go undetected and to allow for novel foods to be sampled with relative safety.

Pigs

There is considerable evidence for directed selection for protein, and this is dealt with in more detail in Chapter 13. As an example, the work of Kyriazakis

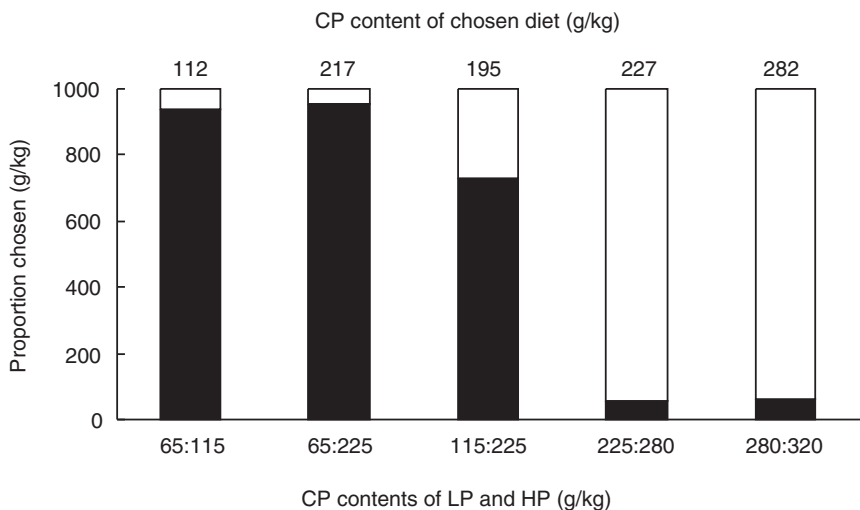


Fig. 7.3. Proportions of HP (solid bars) and LP (open bars) chosen by broiler chickens offered pairs of foods varying in protein content. The CP contents of the two foods on offer are shown at the bottom of each column and the resulting CP content of the diet chosen at the top (from Forbes and Shariatmadari, 1996).

et al. (1990) included choices between two foods with different protein concentrations. When one food contained more, and the other less, than the likely optimum protein level, the pigs selected a mixture which gave almost identical overall protein contents of about 205 g CP/kg (see Fig. 7.4). When both foods had less protein than required (125 and 171 g CP/kg, respectively), more was eaten of the one with the higher protein level; it is, perhaps, surprising that they did not eat entirely or almost entirely from the higher-protein food. When both foods provided too much protein, intake was almost exclusively from the one with the lower protein content, suggesting a strong drive to avoid an excessive protein intake. As shown in Fig. 7.2 (Dalby *et al.*, 1995), there is variation in the selection pattern between a low-protein food (L) and one high in protein (H) by different animals.

In order that animals can make sensible choices between foods they must be able to differentiate between them before they eat them, and the foods used here were clearly different in appearance, smell and taste because of the different ingredients used to achieve the different protein contents. These pigs had the opportunity to balance both energy intake (as a result of their total intake) and protein intake (as a result of the choice they made between HP and LP), whereas pigs given a single food could only meet their energy and protein requirements exactly if the food was perfectly balanced. Even if the diet allowed them to meet their requirements for both energy and protein at one point in time, the same food would no longer be well balanced some time later when the growing animal's protein requirements, relative to energy requirements, had fallen.

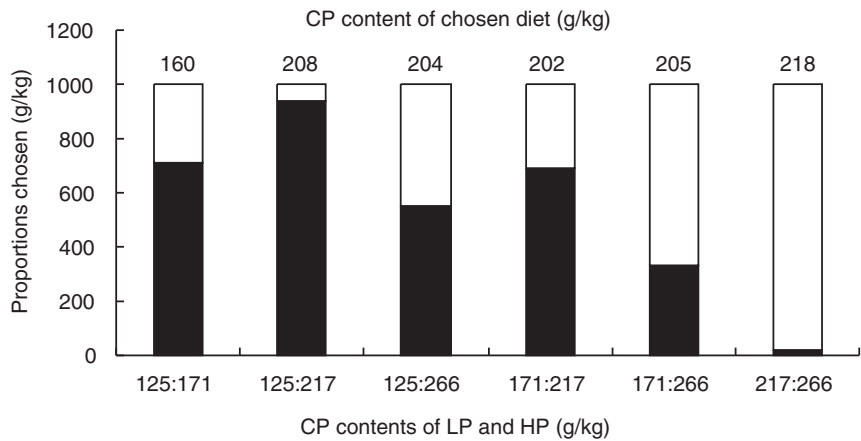


Fig. 7.4. Proportions of HP (solid bars) and LP (open bars) chosen by growing pigs offered pairs of foods varying in protein content. The CP contents of the two foods on offer are shown at the bottom of each column and the resulting CP content of the diet chosen at the top (from Kyriazakis *et al.*, 1990).

Thus, an animal offered a single food has to compromise for much of its life by either: (i) controlling its energy intake and suffering the consequences of eating too much or too little protein; (ii) controlling its protein intake and suffering the consequences of eating too much or too little energy; or (iii) compromising between the two. We will consider in Chapter 10 which of these is the most likely.

Cattle

Experiments with several different pairs of foods given to different individuals, as described elsewhere in this chapter for chickens, pigs and sheep, have not been performed, but a number of demonstrations of the ability of dairy cows to select for CP have been provided by Tolkamp and colleagues, and are detailed in Chapter 13. These have offered two foods of mixed silage and concentrates, the composition of the latter used to manipulate protein content.

A different approach to the study of cows' ability to choose appropriately for protein was adopted by Lawson *et al.* (2000), mindful of the difficulties in practice of providing two mixed foods for large numbers of cows. They offered 24 cows free access to grass silage and, for 3 weeks, a choice between differently flavoured concentrates with 90 or 39 g digestible undegradable protein (DUP)/kg DM, up to a maximum of 5.4 kg DM/day, via computer-controlled out-of-parlour feeders such as could feasibly be provided on a commercial dairy farm. The amounts of the high-protein food eaten as a proportion of total concentrate intake were 0.47, 0.45 and 0.50 for the 3 consecutive weeks, with a much higher standard deviation in the first week (0.372) than in the second (0.265) or third week (0.252).

This greater initial variation in selection is shown clearly in Fig. 7.5, which includes the diet selection pathways for eight of the 24 animals. Two cows ate almost entirely HP; another cow ate almost only LP for the first 6 days; the remaining five ate closer to equal amounts of HP and LP. In all animals but one, however, the selection paths eventually became approximately horizontal, confirming that approximately equal amounts of LP and HP were being eaten once the animals had become accustomed to the choice-feeding situation (and had learned to associate the sensory properties of each food with the metabolic consequences of eating it). The fact that the preference ratio was not significantly different from 0.5 could be due to an indifference on the cows' part as to which concentrate they ate (no selection) or because a roughly equal mixture of the two provided an optimal diet.

Based on previous research on factors affecting food choice in both ruminants and non-ruminants, it would be expected that individuals with high protein requirements would select a higher proportion of HP than animals with low protein requirements. The major need for protein in lactating cows is to support milk protein output, so choice between concentrates – expressed as the proportion of HP in the total intake of concentrates – was regressed against milk protein output immediately before the period of choice feeding began.

It can be seen from Fig. 7.6 that there was a positive relationship ($P < 0.05$); the cow that ate only HP was the one with by far the highest yield of milk protein. Because the regression was carried out with milk protein output measured before the choice-feeding period, when cows were given a single

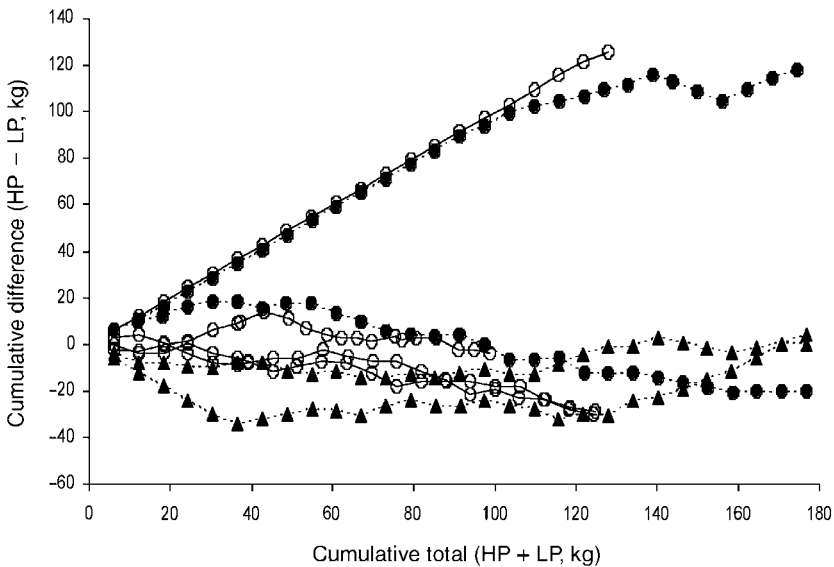


Fig. 7.5. Diet selection pathways for eight lactating cows with access to high (HP) and low (LP) protein concentrates for 21–29 days in mid-lactation. See text for interpretation (from Lawson *et al.*, 2000).

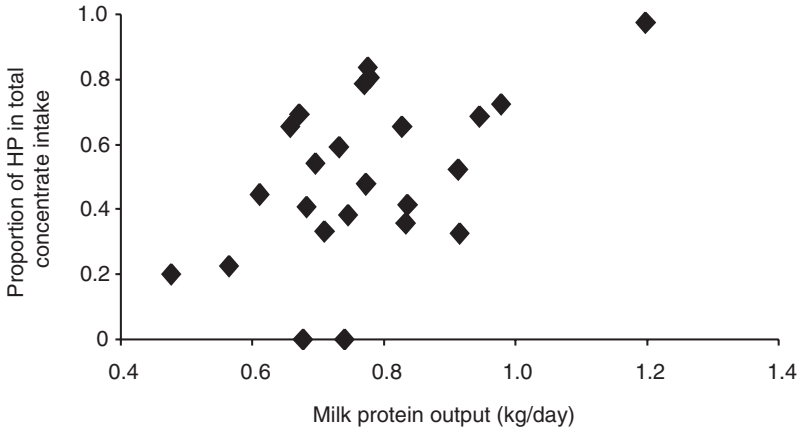


Fig. 7.6. Relationship between milk protein output and the proportion of a high-protein concentrate selected when given in choice with a low-protein concentrate (from Lawson *et al.*, 2000).

balanced concentrate food, this relationship can be interpreted as causal, i.e. the higher pre-existing milk protein output driving the selection of a higher proportion of HP concentrate.

Silage DM intake was significantly higher when, in other periods of the experiment, LP concentrate was offered alone (14.7 kg/day) than it was when HP was given (14.1 kg/day) or when there was a choice (14.2 kg/day). Milk yield was significantly reduced when the concentrate was LP and body condition score significantly increased compared with the HP or choice treatments. This suggests that cows given LP concentrates were trying to increase their protein intake by eating more silage, but that the increase was insufficient to provide the protein intake needed to maintain milk protein output and provided more energy, which was utilized for body fat deposition.

Sheep

Growing lambs have been observed to switch from little discrimination among foods of different digestible energy concentrations, when first introduced to them, to a preference for high-energy foods as they learned the consequences of eating each one (Glimp, 1971). More recently, it has been shown that sheep select proportions of low- and high-protein foods to give a protein intake matched to their presumed requirements for growth (Kyriazakis and Oldham, 1993).

Figure 7.7 shows the results of an experiment in which individually penned growing lambs were offered a high-protein food containing 235 g CP/kg and a lower-protein food containing either 78, 109, 141 or 172 g CP/kg. In the cases of the first three treatments, the lambs chose a mixture providing CP in the

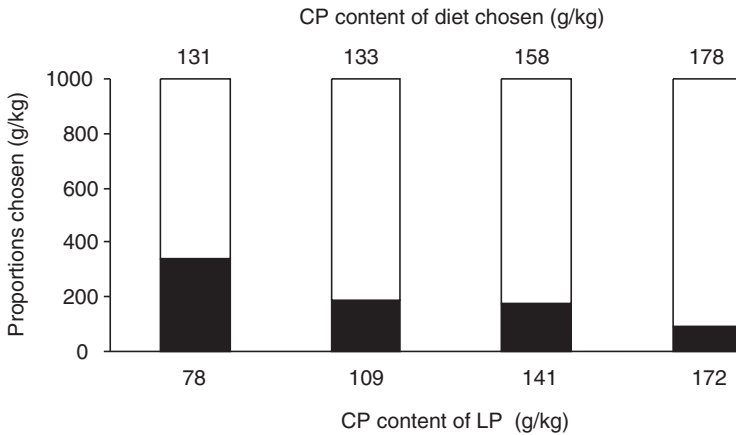


Fig. 7.7. Selection of crude protein (CP) by growing lambs offered HP (235 g CP/kg) and LP foods. The CP contents of the LP foods are shown at the bottom of each column and the resulting CP content of the diet chosen at the top (from Kyriazakis and Oldham, 1993).

range of 130–160 g CP/kg, i.e. within the optimum range. When the low-protein food contained 172 g CP/kg they avoided it almost completely, apparently to avoid a toxic excess of nitrogen in the rumen. The motivation for selection of an adequate protein concentration is strong, as sheep are willing to make at least 30 responses in an operant-conditioning situation to obtain a food reinforcement in order to obtain a ‘balanced’ diet (Hou *et al.*, 1991a).

An attempt to resolve the question as to whether ruminants select diets to optimize rumen degradable protein (RDP) intake was made by James *et al.* (2001), who fed sheep on basal foods formulated and demonstrated to be deficient, adequate or excessive in RDP, and then gave choices between their basal food and the same food with urea (which provides RDP) added. In every case the animals ate more of the urea-supplemented food, even though in the cases of the RDP-sufficient and -excessive foods this provided them with a great excess of RDP. Clearly, these sheep were not managing to control their intake of RDP in order to prevent an excess.

Prerequisites for Diet Selection

Against the background of clearly demonstrated abilities of animals to select in a nutritionally appropriate manner when offered a choice of foods, there are numerous examples of animals that appear not to be making appropriate choices (from the standpoint of the human observer), implying that their food preferences are governed by factors other than, or additional to, nutritional wisdom (ability to match the foods selected to provide the correct balance of nutrients) (Forbes and Kyriazakis, 1995). It is therefore necessary to examine such cases in order to provide guidance on good practice in carrying out studies on food choice and diet selection.

The need for sensory differentiation

Clearly, animals must be able to differentiate between two or more foods if they are to select proportions in order to make up a balanced diet. If the nutrient in question is required only in trace amounts, and especially if it is colourless, it is necessary to give a cue by means, for example, of artificial flavouring and/or colouring. This is not usually a problem with foods differing markedly in protein content, but is surely necessary when a single amino acid is deficient in one food and in excess in the other.

Given that there are these sensory differences, the animal might have an innate preference for one food, e.g. because of its sweet taste. However, nutritional value is not always closely correlated with sweetness, so that the associations the animal learns, between sensory properties and nutritive value, are much more valuable to it than innate preferences. Thus, a bitter flavour imparted to food will cause initial rejection but, if the nutritional value remains balanced, then normal intakes are resumed within a few days. A good example of this is the lack of effect of inclusion of Bitrex, the most bitter substance known to man, on the long-term intake of food by pigs (see Chapter 6). Thus, there is no need to be concerned about the exact nature of the flavours used to differentiate between two foods, as animals soon learn to associate them with the nutrient yields of the foods in which the flavours are incorporated and to eat for nutrients rather than just for taste.

A clear example of the need for sensory differentiation and learning is provided by work with young broiler chicks (Kutlu and Forbes, 1993c), in which mild heat stress increases the requirements for ascorbic acid (vitamin C), offered a choice between a normal food with no supplementary ascorbic acid and an exactly similar food containing 200 mg/kg of protected ascorbic acid. When neither food was coloured, the birds did not differentiate between them and ate at random. When each food was given a different colour (red or green), however, and the birds were trained to associate each colour with the nutritive value of the food by giving them separately in half-day periods for 6 days, they subsequently selected significantly more unsupplemented food when in the thermoneutral environment and significantly more supplemented food when in the hot environment. A sudden change in environmental temperature was followed by a gradual change in the proportions of the two foods eaten as the birds learned that the red (or green) food was no longer the one that made them feel metabolically most comfortable.

In summary, farm animals can select a diet appropriate to their metabolic needs as long as the foods offered are clearly differentiated by flavour or colour and the animals have the opportunity to learn the nutritional difference between the foods.

Training and experience

In order for an appetite for a specific nutrient to develop, it is necessary for animals to learn to associate the sensory properties of each food with its

content of the nutrient in question. In many cases they will learn about two foods if they are introduced simultaneously, but they may learn more quickly if each food is given in turn for a few days. It is evident that some form of 'education' about the foods on offer prior to a choice may aid animals in their later discrimination between foods, but in many cases no advantage of such training has been noted. In group situations, there may be opportunities for animals to learn about food in other ways, and 'training' periods may be less important than for individual animals. A training period may be a hindrance to choice feeding being accepted commercially, due to the high levels of management involved.

Poultry

While large farm animals have been given alternating days on two foods to be offered later as a choice, half-day alternating periods have been used for broiler chickens, on the basis that smaller animals, with a higher rate of turnover of nutrients, need shorter periods of exposure to learn the characteristics of different foods. It takes hens only a few hours to recognize a change in protein content of the food.

Training birds by accustoming them to whole grains at an early age appears to confer benefits at the later stages of growth, in terms of ability to select foods to meet nutrient requirements. Broilers trained from 10–21 days after hatching by giving whole sorghum and protein pellets showed no difference in weight gain compared with complete-fed or untrained choice-fed birds, but the trained birds were significantly more efficient because the inexperienced choice-fed birds ate much greater excess of the protein concentrate in the first 10 days of the experimental period than those with previous experience (Covasa and Forbes, 1993).

No effect was found on subsequent selection for whole wheat of time of access to wheat nor deprivation during the rearing phase, but those birds given wheat alone for part of each day during rearing ate significantly more wheat during the growing phase (Covasa and Forbes, 1995a). They had heavier proventriculus and gizzard than those given mixed wheat and starter crumbs during the rearing phase, but growth and abdominal fat pad weight were unaffected by treatment. Thus, it may be beneficial for subsequent diet selection to remove the standard food while offering whole grains to young chicks during the training period.

Pigs

Kyriazakis *et al.* (1990) trained growing pigs to recognize the difference between HP and LP by offering them as single foods on alternate days for 1 week before offering both in a choice-feeding situation but they did not compare their performance with untrained animals, so whether it is helpful or necessary is not known. Newly weaned pigs do not seem to benefit, in terms of subsequent ability to select between HP and LP, from a period of training such as that advocated by Kyriazakis *et al.* (Dalby *et al.*, 1995). Whether they were

given alternate daily exposure to the foods for 6 days, given one for 3 days and the other for 3 days or given free choice for 6 days, there was no difference in food intake or growth rate over the next 21 days of free-choice feeding, compared with controls fed a single, adequate food throughout, but all choice-fed pigs ate significantly less protein than controls.

Comparisons have been made between selection for protein by trained and untrained growing pigs (Morgan *et al.*, 2003). Groups of four pigs were formed containing either an individual trained to select between two foods or an untrained control animal, and all were offered LP and HP foods. Over a 2-week period there was no effect of the trained pig on the growth rate. However, for the first few hours, the groups with the trained pig were more consistent in selecting a balanced diet close to that of the trained pig, while the untrained groups showed much more variation initially, but stabilized within 3 days. Thus, although this form of training does influence piglets, the untrained piglets learn to achieve a balanced diet so quickly that there is no effect on long-term performance.

Cattle

In a study of training in dairy cows, they were offered two mixtures of grass silage and concentrates, one with a high concentration of protein, the other low in protein (Tolkamp and Kyriazakis, 1997). Some cows were offered both at the start of the experiment, while others had only one food for the first 3 days followed by just the other for the next 3 days. Yet other animals had two such periods of alternate access before being offered both as free choice. After the first week, untrained cows selected 0.66 HP, significantly different from random. From the third week onwards, those given one or two periods of 3-days access to each food alone established similar diet choice: 0.70 HP. It was concluded that, under the circumstances tested, training was not required for cows to distinguish between two mixed foods with different calculated MP/ME ratios and to select proportions significantly different from random.

Identifying 'nutrient requirements' of animals (the need for adequate control)

For the proper design and interpretation of diet selection experiments, we first have to be clear about what food resource(s) it is we are studying. Then we need to formulate foods that provide a greater and a lesser ratio of resource:energy than the animal requires. This entails knowing what the animal's 'requirement' is for the resource in question and for energy, which typically entails the feeding of a range of single foods with different ratios of resource:energy (made as mixtures of the two foods to be given as a choice), building up a dose-response curve that allows us to define the optimum.

In many other diet selection studies, the optimum resource:energy ratio has been taken from the literature, which may be satisfactory in the case of intensively managed animals in which genotype, diet and environment are well characterized. It can, however, be easy to make unwarranted assumptions. It is generally considered, for example, that chicks do not require supplementary

ascorbic acid in their diet, yet they choose a significant proportion of a supplemented food (see Chapter 8), which might be taken as evidence for unwise selection had it not been demonstrated that, under the conditions of the experiments in question, dietary ascorbic acid was beneficial to growth and food intake, especially at high environmental temperatures.

Just because two foods offered in a choice situation intentionally differ in their content of a nutrient, e.g. protein, according to some calculation or limited analysis, does not restrict animals to selecting only on the basis of that nutrient. This is especially true for protein, where it is notoriously difficult to formulate foods with different protein contents but the same ratio of amino acids. Pigs given choices between pairs of foods containing 220/180, 220/140, 220/100 or 180/100 g CP/kg grew well and efficiently, but it was found that the isoleucine content of the chosen diet was almost exactly what would be predicted for optimal growth, suggesting that the pigs might have been selecting in order to obtain the correct amount of this most limiting amino acid rather than CP as intended (Bradford and Gous, 1991). Proper interpretation was not possible, therefore – a situation existing with most protein selection experiments.

Even when diets selected by choice-fed animals are compared with 'control' diets, care must be taken not to draw unwarranted conclusions. For example, broiler chicks given free access to foods containing 456 and 86 g protein/kg selected proportions that gave the same growth as controls (Kaufman *et al.*, 1978). As they grew, the proportion of HP taken in the diet fell to give a decline in the protein content of the selected diet from 250 to 140 g/kg. The authors pointed out that this was a lower protein content than the single food given to controls, implying that the birds had not selected appropriately but, as the control food contained an excessive amount of protein (265 g/kg), this was not surprising.

Previous nutritional history

Animals rendered deficient in a nutrient will, when given access to a choice of foods one of which provides an excess, eat more of that food than do non-deprived control animals. For example, pigs made fat through feeding a low-protein food subsequently selected a much higher protein content when choice-fed (233 g CP/kg) than those previously given a high-protein food (175 g CP/kg); this diet selection enabled them to deposit fat at a slower rate and protein at a faster rate than the latter animals and return their body composition to a 'desired' one (Kyriazakis and Emmans, 1991). It must also be borne in mind that gender influences growth potential and that males chose a diet higher in protein than did females (228 versus 181 g CP/kg).

As the nutrient requirements of animals vary with stage of growth, gender, breed and nutritional history, so diet selection should not be expected to be static or uniform across animals. Great care is needed, therefore, in deciding which is more 'correct', the choices made by selecting animals or the expectations of the human observer, when interpreting the results of diet selection studies. The animal's 'target' might be different from that assumed by

us on their behalf; for example, choice-fed animals are often somewhat fatter than those given a single, commercially optimal food, the implication being that we often 'force' animals to be a little leaner than they 'want' to be.

Concentrations of the resource being studied

It is short-sighted to provide two foods with high and low contents of the nutrient in question such that the optimum diet consists of half of one and half of the other, because equal intakes of the two foods can be interpreted as random eating or directed choice where the optimal is 50:50 (see Lawson *et al.*, 2000). Better to design foods for which an optimum mixture is well away from 50:50, as in the study of Tolkamp and Kyriazakis (1997), so that a statistical comparison of the observed proportion of one food can be tested against the null hypothesis of 0.5.

For animals to make nutritionally meaningful choices, all foods on offer should be nutritionally imbalanced, otherwise there is no benefit to be had in choosing. Many experiments have offered a choice between two foods, neither of which is demonstrably imbalanced. For example, several experiments on amino acid appetite in growing pigs have shown that the pigs could grow perfectly well on either given alone so that, when given a choice between the two, individual animals adopted different choices and overall no significant selection was apparent.

There are instances where animals have been given a choice between two foods in both of which the content of the nutrient under study is below their requirements, either due to miscalculation of their requirements or intentionally. The expectation is that the animal will consume the less limiting food (e.g. the food with slightly lower protein over a food very low in protein) and avoid the more limiting one. With laying hens (Holcombe *et al.*, 1976), broiler chickens (Shariatmadari and Forbes, 1993), growing pigs (Kyriazakis *et al.*, 1990) and sheep (Kyriazakis and Oldham, 1993), animals consumed appreciable amounts of the more limiting food, i.e. more than just occasional sampling. This is puzzling and suggests that they are confused, because neither food provides sufficient protein. Choosing between two limiting foods may be more difficult than choosing between two which can, together, provide a balanced mixture.

Environmental factors

Farm animals are easy to train in operant-conditioning situations in which they have to 'work' for a food by pressing a coloured panel. If the animal has to work harder to obtain one food than the other, then it is likely to bias selection in favour of the food that is obtained with less effort.

Because two foods offered in choice are usually given in different troughs, sometimes one trough will be in a more favoured position than the other. We have observed such an effect due to the positioning of a heater for newly weaned piglets, in which food in the trough closer to the source of heat was

eaten in greater quantities than food further away, to the extent of biasing diet selection against the choice of an optimum diet.

Another constraint on completely free choice between foods would be if one food were to be more difficult to obtain than the other. Ginane and Petit (2005) offered heifers a leafy (L) and a coarse (C) hay, together with a physical and a temporal accessibility constraint given singly or combined. The physical constraint involved covering the trough containing L with a steel grid of 4 cm mesh size, and the temporal constraint limited the daily access time to both hays to 4 h. The physical constraint made the heifers decrease their choice (proportion of feeding time or intake) for L regardless of access time, whereas the temporal constraint had no significant effect on choice (see Fig. 7.8). The presence of mesh over food L caused a reduction in the proportion of L eaten and increased the rate at which L was eaten. Reduction in time of access from 24 to 4 h reduced total food intake while increasing the rate of eating. Even when they were not constrained, the heifers continued to eat some C, thereby showing preference for a mixed diet.

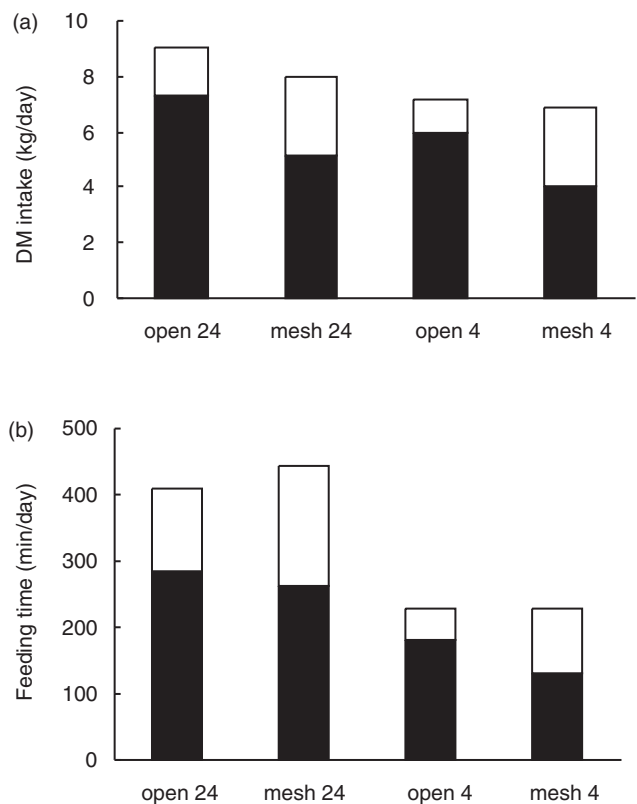


Fig. 7.8. (a) Daily dry matter (DM) intake and (b) feeding time on leafy (open bars) and coarse (solid bars) hays when offered in a choice situation, according to physical (open or 4 cm mesh) and temporal constraints (24 or 4 h of access daily) (from Ginane and Petit, 2005).

We learn from this example that there are complex interactions between rate of eating and food choice that could make it difficult to interpret the results unless we were aware of the effects of the constraints.

Social interactions

When animals are in a group in which a social hierarchy has developed, they often have to compete for access to food(s). An animal low in the pecking order might not be able to gain equal access to both foods, while a dominant animal might feel obliged to maintain its position by eating more of the 'better' food than is optimal for its nutritional status. This situation could be accentuated when the trough space is not sufficient for all animals in the group to eat simultaneously, so that free and continuous access to both foods cannot be achieved. Such bias can be overcome by keeping animals in individual pens or cages. However, it has been shown in some situations that animals learn about foods more quickly when they are in groups than in individual cages (see Chapter 6).

We know that the behaviour of animals in groups can differ markedly from that of individuals, and there is strong evidence of nutritional wisdom being passed between individuals (e.g. mother to offspring, older to younger animals, see Chapter 6). A serious study should be made of the effect of single-penning and the social environment on diet selection, and particularly on the variation in selection between individuals. If the potential to use diet selection methodology to study the optimum nutrition of farm animals is to be realized, then practical problems such as optimum group size and the need for a training period need to be resolved.

Poultry

Most chicks in a choice situation begin to eat from both foods on offer within a fairly short time, but there is often a minority that is slow, and there may be a few individuals who fail to select close to an appropriate diet. However, animals living together in a group tend to copy from each other and there is usually a leader that guides the others to the desired food. Individually caged broilers that did not voluntarily consume any wheat, when given a choice with a standard grower food, immediately started to eat significant amounts when put in pairs, irrespective of whether the partner was formerly a wheat-eater or not.

Within 5 days of being given a choice between a calcium-deficient food and calcite, broilers consumed enough calcium when kept in groups (Joshua and Mueller, 1979). However, individual caging inhibited this ability even when there was visual contact between birds, but birds caged individually after learning to eat calcium in a group took an adequate amount of calcium.

Pigs

One of the 'rules' for successful choice feeding is that animals have access to both choices *ad libitum*. Clearly, this will not always occur when animals are

housed in a group situation. However if the feeding behaviour of pigs is adaptable and the nutritional wisdom 'strong', then pigs may wait for the trough with the 'right' choice to become available.

It is difficult to separate the effects of floor space, group size and feeder access on food intake and performance (see Chapter 17). These may also be confounded by other factors such as floor type, straw provision and environmental temperature. The influence of these factors on dietary selection by pigs may be greater if entrance to only one feeder in a choice situation can be gained. Thus, the number of feeder spaces available may be crucial in a choice situation and is likely to be influenced by the group size and stocking density. The question is raised as to whether pigs will wait for their choice or attempt to quell their hunger by eating from the feeder to which they can gain access.

Sheep

Transfer of learned aversion from mother to offspring has been demonstrated in sheep. Ewes were allowed to eat *Amelanchier alnifolia* (a shrub) and trained, with lithium chloride, to avoid *Cercocarpus montanus* (also a shrub) (Mirza and Provenza, 1994). After training, lambs aged either 6 or 12 weeks were put with their mothers for 5 min each day for 5 days in a small pen with both foods available. Trained ewes ate no *C. montanus*, while control ewes took equal amounts of each. The lambs were then weaned and, 7 days later, tested, at which time trained lambs showed a tendency to prefer *A. alnifolia* (79% and 72% for lambs trained at 6 and 12 weeks, respectively), while lambs from control ewes showed no preference (49% and 53%, respectively).

Familiarity with straw has also been shown to increase its intake by lambs at a later date. After weaning, lambs were fed indoors on concentrates and straw and the intake of straw was higher in those previously exposed to straw when with their dams, especially in the first week, than those not exposed before weaning.

We learn from such examples that experimental studies on diet selection must use animals from a homogeneous social background.

Aversive compounds: toxins

Animals learn to ignore innately aversive cues (e.g. bitter tastes) if they are paired with essential nutrients, but such cues are usually associated with toxic substances, such as tannins. An example of the presence of a toxin in one food biasing diet selection is provided by an experiment in which growing pigs were given choices between an LP food, with too low a protein:energy ratio to support normal growth, and an HP food with an excess of protein:energy, where one food or both contained rapeseed meal, which has a bitter taste and may contain mild toxins (Kyriazakis and Emmans, 1993).

When neither or both foods contained rapeseed meal, the choice was such as to give an optimal dietary protein content (205 and 206 g CP/kg, respectively); however, when HP contained rape the pigs chose a diet containing 155 g CP/kg

while, when it was in LP, they chose 271 g/kg. In other words, they avoided rapeseed meal sufficiently to give themselves grossly imbalanced diets as far as protein was concerned. From these results it might be predicted that rapeseed is toxic, but there was no difference in growth rate between pigs given the food high in rape and those on the low-rape food. It could be that the toxicity of rape is of such low severity that, although it generates mild discomfort, this is not sufficient to depress food intake.

There are many other examples of situations in which animals have to trade off one discomfort with another (see Chapters 6 and 8). Therefore, we must assess the likelihood that one or more toxins, inadvertently included in one food but not the other, bias results in an unexpected manner.

Physical form of food

Some foods are rendered easier or more difficult to prehend by physical treatment, and this can affect animals' selection as one form involves more 'work' to eat than others. For example, broilers were offered maize (either whole grains, cracked or ground) and a protein concentrate (43.7% CP) (Yo *et al.*, 1997b). When maize was fed as whole grains, the proportion of protein concentrate in the selected diet was significantly higher (35.1%) than with cracked (29.3%) or ground maize (29.1%). Although birds could eat the whole grains faster than either the cracked or ground maize, they probably found it more difficult to swallow and digest and therefore ate less of it than when the maize was easier to swallow.

When foods were offered to sheep in pairs, preference was strongly related to rate of eating when that food was offered alone (Kenney and Black, 1984). Reducing the length of straw from 30 to 10 mm increased rate of eating from 5.5 to 12.4 g/min – and also the preference. With rapidly eaten foods (> 24 g/min) there were no differences in preference associated with rate of eating.

These examples teach us that something as simple as physical processing of food can influence the choices animals make and this needs to be taken into account, particularly when making comparisons between the results of different experiments.

Neophobia and familiarity

Although it was stated above that animals continue to sample even those foods they have learned as being imbalanced, there are many examples of animals showing reluctance to sample novel foods. This is particularly true if the familiar food(s) is fairly well balanced with regard to nutrient composition: prior experience can be a very powerful influence in determining food choice.

Lambs show a persistent preference for the type of shrub they had access to from 50–110 days of age, and similarly prefer either an onion- or garlic-flavoured complete food, whichever they experienced, from 30–110 days of age (Nolte and Provenza, 1992). Therefore, familiarity can influence food choice but is not likely to override strong, nutritionally based preferences.

Mechanisms of Diet Selection

Pathways are presumed to exist that transmit information concerning the metabolic effects of a food to the brain to allow development of learned associations with one or more sensory properties of the food. The simplest such pathway would be via the blood. For example, a low blood calcium level arising from eating a low-calcium food might be sensed by the brain, which would respond by increasing the intake of an alternative, high-calcium food.

There have been a number of proposals as to the involvement of neural transmitters in the control of diet selection in rats. For example, carbohydrate intake appears to be enhanced by hypothalamic injections of noradrenaline and neural peptide Y (NPY) and inhibited by 5-HT. There is a steady rise in hypothalamic NPY concentration from birth to puberty, at a time when protein intake increases; however, the optimal protein:energy ratio in the diet declines during this period (see Chapter 8), so the relationship between hypothalamic NPY and selection for protein:energy is not in the direction expected if NPY is indeed solely or mainly responsible for selection between carbohydrate and protein.

There have also been theories of the involvement of individual amino acids in the control of food choice. Given a choice between a tryptophan-deficient food and a control food, chickens preferred the latter but, when the piriform cortex was separated from the rest of the brain, they had difficulty in discriminating between the two foods (Firman and Kuenzel, 1988). It is possible that the piriform cortex monitors amino acid levels, or that its separation disrupted the sense of smell (it is part of the olfactory system), or both of these. However, lesions of the *nucleus taeniae*, which is also a part of the olfactory system, did not affect ability of birds to choose the right food.

As so little is known about neural pathways and transmitters in farm animals, the interested reader is referred to a book reviewing the neurobiology of food choice in laboratory animals (Berthoud and Seeley, 1999).

Timescale of control of diet selection

It might be supposed that animals that start to eat a meal from one food will tend to find the other food more attractive as the meal progresses. Sixty per cent of the meals taken by broilers given free access to high- and low-protein foods are from both foods, i.e. there is a strong tendency to change foods during the meal (Shariatmadari and Forbes, 1992a). As metabolic receptors would not have had time to be significantly influenced by the food eaten earlier in the meal, this suggests that the choice of food is predominantly controlled by learned associations between the foods and their hedonic properties rather than by immediate feedbacks.

In order to look for an explanation as to how short-term feeding behaviour is involved in food choice, Yeates *et al.* (2002) have analysed large amounts of meal data collected automatically from cows given free access to foods high

(HP) and low (LP) in protein, in three experiments. It was concluded that the cows did not attempt to select a consistent diet in terms of protein:energy ratio either within a single meal or in a short sequence of meals, as there was no difference in the proportion of visits to HP and LP during meals compared with random sequences of feeding bouts. The authors concluded: 'Our present analysis does not suggest what the most relevant time scale is, except that is must be longer than a meal'. Further detail is given in Chapter 2.

As an illustration of the greater stability of choice over longer periods, Fig. 7.9 shows the proportion of HP taken by eight cows offered a choice of HP and LP over a period of 28 day (Kyriazakis *et al.*, 1999). Choice in consecutive 8-h periods is very variable and ranges from wholly HP to mostly LP. Cumulating these into 24-h periods greatly reduces, but certainly does not eliminate, the variability, while 7-day means show great consistency, with a steady decline in selection for HP as milk yield declines in mid-lactation. It can be concluded from this that diet selection was being controlled in these cows over a timescale of 1–7 days.

Other research with cows shows selection changing in response to changes in protein content of the foods on offer, starting within 1 day after the change and being complete by about 4 days later (Tolkamp *et al.*, 1998b, Fig. 13.2). It has to be said that in this latter case the changes in food composition were by means of addition or removal of urea from both foods, which leads to rapid changes in ruminal ammonia, whereas in the earlier example (Fig. 7.9) the only change was the very gradual one of advancing lactation.

In sheep the timescales are similar, i.e. regulation of protein content by selection between normal foods with different protein contents to produce a

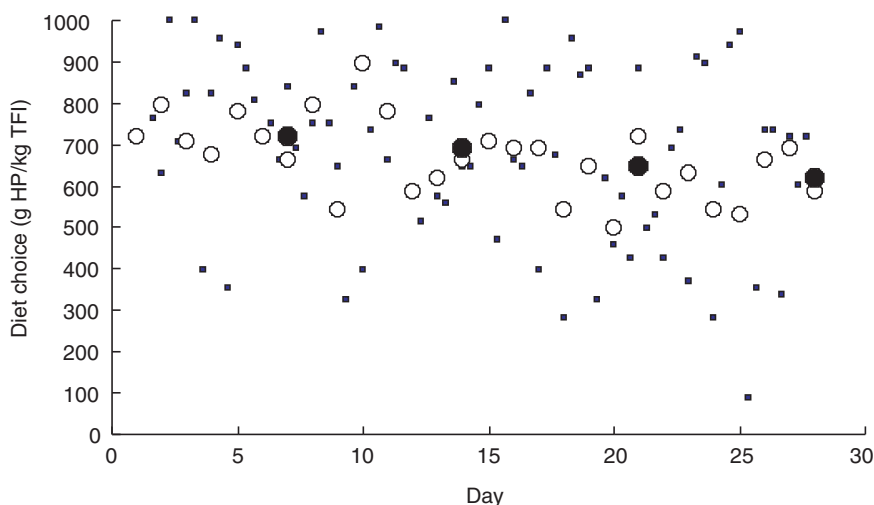


Fig. 7.9. High-protein (HP) food intake as a proportion of total food intake (TFI) by eight lactating cows given a choice of HP and LP over periods of 8 h (■), 24 h (○) and 7 days (●) (from Kyriazakis *et al.*, 1999).

stable diet over 3–7 days (Kyriazakis *et al.*, 1994), but a much more rapid adjustment as a consequence of feeding on a rapidly fermentable food (James and Kyriazakis, 2002). In the opinion of Kyriazakis *et al.* (1999): ‘... the question to be asked in relation to diet selection is not “what time period matters to the animal?” but “how much change or deviation in the internal state is the animal prepared to accept?”’.

In the medium to long term, internal changes in the animal do lead to appropriate changes in selection, presumably in order to control some aspect of the animal’s state rather than to stabilize some short-term changes in blood hormones or metabolites. Examples are given in Chapter 8.

Nutrient infusions and preloads

In order to understand the link between metabolism and learning, numerous experiments have studied the effects of loading a substance or a certain type of food into the digestive tract or bloodstream of animals and observing the effects on diet selection.

Poultry

Mechanisms of diet selection have been investigated in more detail by giving overnight-fasted broilers a meal of either HP or LP, to which they had previously been accustomed, and then offering both a choice. Whether the choice was given immediately after the initial meal or delayed for 1 h, significantly greater amounts of the opposite food were eaten (Forbes and Shariatmadari, 1996) (Fig. 7.10). When the initial meal was given by tube into the crop there was no significant preference subsequently, so it seems as if it is necessary for the bird to taste the food in order to predict its protein content according to its previous experience of the two foods.

The independent control of energy and protein intakes was further demonstrated by force-feeding broilers with 40 g of food containing 60, 135, 215 or 295 g CP/kg daily for 10 days while given free access to foods with 60 and 295 g CP/kg (Shariatmadari and Forbes, 1992b). During the force-feeding period, the higher the protein content the greater the voluntary food intake, but the proportion of HP chosen was lower, resulting in an almost constant level of protein intake across the treatments. After the cessation of force-feeding, the birds which had been force-fed with the two highest levels of protein continued to have higher voluntary food intakes but with a lower proportion of HP, and deposited less protein in the carcass, than birds force-fed with lower-protein foods.

This suggests that, although compensating only partly for the protein given by gavage during the force-feeding part of the experiment and thus ending this period with more carcass protein, the birds force-fed with the higher levels of protein then responded to their higher body protein content by voluntarily consuming a diet with a lower protein concentration than those given lower protein by tube.

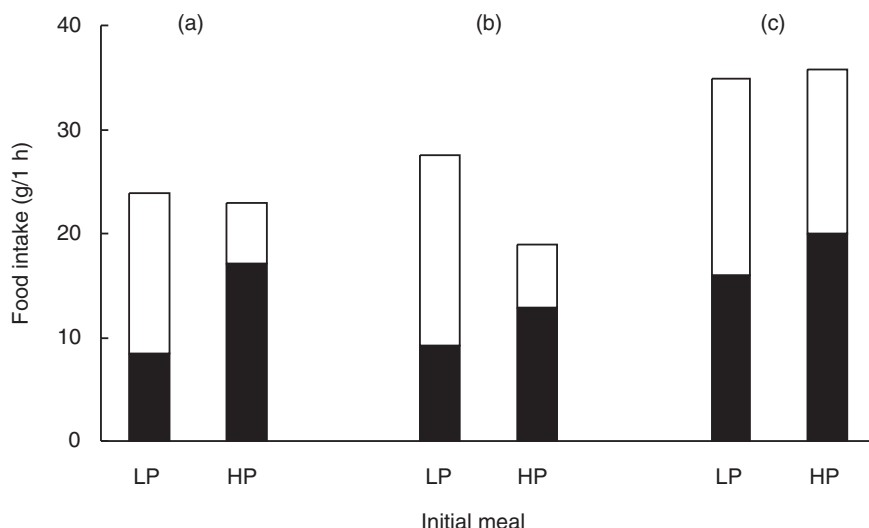


Fig. 7.10. Intake of low-protein (70 g/kg, solid bars) and high-protein (300 g/kg, open bars) foods offered in free choice by broiler chickens given (a) previous access to one food (LP or HP) for 10 min and then immediate access to both; (b) previous access to one food (LP or HP) for 10 min and then access to both after 45 min without food; (c) 20 g of one food given into the crop by gavage and then access to both after 45 min without food (from Forbes and Shariatmadari, 1996).

Sheep

It might be expected in ruminant animals that products of digestion in the rumen would affect diet selection. Infusion of sodium acetate or sodium chloride intra-ruminally in sheep gave large reductions in the intake of concentrates but had no effect on hay intake (Engku Azahan and Forbes, 1992). The effect was almost as great for chloride as it was for acetate, so the major reason for the decreased intake was probably osmotic (see Chapter 3).

Physiological State

Animals' nutrient requirements usually vary over time according to changes in nutrient demand as influenced by growth, pregnancy, lactation, egg laying, disease and season of the year. It is to be anticipated that their choice between high- and low-protein foods would change with this changing optimum protein:energy ratio of the diet.

Differences between individual animals with different genotype, gender and physiology are also expected to influence selection between foods. Thus, males with higher growth potential than females generally choose a diet with a higher protein:energy ratio.

Poultry

As animals grow, the increased cost of maintenance and the increase in rate of fat deposition mean that the optimal ratio of protein:energy in the diet declines. It is to be expected, therefore, that broilers offered a choice of foods higher and lower in protein:energy yield would progressively eat a greater proportion of the food lower in protein; this has been observed to occur with several different combinations of protein content in the two foods (Shariatmadari and Forbes, 1993). Males grow more quickly than females and it is not surprising, therefore, that they choose a high proportion of high-protein food when given a choice with a low-protein food (see Fig. 7.11).

Correlations between selection for protein and rates of deposition of protein and fat in the body might be the cause rather than the result of different growth potentials at different ages or in the two genders. In attempts to resolve cause and effect, corticosterone has been used to reduce the ratio of muscle:adipose tissue being deposited in broiler chickens. In a short-term experiment in which 2-week-old broilers were offered a choice between whole wheat and a balancer food, corticosterone injection at 4 mg/day for 5 days induced a significant preference for the whole wheat and thereby a reduced protein:energy ratio in the diet, as predicted (Covasa and Forbes, 1995b).

In a more comprehensive experiment, male broiler chickens were given free choice of three foods in each of which protein, lipid or carbohydrate was isocalorically substituted for one other macronutrient (Malheiros *et al.*, 2003).

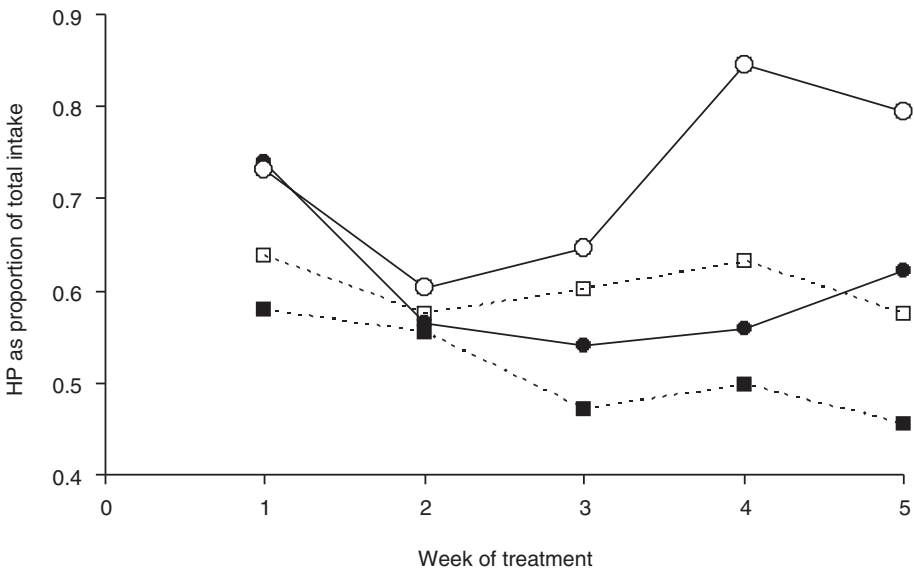


Fig. 7.11. The effect of corticosterone on the proportional intake of HP food in male (circles) and female (squares) broiler chickens. Closed symbols, control; open symbols, corticosterone (from Sahin, 1998).

Treatment with corticosterone (45 mg/kg of food) increased liver and fat pad weight and tended to reduce the dietary content of protein and increased that of fat; there was no effect on daily food intake.

Not all results are as predicted, however. Male and female broilers were offered high- (HP, 285 g CP/kg) and low-protein (LP, 70 g CP/kg) foods and given daily intramuscular injections of 4 mg/kg of corticosterone and had, as a result, a decrease in protein accretion and an increase in total body fat content (Sahin and Forbes, 1997b) (Fig. 7.11). Corticosterone significantly *increased* the intake of HP as a proportion of total food intake from the third week of treatment in males (from 195 to 245 g/kg) and from the second week in females (from 183 to 203 g/kg). Rather than reducing the protein:energy ratio of the diet selected, corticosterone treatment increased the preference for the HP food. This is likely to be due to the increased protein turnover and/or to increased protein degradation to supply the carbon skeleton used for fat synthesis.

Similar increases in the ratio of protein:energy intake were found with inclusion of corticosterone in the diet of broilers (Sahin and Forbes, 1997a) and laying hens, in which it decreased the egg production (Sahin and Forbes, 1999). This might be due to the fact that corticosterone changes the oestradiol profile in plasma, resulting in the change in the route of lipid transport from the yolk to the abdominal fat pad, and then builds the new body profile with an increase in fat anabolism. Therefore, the demand for protein is increased rather than reduced because of the wasteful usage of dietary protein.

Pigs

As with broiler chickens, growing pigs show a decrease in the protein:energy ratio of the diet they choose from high- and low-protein foods (Kyriazakis *et al.*, 1990).

Stimulation of the rate of protein deposition – and depression of fat deposition – in choice-fed growing pigs by daily injections of 4 mg STH significantly depressed food intake. This decrease was accounted for entirely by a reduction in the amount of the low-protein food (120 g CP/kg) selected (the other food contained 240 g CP/kg), so that energy intake was reduced but total protein intake was unaffected (Roberts and Azain, 1997). When the treatment was stopped intake increased, so that within 3 days it had reached pre-treatment levels, but this was by increased consumption of both high- and low-protein foods rather than specifically by normalization of intake of the low-protein food.

Sheep

It has been observed that growing lambs offered high- and low-protein foods chose a diet well matched to their requirements for growth and, even when one of the foods required up to 30 responses to obtain a reinforcement, the lambs responded accordingly to maintain this balanced diet (Hou *et al.*, 1991b).

Pregnant ewes select a significantly greater proportion of a food of high CP concentration than non-pregnant ewes, reflecting their enhanced demand for protein (Cooper *et al.*, 1994). Thus, diet selection is driven not only by the composition of the foods on offer but also by the requirements of the animal, which change in a systematic manner with growth and reproductive cycles.

Conclusions

The theory that animals can select, from a choice of foods, a diet that meets their requirements is difficult to prove, but it is clear that there are many situations in which they show considerable 'nutritional wisdom'. The most widely studied situation is one in which animals are offered two foods, with higher and lower protein contents than required in relation to the energy concentration of the diet. Manipulating the protein content of one or both foods is accompanied by diet selection to maintain a fairly constant protein intake.

A training period, in which the foods are offered alternately, can be useful in ensuring that animals unambiguously associate each food with its nutritional value. Individuals can also learn about the differences between foods indirectly, from conspecifics, particularly the mother.

It is far from clear what internal mechanisms are involved in controlling diet selection; very few studies have been made in this area with farm animals. What is clear is that the principles established in this chapter for protein apply also to many other components of the diet, as will be demonstrated in Chapters 8 and 13.

8

Diet Selection: Practicalities

In Chapter 7 we presented evidence for the ability of animals to select between foods in order to obtain a diet balanced for energy and protein; this is based on learned associations between internal and external stimuli, covered in Chapter 6. We have also discussed the prerequisites for successful studies of diet selection and effects of changes in physiological state, especially growth. In this chapter we bring the subject closer to application by covering those aspects of diet selection that can be utilized in practice and, again, selection for protein is the main focus of research because of the economic and biological importance of protein intake, in relation to energy intake. Examples of appetites for nutrients, including protein, are given in Chapter 13.

The controversial subject of self-medication is discussed; this is of great current interest with the banning of the routine use of antibiotics and other drugs in livestock production and the consequent search for natural remedies for the diseases associated with intensive agriculture. The potential for using applied selection methodology to the commercial situation is also considered.

It has been demonstrated in Chapter 7 that, where two foods differ in the concentration of a nutrient such that one contains more and the other less than optimal, in relation to energy requirements, then animals eat the two in such a ratio that the intake of the nutrient in question is optimized. The higher the demand for the nutrient, the greater should be the proportion of the food high in that nutrient. Note that the animal can cope with mildly imbalanced diets but at a metabolic cost; where possible, it should avoid this cost by eating that amount and mixture of foods that minimizes the cost (discomfort, Chapter 10) of metabolism.

There is a large literature on selection by herbivores at pasture, not surprising given the agricultural and ecological significance of herbivores, especially ruminants. Not only do most grazing animals have to make choices between different species of plant, they also can choose which part of the plant to eat – this ability varies depending on the width of the incisor arcade – and whether to

select against old herbage. As this book does not cover herbage intake, this important subject is omitted, but see the proceedings of relevant conferences (Hodgson and Illius, 1998; Lemaire *et al.*, 2000) and examples of experimental (Parsons *et al.*, 1994) and modelling (Thornley *et al.*, 1994) reports.

Self-medication

In the widest sense, all successful diet selection could be described as self-medication. An animal choosing a greater or lesser proportion of a food in order to match its optimum intake is defending itself against an illness (often covert) – that of nutrient deficiency or excess. However, we will use the term here in its more usual sense, that is the ability of animals to avoid overt illness by making appropriate food choices.

Much of the evidence for self-medication is anecdotal (Engel, 2002), but here we use only examples where well-designed experiments have adopted controlled conditions (Chapter 7).

Toxins

Tannins are a constituent of many plants, including some available to animals grazing on the range. They can be toxic (causing haemorrhagic gastroenteritis, necrosis of the liver and kidney damage), but can also be beneficial by binding proteins to reduce their breakdown in the rumen and thus allow more proteins to enter the intestines, where they can be broken down and absorbed as amino acids.

Polyethylene glycol (PEG) is a substance that attenuates the aversive effects of tannins and when sheep eat foods high in tannins they adjust their intake of PEG to balance the amount of tannin in their diet (Provenza *et al.*, 2000). In some animals, intake of PEG continues for at least 1 week after tannin has been removed from the diet – presumably PEG alone did not cause discomfort so there was no disadvantage in continuing to eat it once it became an accustomed food ingredient. Sheep also seek out locations where they have learned to find PEG when offered nutritious foods high in tannins (Villalba *et al.*, 2002).

Given access to a range of plants, grazing animals usually eat sufficient variety that the intake of one, with its attendant toxins, is not excessive. What, however, if most of the plants eaten deliver toxins? If two or more toxins are detoxified by the same pathway, they depress intake and preference additively (Burritt and Provenza, 2000). However, if the various toxins act on different organs and detoxification pathways, they are less harmful than a large dose of any single toxin. Sheep and goats maintain high levels of intakes when they can select a variety of shrubs that contain different toxins, and the benefit is far greater than that due to medicines such as activated charcoal and PEG (Provenza and Immense, 2006); these medicines have a large effect only when the number of shrubs in the diet is only two or three.

Maintenance of stable ruminal function

It has long been known that excessive intakes of rapidly fermented materials have an adverse effect on ruminal function, leading to low-fat milk due to lack of acetate as a precursor of milk fat synthesis, and a condition known as subacute ruminal acidosis (SARA). Cows suffering from SARA significantly increased their preference ratios for long lucerne over lucerne pellets from 0.60 to 0.85 in an apparent attempt to alleviate the discomfort generated by SARA (Keunen *et al.*, 2002). Further studies with cows in which SARA was induced by a high-starch diet showed no increase in their preference for drinking water that had been supplemented with sodium bicarbonate (an acid-neutralizing agent) at 2.5 g/l over plain water. They did, however, increase their total water intake in an apparent attempt to dilute out the excess acids in the rumen. Extreme acidosis can result in cattle 'cud spitting', i.e. dropping regurgitated boluses from their mouths.

Inclusion of sodium bicarbonate in the diet of sheep given a choice between foods with low- and high-energy density increased the proportion of high-energy food selected, as the bicarbonate ameliorated the low pH induced by the rapid fermentation of the high-energy food (Cooper *et al.*, 1996). However, in subsequent experiments in which sheep were given an energy-dense food or a less dense food, with or without sodium bicarbonate supplementation, there was no effect of bicarbonate on the proportions of the two foods subsequently selected (James and Kyriazakis, 2002).

There was, nevertheless, an effect of dietary energy density such that sheep previously on the less dense food chose a significantly higher proportion of the more dense food than those previously on that high-density food. There was, however, a reduction in choice for urea-containing foods when the basal diet was higher in bicarbonate, explained by the need for urea as a buffer being reduced by the presence of bicarbonate in the diet (James *et al.*, 2002). Effects of diet on buffering may override other diet selection objectives, such as the avoidance of an excess intake of RDP.

Stability of ruminal fermentation is an important requirement for the effective functioning of the microflora. Of particular importance is the regular and sufficient intake of fibrous material and it is observed that, given free choice between forage and concentrates, cattle and goats take about 20% of their DM intake as forage.

Castle (1979) offered dairy cows perennial ryegrass, with median chop lengths of 9, 17 and 72 mm. Voluntary food intake and milk yield increased as chop length decreased, while eating and ruminating times were reduced. Despite this apparent nutritional advantage of the short-chopped grass, cows given a choice of all three ate 16% of the long and 32% of the medium-length grass. Similarly, lambs offered two foods do not totally avoid the bulkier one while lactating goats (J.M. Forbes, unpublished results) and growing heifers (J.H.M. Metz, personal communication) took about 20% of their DM intake as hay when they also had free access to concentrates. Growing lambs offered foods with different nutrient densities but similar ME:CP ratios ate some of the poorer food, and it was suggested that the better foods increased ruminal osmolality or reduced pH to an uncomfortable extent.

Rapidly fermentable nitrogenous compounds also upset the ruminal balance and sheep avoid urea where possible (Kyriazakis and Oldham, 1993), even though this is a good source of nitrogen for the ruminal microflora. When two foods with protein contents above requirements were offered, the sheep consistently ate more of that with the lower content. However, when the choice was between a high-protein food and one supplemented with urea, the HP food was preferred, giving an overall crude protein content of the diet that was greater than required. The sheep preferred to eat too much undegradable protein than too much urea, presumably because of the more toxic effects of an excess of the latter. Thus, tactical adjustment to diet selection by ruminant animals that initially appears as a failure by the animals in obtaining a diet that both meets their requirements and avoids excess can be viewed within the overall feeding strategy of the animal to achieve its long-term goals that depend on healthy ruminal function.

When infused with acid or alkali to increase ruminal osmolality, sheep reduced their intake of a high-energy food but maintained their intake of a low-energy food, apparently in order to maintain the stability of conditions in the rumen (Engku Azahan and Forbes, 1992; Cooper *et al.*, 1995).

In preference studies, Phy and Provenza (1998) offered lambs large (1200 g) or small (400 g) meals of barley followed by a choice between 200 g barley and 200 g lucerne pellets. Lambs given the small amount of barley did not express a strong aversion to it, whereas those given the large amount showed a marked preference for the lucerne. The adverse effects of the excess of readily fermentable carbohydrate provided by the high dose of barley induced an aversion, while the low dose of barley provided a readily available source of energy without disturbing ruminal function unduly.

Although lambs preferred barley to lucerne when given a balanced basal food, this preference was reduced when they were given a basal food with an excessively high ratio of energy:protein (Villalba and Provenza, 1999). As the lucerne has a higher protein:energy ratio than barley (and higher than the basal food), this provides evidence that ruminants select to achieve a diet balanced for energy and protein. Similarly, their preference for whole over ground foods is modified if they need to eat more ground food in order to preserve a balance of energy and protein in their diet. Need for a particular macronutrient generated a stronger preference for a food providing more of that macronutrient, irrespective of its physical properties.

More recently Villalba *et al.* (2006) have shown that sheep learn to recover from overeating grain, tannins and oxalic acid, respectively, by ingesting sources of three medicines – sodium bentonite, polyethylene glycol or dicalcium phosphate – that specifically lead to recovery from illnesses caused by eating these three toxins. This is the first demonstration of multiple malaise–medicine associations.

There is thus ample evidence that ruminants do not always eat for maximum efficiency, as implied by Tolkamp and Ketelaars (1992), but strive to maintain sufficient intake of long fibre or chemical ameliorators of ruminal conditions to aid proper ruminal function.

Gut parasites

Gut parasites often reduce food intake by sheep and this is discussed in Chapter 17.

Tannins can offer some protection from gut parasites, as animals feeding on plants with tannins show lower nematode burdens, lower faecal egg counts and higher body weight gains than those eating similar plants without tannins. Animals can learn to eat foods high in tannins and nutrients in order to overcome internal parasites (Hutchings *et al.*, 2003). Gut immune function is also increased by the increase in protein passing through the rumen undegraded – caused by tannins in the diet.

Anti-emetic drugs

Daily treatment with the anti-emetic metoclopramide increased intake of endophyte¹-infected, but not uninfected, tall fescue by sheep, suggesting that intake of the infected material is limited by feelings of nausea (Aldrich *et al.*, 1993). In addition, anti-emetic drugs attenuated the aversion to several cereals induced by LiCl in sheep (Provenza *et al.*, 1994a), which does induce nausea in many species. Also, sheep receiving anti-emetic drugs ate more grain than those not receiving them; it thus appears that intake of cereal-based foods is limited by mild aversion to abdominal discomfort induced by overeating.

Lameness in chickens

Lameness is a common problem in intensively reared poultry, and administration of the analgesic carprofen allows lame birds to negotiate obstacles more quickly than untreated lame birds, although not as fast as normal birds, evidence that lameness causes pain. In order to discover whether broiler chickens could self-medicate with carprofen, lame and sound broilers were trained to discriminate between different-coloured feeds, one of which contained carprofen (Danbury *et al.*, 2000). Lame birds selected significantly more drugged food than sound birds and, as the severity of the lameness increased, lame birds consumed a significantly higher proportion of the drugged feed. Clearly, they were selecting a dose of the analgesic that relieved the pain or discomfort of lameness.

Practical Uses of Diet Selection

Poultry

Choice feeding may be attractive for small-scale producers in developing countries, as it can avoid the need for grinding or mixing, at least of the cereal

¹ Fungi living within plants.

grains (Henuk and Dingle, 2002). Standard feeding equipment can be used, as birds can select within a trough as long as there are clear visual differences between the foods. Such a system is also widely used in large-scale commercial production, both for laying hens and growing broilers, as detailed below.

Broiler chickens

In a comparison of feeding a complete diet with the choice of whole or ground maize or sorghum to male broilers from 21–56 days of age, no differences in body weight, food consumed, food efficiency, carcass ash, dressing percentage or mortality were found (Olver and Jonker, 1997). The main benefit of choice feeding was said to be the financial savings of feeding whole grains as the main energy source.

Birds trained with alternate days of access to whole wheat and a standard starter food for 4 days, when given the choice between the two, ate a significantly smaller proportion of wheat than birds that had been given a choice throughout (Covasa and Forbes, 1996). It is likely that offering whole wheat alone for 24 h at a time rendered this food aversive, due to its low content of protein and other essential nutrients. In a subsequent experiment, the period of exposure to whole wheat alone was reduced to 2 or 6 h and was followed by significantly higher whole wheat intake than for birds fed to choice throughout. It was concluded that a training period is not necessary as long as birds have experience of whole wheat from an early age.

In a classic experiment, Gous and Swatson (2000) offered broilers choices of two or three foods containing different protein sources: fishmeal, sunflower oilcake meal and soyabean oilcake meal. Their growth and food intake were monitored from 7–21 days of age and compared with those of birds fed 13 different mixtures of the three foods. The design is shown in Fig. 8.1a, with 13 combinations of foods 1, 2 and 3 represented. Fig. 8.1b shows the results in terms of growth rates, and it can be seen that birds chose mixtures that gave them growth very close to optimal; they did not choose mixtures that gave optimal FCE, however, although supplementing the soyabean food with DL-methionine in a second experiment did allow the choice-fed birds to optimize FCE. As a result of this 'severe test', it is possible to state unequivocally that broilers choose to maximize weight gain and FCE when given the opportunity to do so.

WHOLE-GRAIN FEEDING Wheat and barley are attractive ingredients for broiler foods in view of their low price but, because of their low protein content and imbalanced amino acid composition, they must be supplemented, and this necessitates grinding and mixing with supplements before pelleting into a complete manufactured food. Whole grains of cereal can, however, be viewed as low-protein foods that can be offered in free choice with high-protein concentrate pellets, but the extra expense of providing two feeding systems has prevented its large-scale adoption. There is, however, no need to offer the two foods separately, for as long as they are mixed in roughly the right proportions they are visually different and can be separately prehended by the birds. The concentrate is made by removing the cereal from a conventional formulation

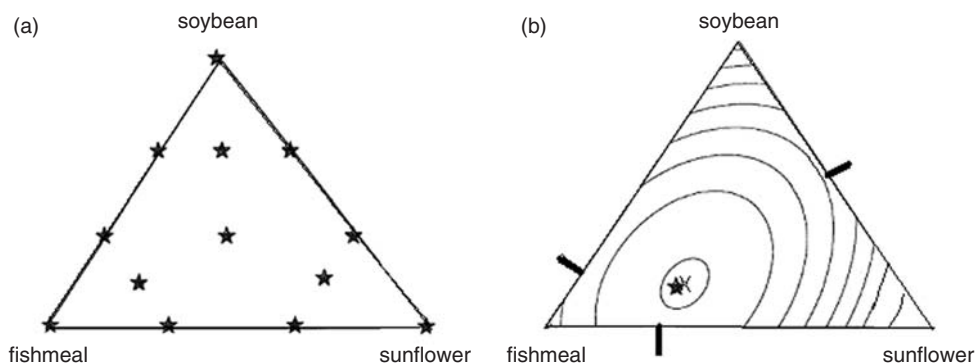


Fig. 8.1. (a) Thirteen combinations of three components making up the optimal design for a 3-component mixture; (b) Contours in a 3-component mixture representing different combinations of soybean oilcake meal, fishmeal and sunflower oilcake meal that result in similar daily weight gains (maximum growth rate (X) and combinations chosen when broilers offered the various 2-way (thick bars) and 3-way (★) choices); the contours are at 1 g/day intervals (from Gous and Swatson, 2000).

with added premix and calcium (note that it is not necessary to formulate a special high-protein food to use as a balancer for wheat. Standard commercial foods are designed to provide sufficient protein for 95% of the birds, which means that the great majority are being over-provided).

Although barley is generally cheaper than wheat, the high content of β -glucans in barley, which slows the rate of food passage through the digestive tract, means that replacement of wheat with barley in a broiler food reduces intake. Treatment of ground barley with a β -glucanase enzyme increases the proportion selected by choice-fed broilers, presumably by overcoming the aversive properties of untreated barley.

Performance of broiler chicks given a choice of concentrate pellets and sorghum grains is about equal to that of pellet-fed controls, but the choice-fed birds ate less protein and converted protein more efficiently. Broilers given a choice of a cereal and a high-protein concentrate performed just as well as controls, whether sorghum, wheat or both were the cereals and, when both wheat and sorghum were on offer, they ate more sorghum than wheat (Cumming, 1983). It is appropriate to provide a small proportion of whole grains from an early age, to give the birds familiarity with their appearance and, hopefully, with their metabolic effects.

Many broiler producers in Northern Europe are now including whole grain in their foods. Adequate mixing takes place during the normal handling of the food through the augers, bins and feeders. Successive batches of food are made with increasing proportions of whole wheat to give a steady increase in the proportion of whole grain, calculated to meet the requirements of the average bird. Results in terms of growth rate and carcass quality are reported to be at least as good as with the commercial grower food fed on its own and, in Scandinavia and other European countries, it is now common practice to feed

a starter food containing 240 g protein/kg throughout and to add increasing amounts of wheat, up to 40%.

While there are scientific grounds for controlling the proportion of whole grain more accurately to match the birds' potential and actual growth, and these are utilized in a comprehensive, computer-monitored and -controlled complete housing and feeding system (the Flockman system, Filmer, 1991), the expense of installing such a system seems unjustified at the moment in view of the good results being achieved with ad hoc methods.

Laying hens and pullets

The large-scale application of choice feeding of caged hens was studied by Tauson and Elwinger (1986) using two narrow, flat-chain feeders, one distributing a mash concentrate, the other whole grain. In a semi-choice treatment the mash was given as a layer on top of the grain, which was provided ad libitum. Two experiments with over 5000 birds showed greater egg size with choice and semi-choice feeding than with conventionally fed controls, with no difference in the number of eggs laid. Egg shell quality and cracks tended to be worse in the choice treatments, however. Profit margin was higher over the two production cycles for both choice-fed groups than control, and these authors concluded that choice feeding from flat feeders is feasible but that further studies would be necessary before similar systems were used in practice.

R.B. Cumming (personal communication) has been a great proponent of choice feeding in practice, and emphasized the importance of exposing pullets during rearing to all the grains that they may be offered later in life. He also observed that water consumption has been found to be lower in choice-fed layers, and the droppings have tended to be drier and to cone more readily under the cages. This may be due to the better gizzard development in birds fed some whole grains, and requires further investigation.

Pullets of a layer strain were given a choice of pelleted protein concentrate (as pellet or mash), whole yellow maize and limestone powder from 7–16 weeks of age and compared with birds fed a complete pullet grower diet in mash form (Olver and Malan, 2000). Choice-fed birds were significantly heavier at first egg than those fed the control diet, even though they ate less food (66.2 versus 68.2 g/day). During the laying period (16–80 weeks), choice-fed hens laid eggs that were significantly heavier, had thicker shells and darker yolks, with better food conversion ratios than those fed the control diet. It was concluded that choice feeding was beneficial for laying hens, and it was suggested that for optimal results the birds should have experience of choice feeding well before the onset of laying.

In summary, under commercial conditions laying hens usually perform well although efficiency is sometimes reduced. There is uncertainty about the optimum methods of training and feeding.

The potential advantages of whole-grain feeding

If animals do make nutritionally wise choices between foods, the following advantages may be seen:

1. There is a saving by not having to grind and pellet as much food and the fact that grain stores better whole, especially in hot, humid areas. Trained birds modify the ratio of intakes of the two foods within a few hours of a change in the energy content of the grain or of the protein content of the concentrate. Under heat stress, they decrease only their grain intake, but not that of concentrate. In the cool of the night they once again eat more grain, and eggs are generally a bit heavier than for birds given a single food, especially in hot weather. Choice diets are cheaper, but broilers take a bit longer to reach a given weight as they lose a day or two while they learn. They may be less susceptible to coccidiosis and usually more efficient financially.
2. Expensive determination and laborious calculations of nutrient requirements for use in food formulations could be avoided by offering a choice of two or more foods and allowing animals to choose a combination that will reflect their needs.
3. Separate-sex feeding will be unnecessary: within a mixed-sex, choice-feeding flock the males and the females will be able to select different diets that reflect the different requirements of the sexes. Differences between individual birds and different strains with different growth potential will be compensated for.
4. Food changes will not be needed: two foods, offered as a choice, could be used throughout the growing and finishing period. In addition, nutrient under-supply (with consequent loss in output) or nutrient oversupply (with no resulting benefit but increased cost and waste) will be avoided since the diet selected by each individual will precisely meet its requirements. Changes in environmental temperature will be accommodated by the birds without the need for reformulation of the foods.
5. Excretion of nitrogenous and other waste will be reduced as individual animals select diets to meet their nutrient requirements. There is potential for a significant reduction in the pollutants generated by intensive animal units.

The potential disadvantages of whole-grain feeding

1. It is an additional task for managers to check that both cereal grains and concentrate are available to all birds to ensure an adequate mixture is provided.
2. The proportion of whole grains eaten tends to increase with the amount of grains provided – in some cases birds seriously overeat whole grain, especially if it is very freely available. There is an advantage in providing the ratio of grain:concentrate that is optimal for the birds in question, i.e. increased management input.
3. Risk of poorer performance: in a comprehensive experiment in which broiler chicks were offered either a single balanced food or a choice of two foods that differed in protein and energy, growth rate and efficiency were reduced by choice feeding, especially in the faster-growing strain (Siegel *et al.*, 1997). Choice-fed birds selected a diet that was lower in protein:energy than optimal, had heavier abdominal fat pads and lighter breasts relative to body weight than those fed a single diet. In another case, although total food intake to 6 weeks of age was not significantly affected by the feeding treatments, broilers on choice

feeding selected diets with a lower percentage of CP and had lower live body weights at 6 weeks than those fed the complete diet (Yo *et al.*, 1998).

Gizzard development and coccidiosis

Grit is not usually offered in intensive poultry production and foods are low in fibre, as a result of which the gizzard is small and the proventriculus may be dilated. This results in food passing very quickly through the stomachs and arriving in the duodenum in a particulate form in which penetration of digestive juices might be slow. This might be conducive to coccidiosis, and Cumming (1987) observed that a higher-fibre food (62.5 g/kg) given to groups of cockerels from 1-day-old to 4 weeks reduced the incidence of coccidiosis compared with a low-fibre food (28.5 g/kg). All birds were dosed with coccidiosis oocysts, and 7/50 died in the low-fibre group, 3 in the high-fibre and none in a third, choice-fed group. The oocyst outputs were 293, 96 and 6, respectively, at 6 days post-infection. It is also advantageous for gizzard development and coccidiosis prevention to offer limestone grit to ensure large particles that stay in the gizzard, rather than as powder incorporated in complete food. Gizzards were significantly heavier in choice-fed birds compared with those given a single complete food.

In well-controlled experiments using *Eimeria acervulina*, it has not been possible to confirm the reduction in oocyst output and improvement of bird performance obtained by Cumming, however, even though gizzard weight was significantly increased by the use of whole wheat, rather than ground, in the diet of broiler chickens (Banfield and Forbes, 2001). It had been proposed that the beneficial effects of whole cereals on coccidial infection were due to the increase in the viscosity of gut contents compared with ground cereals. However, when carboxymethyl cellulose was added to the diet to increase greatly the viscosity of gut contents, there was no benefit in terms of reduced *Eimeria* oocyst output, with the additional disadvantage that food conversion efficiency was reduced (Banfield *et al.*, 2002).

When grit is available to broilers offered whole wheat and a high-protein food, they select a higher proportion of whole wheat as presumably they are better able to grind it in the gizzard in which the grit is stored for this purpose; when access to grit is denied there is a reduction in the intake of the whole grain. When the balancer food for broilers was given in mash form the birds selected more wheat when ground than whole but, if the balancer was pelleted, they selected more wheat when whole. Presumably physical form influences gizzard development and pelleted food improves its ability to grind food and allows birds to make better use of whole wheat. Thus, they select more whole wheat when offered concentrate in the pelleted form rather than mash.

Sequential feeding

One way to cope with the logistical difficulties of providing two foods simultaneously under commercial conditions would be to feed the two alternately. The length of time each food is offered will affect the outcome, as

there is limited storage for many nutrients in the animal's body. If one food is eaten to satiety and another, contrasting, food is then offered, animals usually eat again: this is known as sensory-specific satiety. On the face of it, therefore, offering two or more foods in sequence might be expected to increase total intake but this is not usually the case.

Offering HP and LP to broilers for alternate half-days gave food intakes and growth very similar to birds fed the same two free-choice foods (Forbes and Shariatmadari, 1996), and it appears that alternate feeding would be an effective way of 'choice feeding'. Birds given HP and LP on alternate days had somewhat lower total intakes and significantly less fat in the carcass than those offered free choice. When whole wheat and balancer are given to broilers during alternate 8-h periods, there is good selection: the higher the protein content of the balancer, the greater the proportion of wheat is eaten.

Gous and DuPreez (1975) gave layer cockerels two foods that were individually poorly balanced but complementary in their amino acid composition, in alternating periods of 6 or 12 h. There were no significant differences in food intake or weight gain, either between the two alternating treatments or compared with controls fed the two foods mixed together. Thus, the growing bird appears to have the ability to compensate for short periods on amino acid-imbalanced foods.

Chicks offered a choice between high- and low-protein foods during the 12 h of daylight but a food with an adequate protein content at night adopted a nocturnal feeding pattern, but did not completely eliminate daytime meals. Thus, although normally a diurnal feeder, if necessary the chick will eat at night in order to get a single, complete food. This suggests they prefer to eat a single, balanced food rather than making up their own balanced diet. Chicks exposed to cold conditions at night ate more and selected a higher energy:protein ratio than controls kept continuously in the warm, and chicks kept in permanently cool conditions ate more food, with a higher energy:protein ratio, than those put in the warm at night (Hayne *et al.*, 1986). The chick has the ability, therefore, to compensate for changed nutrient requirements at one time of day by altering its diet selection at other times.

In a comprehensive series of experiments, Rose *et al.* (1995) compared alternating periods of access to whole wheat and a balancer food with free access to both or a single, complete food. The proportion of the diet taken as whole wheat was low with choice- and 4-h sequential-feeding, but higher with sequential periods of 8, 12 or 24 h (see Fig. 8.2). Weight gains were similar for the complete, choice, 4-h and 8-h treatments, but lower for the 12-h and lower still for the 24-h sequential treatments.

When the foods were given in alternating 4-h periods, it can be assumed that the chicks learned that they did not have to wait very long before the preferred balanced food became available again, whereas with the 12-h and 24-h alternating periods they became hungry and this encouraged them to eat more of the whole wheat. When the 8-h sequential treatment was compared with a single complete food, both in small group cages and in larger groups in floor pens, the sequential treatment gave growth rates that were 7% and 5% lower, respectively. However, because of the reduced need for food processing

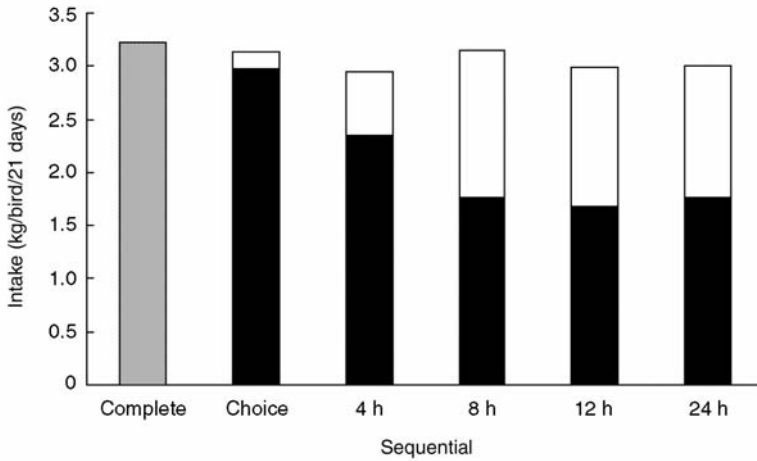


Fig. 8.2. Food intakes of broiler chickens fed a complete food (grey bar), free choice between a balancer food (solid bars) and whole wheat (open bars) of these two foods in sequence for alternating periods of 4, 8, 12 or 24 h (from Rose *et al.*, 1995).

and transport in the sequential treatment, the cost of food/kg of weight gain was lower (36.1 p²/kg) than for the complete food (38.6 p/kg). Because of the slower growth of sequentially fed birds, the authors' opinion was that this method of feeding is not to be favoured for intensive broiler production.

Nutrient solutions

Almost all animals are choice-fed almost all of the time in that they are given food and water; water intake is covered in Chapter 12. Other nutrients can be included in the drinking water and the situation is then more obviously choice feeding.

Feeding a low-energy food increased the preference by domestic chickens for a 100 g/l solution of sucrose, compared with feeding a normal or a high-energy food (Kare and Maller, 1967). In contrast, jungle fowl selected significantly more sugar solution than water irrespective of the energy and protein content of the foods, which were a 200 g/kg protein food diluted or enriched with 250 g/kg of cellulose or corn oil. Jungle fowl have a low potential growth rate and therefore a low protein:energy requirement, and so choose to reduce the protein concentration of their diet by drinking sucrose solution.

The inclusion of 9% of glucose in the drinking water of cockerels of a laying strain did not reduce food intake, but weight gains were not increased and it was suggested that the extra energy was mainly stored as fat. In other experiments with broiler chickens, intake was depressed by glucose solutions to maintain a constant total energy intake (Engku Azahan and Forbes, 1989). To see whether the different response might be due to differences in the protein content of the food in relation to potential growth rate, either water or a 9% solution of glucose was offered to male broiler chicks fed on either low-

² UK currency, 100 p = £1.

(150 g/kg) or adequate (195 g/kg) protein foods. Compared with those on tap water, those birds having dextrose in the water ate significantly less food but there was a highly significant interaction between the effects of dietary protein level and type of fluid offered, glucose depressing intake of the medium-protein food but stimulating it with the high-protein diet (see Fig. 8.3).

Fluid intake was generally closely related to food intake and did not differ between types of fluid on offer. On the high-protein food, glucose solution had no effect on food intake but allowed increased protein and fat deposition, whereas with the medium-protein food, intake, protein and fat were all depressed, presumably due to lack of protein to balance the increased energy intake from glucose. It appears that chickens consider glucose solution to be a drink rather than a food and that, having taken in extra energy, respond according to the new protein:energy ratio of the diet.

Pigs

Choice feeding has not been practised on a commercial scale to any significant extent as, unlike the situation with whole-grain feeding in poultry, no consistent economic benefits have been found. However, results from research under commercial conditions suggest that there is potential for choice feeding of pigs (Dalby *et al.*, 1997; Lawlor and Lynch, 2003). Choice feeding frequently leads to more efficient utilization of food protein (e.g. Dalby *et al.*, 1995), although there has been a tendency towards a lower food conversion efficiency in some experiments. This may indicate that the animals are depositing higher levels of fat tissue, and this is corroborated by greater thickness of back fat in choice-fed animals in some cases, but by no means all.

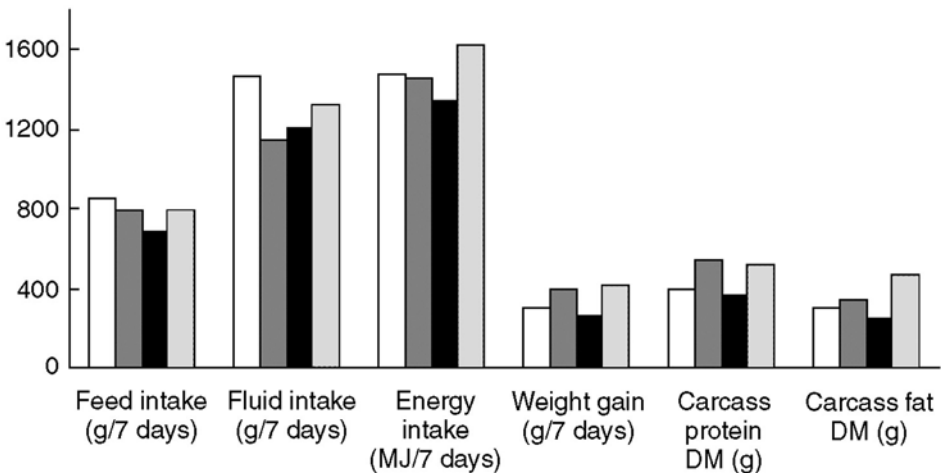


Fig. 8.3. Intakes of feed and fluid, weight gain and carcass composition of broilers offered water with either 150 (open bars) or 195 (dark grey bars) g CP/kg or 90 g/kg glucose solution with either 150 (solid bars) or 195 (light grey bars) g CP/kg (from Engku Azahan and Forbes, 1989).

Nitrogen excretion and pollution

The environmental consequences of diets that are offered to pigs must now be considered. In several European countries pollution with phosphorus and nitrogen from animal manures is a major problem, and nutritional strategies to increase utilization should be investigated. Choice-feeding experiments have generally shown that choice-fed pigs eat lower levels of protein with no significant reduction in live weight gain when compared with pigs offered a single food with fixed protein level. From this it can be estimated that there will be lower levels of nitrogen excretion from the pigs selecting their own diet, as the protein is utilized more efficiently, although similar results can be obtained by feeding lower than normal levels of protein that are balanced by the inclusion of synthetic amino acids.

Sequential feeding

Fowler *et al.* (1984) studied the effects of dietary novelty and frequency of feeding on the food intake and performance of growing pigs. From 25–90 kg body weight they were offered nine foods in sequence or as a mixture given nine times or twice per day. Initially, the sequentially fed groups ate more but, at the end, intakes were similar at 2.32, 2.35 and 2.33 kg/day and live weight gains and food conversion efficiencies were not different between groups.

Ruminants

Selection within a single food

When grass or hay is offered in the long, unchopped form, animals have the opportunity to select between stem and leaf. The proportion of leaf selected by sheep increases with the amount of straw offered. Sheep given unchopped barley straw in sufficient amounts so as to leave uneaten 20, 30, 40, 50 or 70% of that on offer ate increasing amounts of leaf blade as the allowance increased, in a linear manner, at the expense of stem; leaf sheath was little affected (Bhargava *et al.*, 1988). Little stem was eaten until refusals were < 40% of the amount offered, and the DM digestibility of the whole diet increased from 0.59 to 0.64 with increasing allowance from 20 to 70% excess.

Ruminants select leaves in preference to stems when given an excess of hay – the former have a lower content of fibre and higher levels of soluble carbohydrates and protein. Wahed *et al.* (1990) offered goats 50% more straw than they would eat and noted a significantly higher DM intake (18.9 g DM/kg^{0.75}/day) than those offered 20% more than ad libitum (14.4 g DM). Further work with goats and sheep confirmed this, as shown in Fig. 8.4, i.e. very worthwhile increases in levels of nutrition. The refused straw can be utilized as bedding or fuel.

Oosting and Nordheim (1999) have developed a theory of the proportion of the offered food sheep select as the amount of forage on offer is increased. Below a certain threshold, animals eat all that is put in front of them (phase 1); above

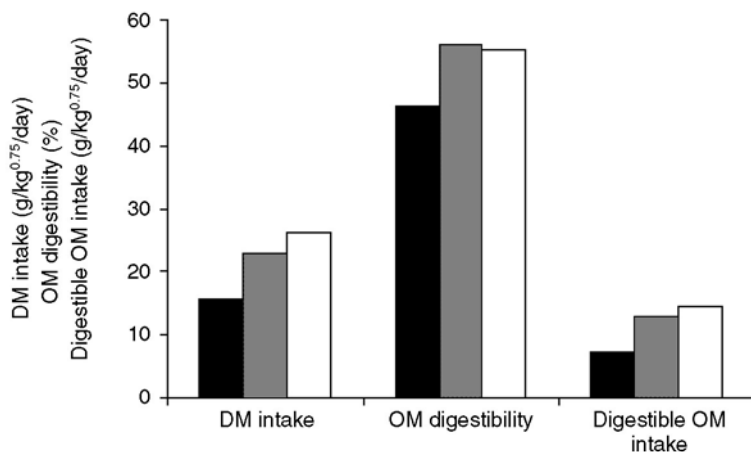


Fig. 8.4. Effect of allowing sheep and goats 13% (solid bars), 57% (grey bars) or 70% (open bars) excess straw over intake on voluntary intake, organic matter (OM) digestibility and digestible OM intake (from Wahed *et al.*, 1990).

this point they choose to eat an amount of food according to the efficiency with which ME is used for maintenance and growth (see Chapter 9). Once the amount of food on offer gives an efficiency of 0.6, over this level refusals are left in such amounts as the intake is such that efficiency stays at 0.6 (phase 2). Eventually, as the amount of offer increases further, a point will be reached at which there is no further increase in intake (phase 3); the transition points and gradients will vary for different food materials, as illustrated in Fig. 8.5.

Matching Food Composition with Requirements

Diet formulation

In commercial practice the protein content of food given to broiler chickens and growing pigs is reduced in a stepwise manner to match the changing needs of the animals as they grow. Even if choice feeding is difficult to apply commercially, it has the potential to be used to define more precisely the changes in requirements to allow more accurate formulation of rations. In particular, the optimum level of amino acids for animals of particular genotypes at different stages of growth can be assessed more comprehensively by diet selection experiments than by complex factorial experiments in which different groups of animals are given all combinations of likely amino acids at different stages of growth (Forbes and Covasa, 1995).

Based on results with choice feeding, the optimum single foods to be given to birds under different environmental temperatures have been recommended, as have levels of methionine inclusion in broiler foods and lysine inclusion in food for growing pigs.

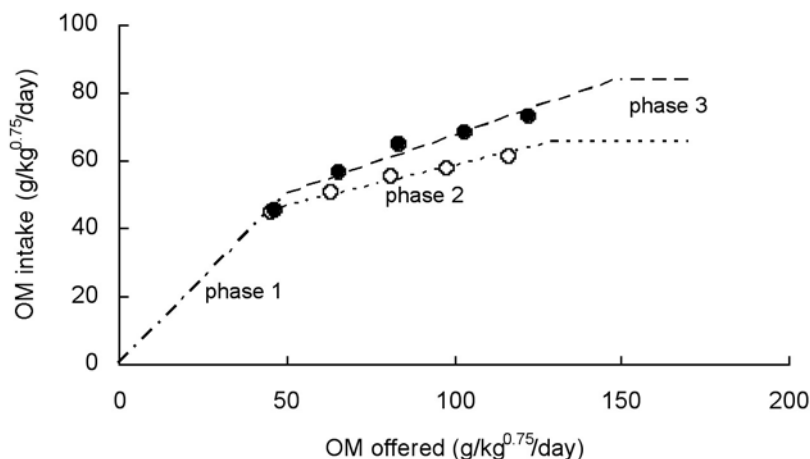


Fig. 8.5. Relation between amount of food organic matter (OM) offered and amount eaten according to the model of Oosting and Nordheim (1999). Phase 1, all offered food is eaten; phase 2, intake increases with amount offered, according to theory of efficiency of utilization of ME; phase 3, further addition of food does not result in increased intake. Symbols are observed intakes: ○, untreated; ●, urea-treated rice straw.

New genotypes

If diet selection can be used to define more precisely the optimum content of protein, amino acids and any other essential nutrient, for existing genotypes, then it can also be used for novel genotypes, such as may be produced by genetic engineering techniques in the foreseeable future. Leaving aside the moral issues, there are likely to be major technical problems with the feeding and management of animals whose potential for growth has been elevated considerably but whose ability to ingest, digest and metabolize the food to support such growth is unknown. Diet selection experiments are likely to lead more rapidly to a resolution of these problems than classical factorial experiments but the limits of diet selection as a technique for assessing optimal nutrition have yet to be defined, and much more basic research is needed at this stage so that we are not to be taken unawares if, and when, novel genotypes are produced for commercial use.

New genotypes of crop plants can also be assessed as animal foods by diet selection techniques.

Conclusions

Given the appropriate conditions, diet selection methodology provides a very powerful tool for nutritional and behavioural scientists and has great commercial potential.

Currently, however, there are only two situations in which farm animals are offered choices in practice. One is grazing, which is not covered specifically in

this book. The other is the apparently widespread practice of offering poultry a mixture of whole cereal and a pelleted balancer food, either in separate troughs or, more usually, in the same trough. However, there is little evidence to date that individual birds improve their diet by choosing disproportionate amounts of the two foods.

Questions still to be answered include:

- Is it better to offer a standard complete food in choice with whole grain or to formulate a high-protein balancer to complement the cereal?
- Is the welfare of animals better served by offering them a choice of two or more foods?

Ultimately, it is economics that will dictate whether choice feeding is implemented commercially. In most research, non-standard foods have usually been used to try to ensure that selection is for or against a nutrient rather than an ingredient. In commercial practice least-cost formulation determines the raw materials to be used as ingredients, and some of these have sensory properties rendering them more or less attractive to animals and distorting their choice away from constructing for themselves a balanced diet. It remains to be seen whether choice feeding will be suitable in practice, especially for pigs.

9

Integrative Theories of Food Intake Control

This chapter deals with mechanistic modelling of voluntary food intake and diet selection over periods of 1 day or more. The philosophy of modelling, together with many examples from ruminant digestion and metabolism, is included in the book edited by Dijkstra *et al.* (2005), while Yearsley *et al.* (2001) discuss modelling of food intake in herbivores, with particular reference to extensive systems.

Some of the theories that have been put forward to explain the control of intake in birds and mammals are described. In many cases they are developments of simpler hypotheses described briefly in Chapter 1, which postulated that feeding is controlled by a single factor, usually acting in a negative feedback manner. Stomach distension (Chapter 3), hypothalamic temperature (Chapter 5), blood glucose concentration (Chapter 4), body fat stores (Chapters 4 and 15) and plasma amino acids (Chapter 4) have all, in their turn, been proposed as the factor whereby intake is controlled to match requirements. However, none of these theories outlined so far can explain how intake is controlled under all circumstances. Balch and Campling (1962), having reviewed the control of voluntary food intake in non-ruminants, concluded that: '... food intake is unlikely to be regulated by any single mechanism and ... oropharyngeal sensations, gastric contractions and distension, changes in heat production and changes in the levels of circulating metabolites, may severally be implicated'.

In a complex situation it is often helpful to construct a model to study the likely consequences of integrating the various parts of the system in a quantitative manner. At the very least, the attempt at model-building forces the would-be modeller to consider the main factors involved in the system under study and can usually point to what critical experiments are required in order to fill in gaps in concepts or data.

In the first edition of this book (Forbes, 1995), prediction of food intake was given a chapter to itself. In this edition this subject is incorporated into the appropriate parts of the text, including this chapter, because it is the aim of

theorists and modellers to develop quantitative hypotheses that reflect the main features of the intake control systems and should thereby produce good predictions of intake.

Energostasis

Several of the single-factor theories have in common the idea that some function of energy intake or storage is monitored by the brain, which then controls intake in order to preserve the constancy of a bodily function (glucose concentration or utilization, deep body temperature, body fat stores, etc.). It is clear that any attempt at formulating a more complex hypothesis must rely on energy as the principle commodity. So far as we know, the body cannot measure energy per se, although several recent theories imply monitoring of energy flows.

Le Magnen and colleagues (summarized in 1985), realizing the limitations of the 'classical' theories, have accumulated evidence to support the concept that the energy supply to some tissues is monitored and used to control food intake. They showed that, during the day, the rat has a lower metabolic rate than at night and speculated that this might be the cause, rather than the result, of the reduced frequency of meals during the day, compared with the night. They concluded that the amount of food eaten from the onset to the termination of a meal, or meal size, is mainly determined by the peripheral, i.e. oral and gastrointestinal action of ingested foods.

Meal-to-meal intervals, and therefore the meal frequency, are mainly dependent on post-absorptive and metabolic factors. Another way of putting this is to say that meal termination is not finely controlled, as it seems to be caused by numerous factors acting in concert, many of which are not directly related to the eventual nutrient yield of the meal. However, the products of the meal in question can be more accurately monitored during the subsequent inter-meal interval and used to determine the onset of the next meal.

The same idea was expressed by Stricker and McCann (1985): 'when eating, increasing gastric fill and increasing hepatic delivery of calories both serve to reduce the likelihood that animals will continue to feed. Once they stop eating ... they will remain satiated despite an empty stomach so long as the liver continues to get utilizable calories from the intestines.'

Whatever the mechanism, the idea that 'animals eat for calories' has pervaded the subject, even though it has been clear for many years that increasing the caloric density of food by the addition of fat results in increases in the intake of digestible energy and weight gain (see Chapter 11).

Limitation of Intake by Bulk

The concept that animals try to meet their energy requirement by eating an appropriate amount of food is central to theories of the control of food intake. In many situations, however, particularly with ruminants, there are constraints

that limit intake to below the optimal. The history of studies on voluntary food intake in farmed ruminants shows that initially (up to the 1960s) all the emphasis was on a *positive* relationship between the digestibility of the food and how much animals would eat, rather than the *negative* relationship predominantly seen in simple-stomached animals.

With unchopped forages it is likely that intake is constrained by the capacity of the digestive tract and the dynamics of breakdown and passage of food particles (see Chapter 3). This assumption is made in the model of Illius and Gordon (1991), and no account is taken of any metabolic factors that might be involved. The model is run with three equally spaced meals per day until it reaches a semi-steady state; the number of meals per day is then increased until the mean daytime digesta load reaches 21 g DM/kg body weight (the mean digesta load found from the literature).

Predictions of forage intake were highly correlated with observed values ($r = 0.78$) and, not surprisingly, were found to be particularly sensitive to changes in the model of the permitted average DM contents of the rumen, the digestible cell wall content of the forage and the rate of passage of particles out of the rumen. Further discussion of models based on the physical limitation of intake is provided by Illius *et al.* (2000).

Constraints Models and the Two-phase Hypothesis

With the increasing use of high-concentrate diets on farms in the 1960s, it became clear that when constraints such as bulk were not limiting, ruminants control their intake of food to achieve an approximate constancy of metabolizable energy intake (see Chapter 11). It was necessary, therefore, to combine so-called 'metabolic' and 'physical' controls of intake into an overall picture of how intake might be controlled.

Animals eat in order to satisfy their requirements for energy unless prevented from doing so by limiting factors, of which the bulk of the food is the most commonly considered. Figure 11.6 summarizes data from numerous experiments and it can be seen that, in general, intake (of both DM and energy) increases with increasing DE yield (digestibility of energy, reducing bulk) until energy requirements are being met. Further increases in DE yield do not result in any further increase in energy intake, so that DM intake actually decreases. The concept of a sudden change from 'physical' limitation of intake to 'metabolic' control, although physiologically unrealistic (see below), has been widely accepted and named the two-phase hypothesis (TPH), by Pittroff and Kothmann (1999).

It must be made clear that physical limitation of intake by gut capacity is not the only constraint that might be applied to food intake. Heat load and the need to maintain body temperature is another constraint when intakes and/or effective environmental temperatures are high. In some situations, therefore, more than one constraint should be included simultaneously, and approaches to doing this will be covered later in this chapter and in Chapter 10.

Poultry

Although acknowledged as a possibility, physical limitation of intake has not been seriously considered, presumably because poultry are normally offered highly digestible foods. A TPH has, therefore, not been developed for birds.

Pigs

While principally applied to ruminants, the TPH concept has been applied to pigs (Kyriazakis and Emmans, 1999) based on evidence from experimental work involving bulky foods. In order to test whether pigs behaved in a manner consistent with the TPH or with an hypothesis of optimization of biological efficiency (Tolkamp and Ketelaars, 1992), Whittemore *et al.* (2001b) fed growing pigs – kept at a thermoneutral or low environmental temperature – either on a highly digestible food or on a high-bulk food incorporating 650 g of sugar beet pulp/kg.

While both theories predict that lowering the temperature will increase the intake of a high-quality food, the THP predicts that intake of a bulk-limited food will not be increased by such treatment. The results showed a highly significant food \times temperature interaction for food intake, whereby reduction in temperature resulted in an increase in food intake of the high-quality food but had no effect on the intake of the bulk-limiting food, thereby agreeing with the TPH.

In a further test of these two frameworks, foods with low (L), medium (M) and high (H) bulk characteristics were used (Whittemore *et al.*, 2001c). Compared to L fed throughout, a period on H followed by L resulted in compensation of the reduced intake and growth in period 1, while H followed by M did not give such high intakes or growth rates, suggesting that food M was preventing the full expression of compensation for the period on H. While not clear-cut, the results were in closer agreement with the TPH than with the efficiency theory.

Ruminants

Evidence that can be interpreted as supporting the TPH is presented in Chapter 11, and its use in models of intake and ruminants has involved assumptions that sheep (Forbes, 1977b) and lactating cows (Forbes, 1977a) will eat daily sufficient metabolizable energy to meet the animal's requirements for maintenance, production and fattening, unless physical limitations intervene. The daily intake of food supplies energy to the body pool, which is utilized for maintenance, pregnancy, lactation and fattening. Food intake also leads to stomach distension, and this is compared with the abdominal space available (taking the size of the uterus and abdominal fat into account) to determine a physical limit to feeding. If the physically limited intake is less than the metabolically controlled intake, then the former value is used and the shortfall in energy supply made up by fat mobilization.

An important principle in this model is that fat deposition (in addition to maintenance, growth and lactation) is seen to be driving food intake in that it is assumed that the sheep tries to deposit 100 g of fat/day if the quality of the food is good enough to avoid physical limitation of intake. Of course, if intake is physically limited then fat deposition cannot reach this target and may even be mobilized if intake is very low. The deposition or mobilization of fat increases or reduces the volume of abdominal fat which, in turn, reduces or increases the space available for the rumen and hence for food intake.

This type of model produces a much steeper increase in daily intake in the period immediately after parturition than that seen in ewes or cows. The sharp rise is due to the sudden reduction in the volume of the uterus, which releases the animal from physical limitation of intake and allows it to satisfy its greatly increased energy requirements for lactation. To cope with this anomaly the model was provided with a limit to the rate at which intake could increase, but this is artificial as we do not know the physiological reasons for the unexpectedly slow increase in intake in early lactation (but see Chapter 16).

While there are numerous reasons to doubt the TPH as representing what occurs physiologically, Emmans and Kyriazakis (2001) have vigorously defended it as a tool for predicting intake in practical situations. One of their objections to attempting to include numerous physiological factors in ruminant models is that the effects of the different presumed signals need to be expressed in a common currency. They state that it will be necessary to know the strength of all relevant signals in order to calibrate them and combine them and that there is still considerable uncertainty as to what signals are involved, never mind their quantification. Concepts that involve more complex integration of signals than the TPH are dismissed by them as having no contribution to make to the accurate prediction of food intake.

With those in mind who draw a distinction between 'understanding' and 'ability to predict', Emmans and Kyriazakis (2001) state that: 'The test of whether we understand a system is always whether we can make accurate predictions of its behaviour'. They do not denounce attempts to describe in detail the systems controlling intake outright, but consider that such approaches have no immediate prospect of predicting intake.

In order to predict intake for a given kind of animal it is necessary to consider the food contents of protein, fat and carbohydrate, the amino acid contents of the protein and the contents of minerals, vitamins, water and the indigestible – or only slowly digestible – components such as fibre. It is also necessary to know the climatic environment, as energy requirement can be increased in a cold environment, and a hot environment can limit the rate at which the animal can dispose of heat. To these factors must be added a description of the animal, to allow animals of different potentials to be included in the prediction model. The description of the animal will include growth rate and body composition, or milk yield and composition.

The paper by Emmans and Kyriazakis (2001) provides equations for the calculation of energy requirements, considered to be the driver for food intake, but does not address constraints other than to mention that it is sensible to select animals for heat tolerance where intake is limited by a hot environment, and for higher capacity for forages in situations where forage is cheaper than concentrates.

Multiple constraints

A more comprehensive constraints model for growing cattle is proposed by Poppi *et al.* (1994), in which six potential limits to intake are calculated and whichever gives the lowest predicted intake is assumed to be the limiting factor; no attempt is made to integrate or add these limiting factors. Nevertheless, there are several interesting ideas in this model. The six factors are:

1. Rate of eating; this is of importance as it is likely that there is an amount of time per day above which the animal will not eat, which is thought to be 12–13 h/day for ruminants. However, motivation to eat, and thus maximum time per day spent eating, is likely to be flexible and to depend on demand for nutrients.
2. Faecal output; faecal output of steers for forage-based diets has been found to be 9.6 g DM/kg body weight/day. In practice, the rumen is likely to be the limiting part of the digestive tract, but this cannot be predicted from faecal output unless digesta flow is known.
3. Ruminal turnover; this essentially is the rate at which the cell wall is digested and its particles leave the rumen.
4. Nutrient requirements; this is expressed as the potential for protein deposition and is acknowledged as being a difficult area in view of the fact that the level of food intake to some extent affects the rate of growth, milk yield, etc. and thus the 'nutrient requirements'.
5. Heat dissipation; there is a physical limit to the rate at which heat can be lost, depending on environmental factors such as air temperature, wind speed and humidity. Heat produced in excess of the capacity to lose it results in a rise in body temperature and a defensive reduction in voluntary intake.
6. Metabolism; a common factor is fluxes of ATP; ATP must be degraded with imbalanced diets, and an upper limit can be set for this metabolism in order to limit intake.

As the authors did not consider that there was a good concept of how the short-term effects on intake, which might be additive, are used in the long term, they used the most limiting factor at any moment in time to predict intake. Seven diets were chosen to be representative; values for nutrient absorption were obtained from the literature and the model solved for the equations predicting the strength of each of the six limiting factors.

For a steer of 100 kg empty live weight and starting with 15.4 kg of protein and 4.4 kg fat in the body, initial pool sizes were: ATP, 292 mol; C₂ equivalents, 5.8 mol; C₆ equivalents, 23.8 mol. Rates of eating of 3–30 g/min were used, from the literature. Maximum capacity of the rumen was set at 13.8 g NDF/kg body weight and maximum faecal output was set at 9.6 g/day/kg body weight. Particles can leave the rumen when 80% has been digested. Literature values were used for NDF content and rates of digestion of NDF, and the genetic potential for protein deposition was set at 298 g/day.

Duodenal absorption of protein from the different foods was used to estimate how much food could be eaten before excess limited intake, assuming a value of 80% for efficiency of utilization of amino acids. An upper limit of

1100 kJ/kg wt^{0.75}/day at 20°C was used for heat dissipation; heat production is calculated from the inefficiency of utilization of ME, calculated from the ATP utilization and energy retained as fat and protein. The rate of ATP degradation is speculative, but was subjected to sensitivity analysis. A standard value of 45 mol ATP degradation/day was taken, arrived at by iteration of the model.

In general, there was good agreement between the model's predictions and literature values, but predicted intakes were usually somewhat higher (see Table 9.1). Substrate cycling was a limiting factor for all foods, while rate of eating did not pose a limit with any of the diets used, but is probably important in grazing animals. Assuming a constant maximum fill of NDF may be wrong in view of the likelihood that different signals are interpreted additively by the CNS (see Chapter 10). Fractional digestion rate is not sufficiently well documented and, as digestion approaches its plateau, small differences in the rate of digestion will make big differences to the time taken to reach that point and therefore the residence time.

The fact that rumen fill needs to be set lower than the assumed maximum supports the concept that animals often do not utilize their full ruminal capacity. Substrate cycling limits intake in many of the simulations, implying that nutrient imbalances are often limiting intake. Where two or more factors are almost equally limiting, removal of one may not increase intake, and thereby lead to the conclusion that it is not important; however, it is highly unlikely that various signals are used in an exclusive manner but that they are integrated, perhaps additively. If this is true then the model of Poppi *et al.* (1994) should be modified to integrate the various limiting factors in a more physiological manner, along the lines suggested below and in Chapter 10.

This type of model, based on a time interval of less than one day but more than a few minutes, is particularly useful as it allows integration of voluntary intake into well-developed models of digestion and metabolism. It does not, however, allow meal patterns to be studied or simulated in a realistic way.

Table 9.1. Observed and predicted dry matter intake by a Friesian steer of 100 kg empty body weight consuming various feedstuffs. *, limiting factor(s) (from Poppi *et al.*, 1994).

Food type	Dry matter intake (kg/day)						
	Observed	Rate of intake	Faecal output	Predicted from:			
				Ruminal turnover	Genetic potential	Heat dissipation	ATP degradation
Concentrate	2.3–2.7	33.4	3.7	6.0	4.3	4.0	2.2*
Legume	> 2.6	7.9	4.2	16.5	2.9*	4.3	2.4*
Grass	2.6	11.8	5.3	6.2	3.9	4.1	2.2*
High-D silage	> 1.8	3.8	4.0	5.3	3.9	3.9	2.2*
Low-D silage	1.8	3.8	2.7*	2.9*	5.3	4.7	2.7*
High-D dried grass	2.5–2.8	11.1	4.0	5.9	4.6	4.8	2.4*
Low-D dried grass	2.2–2.4	7.7	3.1*	3.3*	4.4	5.5	3.0*

Comparisons and criticisms of constraints models

The basis of constraints theories – that each limiting factor is considered to have no effect on intake until its constraining limit is reached, at which point no further intake is allowed – seems untenable. Under this concept it is imagined that stimulation of receptors sensing rumen fill, for example, should contribute nothing to intake control until a certain degree of stretch is reached, at which point rumen fill suddenly becomes the only factor to control food intake.

Pittroff and Kothmann (2001a, b) have criticized much of the modelling work on food intake by ruminants and have been particularly critical of the TPH, starting from the basis that it has been used in many models of ruminant food intake over the past 30 years and has yielded no consistently successful predictive system. They found weak concepts in the sense of ability to accommodate experimental data; rarely did they find a serious attempt at sensitivity analysis or proper validation. Also, the mathematical properties of models were frequently questionable and they claimed that the modelling approaches they reviewed provided a distinct lack of direction for future research, i.e. an absence of new hypotheses. Suggestions were made for improved model development, implementation and documentation.

Pittroff and Kothmann (2001c) reviewed 11 published prediction models for sheep and 12 for cattle, mainly for intake at pasture. There was a wide range of predictions, in which the highest was approximately double the lowest, and the authors dismissed the modelling approaches used as unsuitable bases for predicting the voluntary intake of forage. In particular, they were strongly critical of the lack of a formal approach to modelling in most of the cases cited, i.e. a failure to state the limits within which the model is designed to operate; a failure to present examples of calculations from their models and discuss the goodness of fit with published observational data on food intake.

They highlight the need for robust, testable theory on how intake and diet selection are controlled in ruminant animals and for experiments designed to test specific hypotheses, rather than just being used to collect yet more data:

... the analysis provides disturbing evidence of the failure of model developers to thoroughly examine the theoretical basis of key assumptions upon which their models rest. Although it would be clearly more appropriate to formulate models as researchable hypotheses, given the current state of knowledge of intake regulation in ruminants, this is generally not done.

(Pittroff and Kothmann, 2001c)

Fisher *et al.* (1987) were also concerned with progress in modelling intake, observing that previous models had used only the physically limited intake or, when the metabolically controlled intake was included, whichever was the lower was used as the predicted level of intake. They proceeded, therefore, to incorporate both simultaneously to take into account the likelihood (see below and Chapter 10) that the factors that control intake do so in concert rather than separately.

On the one hand, they used a simulation of digestion and passage (Mertens and Ely, 1979) as a basis for the physical limit; fibre was classified into three particle size classes, each with different digestibility classes and a maximum rumen DM fill of 1.9% of body weight was assumed. On the other hand, they

supposed the optimal flow of nutrients to be that absorbed from a food of 650 g/kg DM digestibility, this being approximately the point above which intake appears to be controlled metabolically. Rate of intake (I) was assumed to be based on the ratio of current rumen contents to maximum contents (D) and the ratio of current nutrient flow to optimal flow (C) according to the equation

$$I_{t+1} = I_t DC^{aD^b} \quad (9.1)$$

in which the exponent a limited the chemostatic effect relative to distension and the exponent b gave an increased chemostatic effect at low levels of distension. When a and b were set to zero to eliminate the chemostatic feedback, intake increased with increasing digestibility (decreasing NDF content) in a curvilinear manner right up to the highest digestibility, as expected. Setting a to 0.2 and b to 5 reduced the increase in intake per unit increase in digestibility and gave reduced intakes at very high digestibilities.

Whereas rumen fill was constant when no chemostatic feedbacks were included, it decreased with increasing diet quality when such feedbacks were used. Daily intake declined with increasing NDF content and increased with increasing energy demand by the animal, although no quantitative information on the latter point is presented.

Combinations of Relationships into Predictive Models

Even the most complex equation cannot adequately represent what we know to be the range of factors that affect intake and can therefore be used in its prediction. Some of these factors are discontinuous while others are conditional. Several prediction systems have been developed with the aim of making them more flexible and general than any one single equation. Some approaches involve iterative calculations and are as much to explore the limits of our understanding as they are to be used for predictions under practical conditions.

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A comprehensively documented system of prediction of food intake by ruminants has been developed by Jarrige and his colleagues at the National Institute for Agricultural Research of France (Jarrige *et al.*, 1986). This system depends on knowledge or prediction of the animal's ingestion capacity for a standard food, the ingestibility of a food relative to that of a standard food by a standard animal and substitution rates for concentrates in place of forages.

The animal's ingestion capacity for a standard food

Observations of food intake of cows on 59 different dietary regimes, corrected to 600 kg live weight, showed that the ingestion capacity (bulk units for cattle, BUC) was closely related ($r = 0.88$) to milk yield (kg of fat-corrected milk/day, MY):

$$BUC = 10.43 + 0.26MY \quad (9.2)$$

The data were for cows having a mean yield of 17 kg/day (range 10–28), at which level the capacity is 14.9 BUC. During the first month of lactation, and for the whole of the first lactation, ingestion capacity is reduced by 0.15 because heifers and recently calved cows have low voluntary intakes. Intake capacity (IC, kg/day) was predicted from:

$$IC = 22 - 8.25 \exp(-0.02MP) + 0.01(LW - 600) \quad (9.3)$$

where MP is milk production (kg FCM/day) and LW is live weight (kg). Ingestion capacities for suckler beef cows are also tabulated by INRA (1979).

The ingestibility of a food relative to that of a standard food by a standard animal

The ingestibilities of some 2500 forages by ‘standard’ sheep (castrated males aged 1–3 years and weighing 40–75 kg) have been determined. A pasture grass which was used as the standard food had a mean intake by such sheep of 75 g/kg^{0.75}; on average, this grass contained 150 g CP/kg DM and 250 g CF/kg DM with an organic matter digestibility of 770 g/kg. By definition, 1 kg DM of this standard food has a bulk value of 1 bulk unit for sheep (BUS). Thus the BUS value for other forages is 75 divided by the amount of that forage consumed by the standard sheep/unit of metabolic live weight. Typically, green leguminous plants have a BUS of around 0.8 while straws are 2.0–2.5 BUS.

The ingestibility of forages by cattle is higher than by sheep, for any given food. Data from a large number of feeding trials in which the same forage was offered ad libitum to both sheep and cattle were used to allow BUC to be predicted from BUS:

$$BUC = 57 + 0.87BUS \quad (9.4)$$

Thus the standard grass has an ingestibility for cows of 122.6 g DM/kg^{0.75} which, for a 600 kg cow, is 14.9 kg DM. The bulk value for a forage for cattle is therefore 122.6 divided by its ingestibility in cattle.

Substitution rates for concentrates in place of forages

The INRA algorithm for this is covered in Chapter 11.

The system devised by INRA (1979) is designed to be used in situations where physical factors are predominant in the control of intake. That is, forages are to be used as much as possible, concentrate supplements being given only to the extent demanded by the desired level of production. However, there is now a recognition that nutrient demand can exert some influence on voluntary intake of forages, so it will be interesting to see how well the principles and procedures adopted in the INRA system cope with the needs of farmers and advisors.

Interactions between Factors Affecting Food Intake

To suppress feeding in rats completely (cause satiety?) it is necessary to infuse not just a supply of energy but also fat and protein, and it is abundantly clear that satiety is not induced by a single mediator acting on a single group of receptors in a single target organ. Any experimental treatment given on its own must usually be applied at a level far above that achieved in the normal animal in order to prevent feeding completely.

For example, in order to suppress feeding totally by infusion of glucose into the hepatic portal vein it is necessary to give quantities greatly in excess of those normally flowing in the portal vein, even after a very large meal. Thus, if all of the pathways described above are involved in controlling intake, their signals must be integrated by the appropriate circuits in the brain. Presumably these signals which fluctuate rapidly in relation to meals are added to a more stable signal coming from adipose tissue, and a relatively small change in the strength of the signal from adipose tissue will, in the long term, play a significant part in controlling intake.

Food intake is also affected by positive signals, such as the sight or sound of other animals eating, and the delivery of fresh food. These are presumably integrated with the negative signals coming from the visceral receptors to determine whether or not feeding should occur.

Although the discussion of 'modern' theories of the control of intake started off with energostasis, it is necessary to include other factors, particularly the physical fill of the digestive tract and the sensory characteristics of the food. There are many ways in which these signals might be combined in order to generate the final outcome in terms of feeding; two possibilities are that they are either added or multiplied.

Consider one set of receptors sensitive to stretch in the stomach wall and another set of chemoreceptors in the liver, both responding to increases in stimulation during and after a meal. The signal from the stretch receptors will be $S \times N_s$, where S is the degree of stretch and N_s is the number of receptors. Similarly, the signal from the chemoreceptors will be $C \times N_c$, where C is the concentration of the chemical(s) to which the liver receptors are exposed and N_c is the number of such receptors. Geometric combination of the two signals would give:

$$IS = (S \times N_s) \times (C \times N_c) \quad (9.5)$$

where IS is the strength of the integrated signal. However, should either of the families of receptors not be stimulated (as may occur with a highly concentrated food that does not stretch the gut wall or a totally indigestible 'food' that does not yield any nutrients to stimulate the liver) and S or C are therefore zero, then the combined signal will be zero:

$$IS = (0 \times N_s) \times (C \times N_c) = 0 \quad (9.6)$$

or

$$IS = (S \times N_s) \times (0 \times N_c) = 0 \quad (9.7)$$

and intake will be uncontrolled. This led to an alternative possibility: that the effects on intake of stimulation of different groups of receptors are additive:

$$IS = (S \times N_s) + (C \times N_c) \quad (9.8)$$

Booth (1978) found it necessary, in order to prevent excessively large meals, to include distension as well as energy feedbacks in a rat model in an additive manner, equating distension with Joules and adding this to the genuine energy signal. This is in contrast to models based on the TPH, in which feeding was stopped by energy supply or gut fill, whichever was first to reach a critical level. There is sufficient evidence to be able to conclude now that some feedback signals combine additively in their effects on intake, rather than being mutually exclusive, and experimental evidence for additivity of feedback signals in support of this equation is presented in Chapter 10.

Maximizing efficiency

Dissatisfied with the concepts of distension and chemical feedback as controllers of intake in ruminants, Ketelaars and Tolkamp (Ketelaars and Tolkamp, 1992a, b; Tolkamp and Ketelaars, 1992) have explored theoretically the costs and benefits of food consumption and proposed that intake is controlled to optimize the ratio of oxygen consumed to net energy made available.

They give several examples of animals behaving in ways that minimize the ratio of oxygen consumed to work done, showing that, for example, horses prefer to walk, trot or gallop at speeds at which they are most efficient. Using data collated by the Agricultural Research Council (ARC, 1980), they have sought to demonstrate that ruminants eat that amount of food/day at which net energy production per mole of oxygen is maximized.

Figure 9.1 shows the relationships between the efficiency of obtaining net energy by oxidation (ratio of net energy intake (NEI):oxygen consumption) and the level of food intake (ratio of net energy intake:net energy required for maintenance) for foods of several metabolizabilities which, according to the equations of ARC (1980), reach maximum values at points at which animals are predicted to consume each food voluntarily. For example, a food with a metabolizability (q) of 0.55 shows a peak of NEI: O_2 consumption at the same level of intake of this food ($1.4 \times$ maintenance) that sheep consume voluntarily.

In attempting to answer the question 'How can oxygen utilization be measured?', Ketelaars and Tolkamp suggest that intracellular pH is capable of being monitored and is, in part at least, influenced by oxygen consumption. However, intracellular pH is influenced by numerous other factors and would be an unreliable indicator of oxygen consumption. Even if the latter could be measured, why should animals seek to be optimally efficient? Presumably through evolution, gross inefficiency has been avoided but there is no more evidence that animals want to be efficient than that they want to be comfortable. Although such a novel approach is refreshing, there is too little evidence on which to accept their claims at the present time.

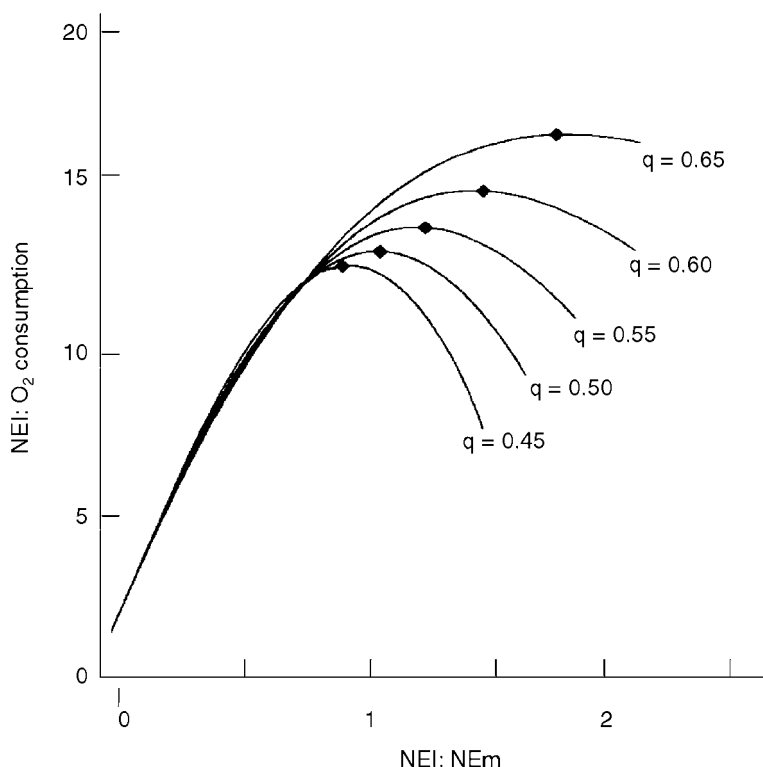


Fig. 9.1. The efficiency of oxygen utilization (NEI:O₂ consumption) as a function of NEI for roughages of metabolizabilities (q) 0.45–0.65. ◆, values corresponding to the average observed voluntary intake of such feed by sheep (Tolkamp and Ketelaars, 1992, using equations from ARC, 1980).

In a recent development (Tolkamp *et al.*, 2007), the investigators have extended their coverage of this theory to fattening animals, with very encouraging results, and this is covered in Chapter 15.

Concept of Weston (1996)

A recurring theme in food intake control, especially for ruminants, is the idea that animals eat to meet their nutrient (energy) requirements unless prevented from doing so by one or more constraints, of which the constraint of gut fill is the most common. This is expressed in the two-phase hypothesis (TPH, see above). Concerns about the validity of the TPH in its simple form led Weston (1996) to revisit the subject and to present his concept of the principles on which ruminants control their food intake.

His assumptions included the common one that the animal's capacity to use energy is the sum of the requirements for maintenance plus growth plus reproductive activities, including lactation; this capacity is reduced when

pathways of oxidation or synthesis are blocked, e.g. by inadequate levels of essential nutrients (including glucogenic substrates) or when climatic conditions limit rate of heat loss.

He proceeded to propose that energy deficit generates hunger signals, the strength of which is linearly related to magnitude of deficit. His other basic assumption was that forage constraints include resistance of flow of OM from the rumen, difficulties of harvesting and prehension, environmental stresses and 'low diet palatability', whatever is meant by this. He observed that the clearance rate of digesta OM from the rumen and quantity of OM in rumen are directly related, but with a limit to the increase in OM removal. The digesta load generates a satiety signal, directly related to rumen load once a threshold is reached. Weston viewed such factors as stretch, osmolality, chemical effects and hormones as warning signals preventing overloading of the system rather than as satiety factors per se, and points out that feeding pattern can easily be disturbed without much change in daily intake. However, we must consider their roles as US in the development of conditioning (see Chapter 6).

Critically, Weston then proposed that feeding drive is overcome when the combined inhibitory signals more than balance the hunger signals. As evidence of the interplay between ruminal digesta load and energy deficit, he pointed to the increase in ruminal digesta load when voluntary intake of a low-energy food (forage) is low. Also, infusion of a nutrient solution into the abomasum of lambs fed low-quality forage decreased *both* intake and ruminal digesta load, showing that intake was no longer limited by capacity, even if it had been before the infusion. While glucose infusion i.v. into lambs fed high-quality food reduces voluntary intake with almost exact energy compensation, with poor forage similar infusions do not decrease intake sufficiently to give complete caloric compensation. It indicates that both physical and metabolic factors can be acting *at the same time*.

Whereas the inverse relationship between digesta load and energy supply is seen in animals of similar physiological state, when energy demand changes there are changes in load and energy intake – e.g. lactation, in which energy intake increases and digesta load increases. Thus, load can be the same at various energy intakes because of differences in capacity to use energy.

Figure 9.2 is the conceptual relationship between the ruminal digesta 'load' and energy deficit for forages without (ABCD) or with (EFGD) constraints such as 'low palatability'. Weston places great emphasis on energy deficit (the shortfall in energy supply being the difference between the current supply from the food and the optimal supply to satisfy all requirements). When energy deficit is zero (A) then reducing the yield of DOM/kg of food (digestibility) causes an increase in DM intake and ruminal digesta load (B). Further reduction in digestibility results in a further increase in rumen load, but not sufficient to prevent a decrease in energy intake, giving the linear relationship from B to C. On reaching C, further reduction in the digestibility does not result in further increase in rumen load as the rumen is 'full' (CD). The concept that BC is linear suggests that Weston viewed hunger and satiety signals as being *additive*, at least up to a certain point.

A further proposition is that limiting factors move the relationship to the right, i.e. for any given energy deficit, intake and rumen load is lower than for a food

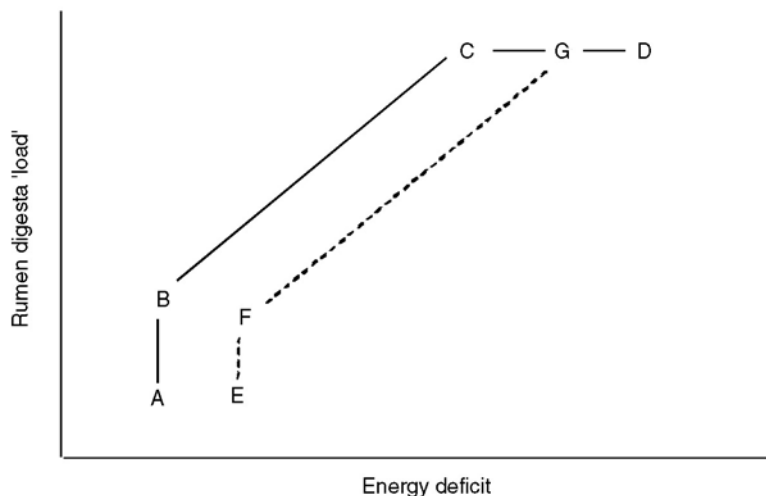


Fig. 9.2. Conceptual relationship between energy deficit in sheep and rumen digesta load. Solid line is without, and dotted line with, inhibitory factor(s) such as low palatability (from Weston, 1996).

without such constraints. Although Weston puts forward 'palatability' as being a particularly important example of a constraint, he does acknowledge that: 'The significance of low palatability as an intake constraint remains a vexed question'.

Note that rumen load in Weston's concept has a fixed upper limit, in contrast to some others in which it changes according to metabolic state (e.g. Mertens, 1994). However, is the notion realistic that the rumen allows itself to be filled until a sudden, fixed limit is reached? The question is addressed in Chapter 10 through the MTD hypothesis.

Conclusions

Many theories of the control of voluntary intake have concentrated on single factors such as gastric distension, blood glucose concentration, body temperature or fat stores. In ruminants, distension of the rumen and infusion of short-chain fatty acids have additive effects on intake but this has not been properly incorporated into models of intake by ruminants, although additivity of distension and metabolic signals is a feature of the early rat models.

More recent theories of intake control have included those in which the efficiency of utilization of oxygen for net energy production is maximized, and this may in some way be coupled to feelings of metabolic 'comfort', which animals presumably seek to maximize.

Mathematical models help us to understand the relative importance of different factors affecting and controlling intake. Models are only as good as the concepts and data from which they are built, but play a vital part in the advancement of our understanding of what controls food intake.

10 Minimal Total Discomfort

In previous chapters it has been shown that many factors affect food intake, but it is uncertain as to whether each factor in question plays a significant role in the normal control of intake. Some of these difficulties can be overcome by a hypothesis that negative feedback signals are interpreted by the CNS in an additive manner. In this chapter the evidence for the integration of signals, particularly by addition of their effects on intake, is presented. This is followed by the development of the Minimal Total Discomfort (MTD) hypothesis, in which it is proposed that animals eat that amount of food, and such a mixture of foods where more than one is available, so as to minimize the 'discomfort' emanating from the integrated sum of the deviations of the various factors from their optimal.

Evidence for Additivity

Poultry

The effects on the food intake of cockerels of various combinations of loading the crop with glucose solution and infusion of glucose into the portal vein on 3-h intake are additive (Shurlock and Forbes, 1981a). Not only are the effects of the same nutrient administered into different sites additive, but also different nutrients given into the same site. A mixture of amino acids depressed intake much more when infused into the portal vein than into the jugular vein (Shurlock and Forbes, 1984), and several combinations of amino acid mixture and glucose given into the portal vein had similar effects on food intake during the 3-h infusion.

Similarly, lysine and glucose infusions into the portal vein have additive effects (Rusby and Forbes, 1987a); whereas the birds ate 71 g during the 3-h infusion of saline, intakes were depressed to 54 and 61 g with 300 mg lysine

and 1260 mg glucose, respectively. When both metabolites were given together the intake was 46 g, which is almost exactly the sum of the depressions caused by the two given separately (see Fig. 4.2).

Cattle

To test the hypothesis of additivity of negative feedback signals in lactating cows, Mbanya *et al.* (1993) applied distension of the rumen by a balloon (10.0 l), infusion of acetate (9.0 mol/3 h) into the rumen and infusion of propionate (4.0 mol/3 h) into the rumen, each of which had a small and non-significant effect on silage intake. When given in combination there were additive effects in most cases, to give significant depressions in intake (see Fig. 10.1).

The only exception to the general observation of additivity was when sodium acetate infusion was combined with sodium propionate infusion. While it is possible that this is a chance finding, it can also be explained in terms of an imbalance of nutrients. Infusion of a single metabolite, such as acetate, upsets the normal balance of volatile fatty acids, which makes the animal feel uncomfortable. A simultaneous infusion of propionate, in a ratio with acetate similar to that normally produced by fermentation, corrects the imbalance, making the animal more comfortable and therefore not depressing intake. Overall, however, the evidence is for additivity.

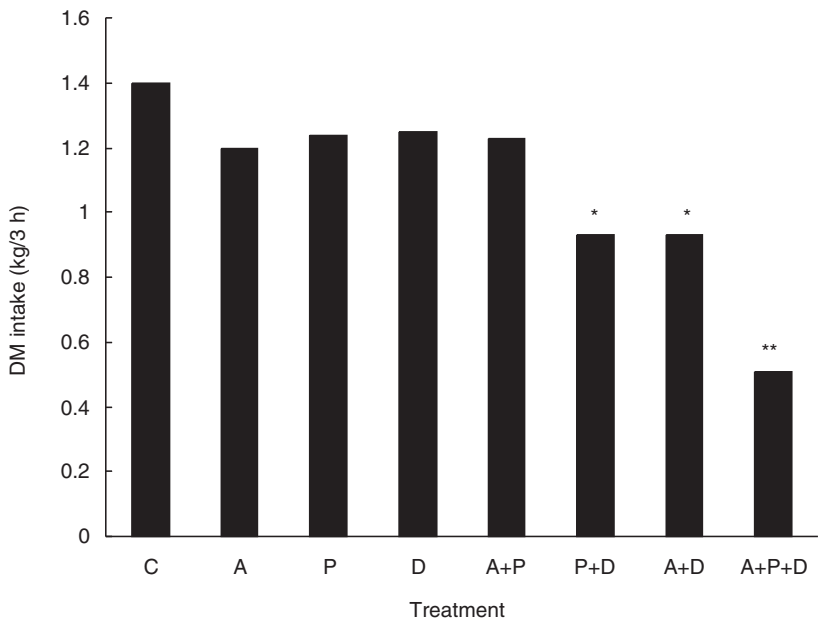


Fig. 10.1. Intake of silage DM by dairy cows given distension of the rumen (D, 10.0 l for 3 h), intra-ruminal infusion of acetate (A, 9.0 mol/3 h) and propionate (P, 4.9 mol/3 h) either separately or in combination). Significantly different from control (C): * $P<0.05$, ** $P<0.01$ (from Mbanya *et al.*, 1993).

Sheep

Equivalent experiments with sheep have given similar results. Sodium propionate solution at 0.6 mmol/min into the hepatic portal vein depressed intake additively with sodium acetate into the rumen at 2 mmol/min for 3 h, as did ruminal acetate infusion and balloon distension (1 l) (Adams and Forbes, 1981).

If one negative feedback factor is administered experimentally at a rate that initially completely suppresses feeding, it is to be expected that eventually, when other negative factors have declined to low levels due to an abnormally long period without food, the exogenous treatment will no longer be sufficient to prevent feeding. Infusion of sodium propionate into the hepatic portal vein of sheep at 1.2 mmol/min for 3 h prevents feeding for the whole of this period (Anil and Forbes, 1980b). When infusion continued for longer periods, small meals started to occur after about 6 h of treatment and were then more frequent than on control days (P.M. Driver and J.M. Forbes, unpublished results). Although intake was significantly depressed during 7 h of infusion, the fact that eating did resume agrees with the general theory of additivity.

If one set of receptors is denervated and the brain is no longer aware of the extent of stimulation by negative feedback factors, the animal might be expected to continue feeding for a longer time during each meal than before the denervation. Because of these large meals, levels of all negative feedback signals will rise to higher levels and for longer than usual, which will lead to a longer interval before the next meal occurs. This happens when the liver is denervated in rabbits (Rezek *et al.*, 1975), sheep (Anil and Forbes, 1980b) and chickens (Rusby *et al.*, 1987).

So far, our examples of additivity have been for signals that inhibit feeding. Aydinoglu and Forbes (1985) studied combinations of noradrenaline injected into the lateral ventricles of sheep (a potent stimulus to feeding, see Chapter 5) with infusions of acetate into the rumen; additivity is, once again, quite clear: while noradrenaline stimulated intake (292 g versus 217 g/3 h for control) and acetate inhibited feeding (18 g/3 h), noradrenaline partly reversed the effect of acetate when both were given together (98 g/3 h), i.e. almost exact additivity.

There is general agreement, then, that small, experimentally induced changes in several signals that might be involved in food intake act together to reduce food intake. The sum of such small changes that occur during a spontaneous meal might be sufficient to be satiating.

The concept of additivity is useful in understanding situations, such as lactation, where there is a very high rate of utilization of metabolites, leading to the under-stimulation of chemoreceptors. The animal can therefore suffer a greater degree of distension before the total of the negative feedback signals reaches the level at which feeding is switched off.

Egan (1970) added casein to a straw diet or infused casein into the duodenum and saw increased voluntary intake by sheep. The volume of ruminal contents was increased, and Egan suggested that there is a mechanism that allows greater fill when protein nutrition is improved. He also saw the possibility that concentrate intake might be regulated by ruminal volume being 'set' at a lower level than for forages; these ideas do not now seem so speculative as they

did in 1970. Improving the protein status of the sheep allowed a more rapid utilization of nutrients and thus a greater degree of ruminal distension before their combined signal became satiating.

It might be, therefore, that additivity is a general phenomenon involving many factors affecting food intake, not simply the negative feedbacks from the viscera, and that intake and body weight are the net result of the effects of these many factors. This theory helps to resolve the conceptual difficulty of coping with the many factors that affect intake and may be involved in its control.

No longer do we have to take the pessimistic view, expressed by an eminent animal scientist, that: 'The problem in research in intake regulation is the establishment of evidence for or against *mutually exclusive* alternative hypotheses'. For such a view to be valid it would be necessary to assume that a feedback signal, say stomach distension, which was controlling intake with a poor-quality food, suddenly disappeared (or was suddenly ignored by the CNS) when the quality of the food was improved so as to bring it into the 'metabolic' range. It seems highly unlikely that this would be the case.

Maximal stimulation of one population of receptors, perhaps causing pain, may saturate the control system and prevent other stimuli having additive effects on feeding. Grovum (1979) found that distension of the reticulum with 800 ml of water in a balloon depressed intake to a marked extent, but that simultaneous abomasal distension had no further effect. This result might be explained by the likelihood that mechanoreceptors in the reticulum were grossly affected by a balloon of such large size in relation to the capacity of that viscus, especially as the reticular wall is relatively inelastic.

Afferent pathways for negative feedbacks

This section presents anatomical and physiological evidence that signals from metabolic receptors converge with those from other classes of receptor, such as those monitoring visceral distension, osmolality and adiposity, to provide the CNS with a composite picture of comfort/discomfort and thus to play a vital part in influencing intake and preferences for food.

From the mouth to the anus, food and digesta provide a continuously changing set of stimuli to stretch and tactile receptors. There is considerable convergence in the afferent branches of the autonomic nervous system that relays the impulses to the CNS (Forbes, 1996). The work of Leek and colleagues showed how physical and chemical stimulation of receptors in the digestive tract activates vagal afferent pathways to the gastric centre of the *medulla oblongata* (Forbes and Barrio, 1992). In addition, the liver is sensitive to propionate, once again relaying its information to the CNS via autonomic afferents (Anil and Forbes, 1987) and providing a comprehensive assessment of the energy supply via the liver.

It seems unlikely that the CNS could interpret individually the nature and degree of stimulation of each receptor in the viscera, as there are both polymodal and polytopic integration of visceral signals with convergence in ganglia and in hind-, mid- and forebrains.

Pain?

If we are to place reliance on a smooth relationship between stimulus and response in the context of feedback signals from the viscera and food intake, we must address the question of whether the supraphysiological stimulation required to depress food intake significantly represents an extremity of a dose–response relationship that includes also a small (and often non-significant) depression in intake caused by mild and physiological stimulation of one type of receptor. Cervero (1994) says that visceral sensations (including pain) are carried by spinal afferents while reflex regulation of visceral function is managed through vagal fibres, i.e. physiological and supraphysiological sensations are relayed to the CNS via different pathways.

However, Janig and Morrison (1987) see abdominal pain as an extension of normal sensitivity to stimuli such as distension of a viscus or irritation of a mucosal surface by chemicals, i.e. the afferents responsible for relaying abdominal pain are the same as for physiological functions, but that different ranges of stimulation are involved. They observe that most neural units studied in various abdominal viscera have stimulus–response functions covering the normal and supranormal ranges of pressure in a single curve. This agrees with the effects of different degrees of distension, and different rates of infusion of VFA salts into the rumen, on food intake by ruminants (see Chapter 3), where a single dose–response curve fits the data for dose ranging from physiological to well above the physiological range.

Thus, while a large stimulus is required to induce a statistically significant reduction in food intake, the effects of smaller stimuli, within the physiological range, are part of a continuum with the more extreme doses; they can be considered to cause discomfort rather than pain. Additivity of feedback signals, discussed above, could account for satiety, with modest changes in many signals being summed to provide a general, total signal of visceral stimulation.

Minimizing Discomfort

Knowing that animals learn to associate discomfort induced by ingestion of toxic or imbalanced foods with the sensory properties of those foods (see Chapter 6), it seems reasonable to propose that animals eat to optimize their comfort. It is, as we know, uncomfortable to have an insufficient supply of nutrients, so we eat to reduce the discomfort of hunger. It is also uncomfortable, and sometimes painful, to eat too much food or to eat poisonous materials, so we avoid eating too much and avoid eating poisonous foods. Thus, by eating for minimum discomfort, we integrate positive and negative signals but then rely to a great extent on what we have learned to be the consequences, in terms of discomfort, of eating foods on previous occasions.

The use of the term ‘discomfort’¹ in this context has been criticized, but is justified on the grounds that animals would prefer not to suffer discomfort and

¹ Something that causes difficulty, trouble or lack of ease (<http://www.answers.com/topic/discomfort>).

will behave in such a way as to minimize it – preferring a balanced diet to an unbalanced one is an example of avoiding a discomfort.

Theories based on discomfort have to rely on human experience and such animal feelings as can be deduced from learned associations, preferences and operant conditioning. Science progresses by dissatisfaction with current explanations, leading to new or modified theories and then to experiments to demonstrate or otherwise the validity of these theories. The challenge now is to develop experimental methodologies to measure animals' comfort ratings. Given that metabolic comfort is primarily subconscious, this is a significant challenge.

Minimal Total 'Discomfort' (MTD)

Why talk about 'minimizing discomfort' rather than 'maximizing comfort'? Because there is no quantitative way of defining what is maximum comfort, whereas the minimum for discomfort is clearly zero.

It is apparent that animals are eating to obtain the nutrients they need to survive and to ensure their genes survive. The physiological state of the animal determines the optimum rate at which each tissue takes up each nutrient from the blood in order to meet genetic targets, and an inability to supply these in full leads to signals whereby the state of deficiency is transmitted to the central nervous system.

An excess leads to signals of toxicity. Moderate deficiencies or toxicities can be tolerated – the tissue in question, or another tissue(s), adapts to cope with the situation but, the more extreme the difference between supply and demand, the stronger the message becomes and the more urgently is the animal driven to redress the imbalance – to reduce the discomfort (for the purposes of this discussion we classify energy as a 'nutrient' – more correctly we could encompass nutrients, energy, bulk and flavour as 'properties' of foods or of 'resources' provided by foods). In addition, factors such as the bulk of food, difficulty of losing sufficient heat to the environment and limitations on grazing time per day (constraints) can all be viewed as generating discomforts; so can environmental and social factors.

There are numerous food properties that can be presumed to generate negative feedback signals because experimental addition of these to the diet, or introduction directly into the animal enterally or parenterally, generates dose-related reductions in voluntary food intake (see Chapters 3 and 4). It seems likely that the signals generated by the various families of chemo- and mechanoreceptors in the abdomen are integrated by the CNS in an additive manner (see above) but, when it comes to using this concept to predict food intake, the problem of expressing the various factors in a common currency has to be faced.

We can propose that the difference between the rate at which a food property is supplied and the optimal rate for body functioning generates 'discomfort' in proportion to the magnitude – but not the sign – of the deviation, expressed as a proportion of the optimal rate. We then square the relative discomforts before adding them, justified as follows.

We will start by considering the very simple case involving just two food properties, energy and protein. In Fig. 10.2, the intake of each is represented along an axis of the two-dimensional relationship between the two properties. If the animal's current food intake provides energy and protein in amounts represented by point A and its optimal intakes of energy and protein are at point B, then its desired trajectory is indicated by the arrow from A to B. The strength of the combined deviation in energy and protein supplied is represented by the length of this arrow, which is calculated (Pythagoras) as the square root of the sum of $(A - B)^2$ and $(B - C)^2$. Thus, the combined discomfort (d) generated from energy (E) and protein (P) can be calculated from the squares of the two separate deviations.

$$dEP = \text{sqrt}(dE^2 + dP^2) \quad (10.1)$$

Squaring the deviations provides two practical benefits: (i) discomforts are always positive, whether more or less than the optimal quantity of a resource is currently being consumed; and (ii) large deviations have a disproportionately greater feedback effect than small ones, in line with physiological expectations. A sheep with an optimal supply of ME of 20 MJ/day, but only eating an amount of food that provides 15 MJ, will have a relative discomfort from lack of ME of $(20 - 15)/20 = +0.25$, as would a similar sheep receiving 25 MJ/day in its diet $((20 - 25)/20 = -0.25)$. Squaring each of these gives the same result: $+0.063$.

It is possible, of course that the animal is influenced by each of the deviations in sequence, rather than in parallel as implied by the diagonal arrow in Fig. 10.2, in which case it would first change its food intake to reach its desired intake of one of the properties (energy or protein) and afterwards modulate its intake to optimize the balance between the two properties.

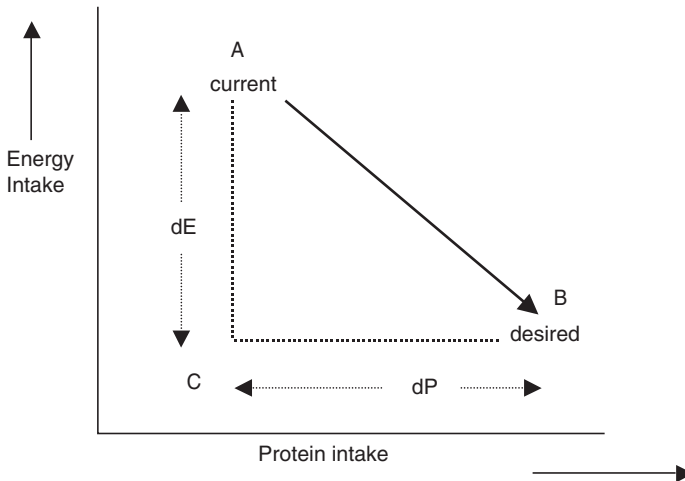


Fig. 10.2. Notional pathways between an animal's current intakes of energy and protein and its desired intakes (see text for description).

To determine whether the solution is Pythagorean or rectangular would involve designing appropriate experiments in which animals' intakes were monitored closely after a change of diet. A possible design would be similar to that of Ferguson *et al.* (2002), in which growing pigs were given choices between three foods. Although the changes in intake with time are not presented in detail, the authors conclude that: 'Preference was firstly against potentially harmful substances in the food (e.g. tannin) or an anti-nutritive factor (e.g. cottonseed oilcake), and then for better-balanced or higher protein-value feeds'. Whether this sequential, rather than parallel, response is general can be answered only by further relevant experiments.

This line of reasoning can be extended to more dimensions, each representing a different source of discomfort, be it food- or environmentally related. Figure 10.3 shows the case for three food factors, energy, protein and calcium, while environmentally related factors are considered in Chapter 18. The relationship between energy and protein is the same as above, while calcium (C) is represented by the third dimension.

$$\text{As } dEP = \sqrt{dE^2 + dP^2} \text{ and } dEC = \sqrt{dE^2 + dC^2} \quad (10.2)$$

then

$$dEPC = \sqrt{dEP^2 + dC^2} = \sqrt{dE^2 + dP^2 + dC^2} \quad (10.3)$$

More generally:

$$\text{Total discomfort} = \sqrt{\sum_{j=1}^i w_j ((o_j - c_j) / o_j)^2} \quad (10.4)$$

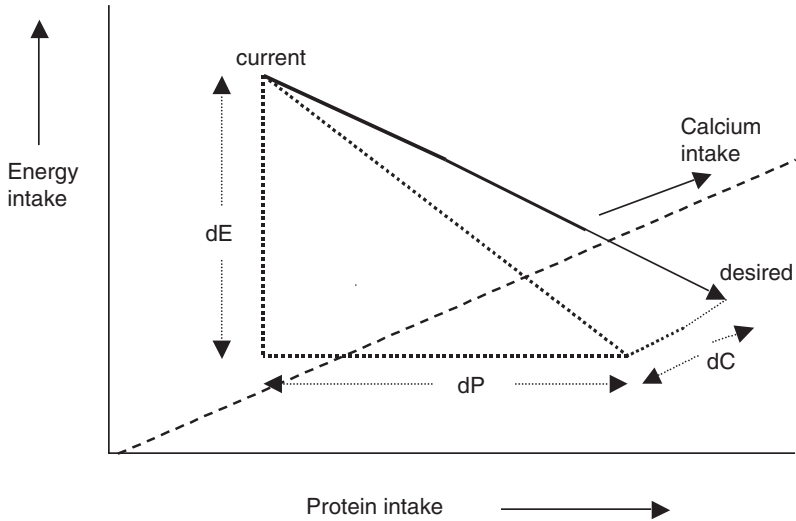


Fig. 10.3. Notional pathways between an animal's current intakes of energy, protein and calcium and its desired intakes (see text for description).

where the total discomfort is generated by the discomforts of each of an array of i items – food and environmental properties, where w , c and o are the weighting, current and optimal rate of supply for resource j out of the set of i resources. All the weightings are set to 1 in this example.

A worked example

As an example, we will take a growing lamb of high genetic merit for which we can specify the approximate ‘nutrient requirements’: e.g. 20.0 MJ ME/day, 0.25 kg crude protein/day, with an effect of bulk becoming increasingly strong above an intake of NDF of 0.4 kg/day and an increasing discomfort if the time spent eating exceeds 10 h/day (grazing time does not normally go above 13 h for sheep and 15 h/24 h for cattle). The forage offered contains 10.00 MJ ME/kg DM, 0.10 kg CP/kg DM and 0.6 kg NDF/kg DM, eaten at a rate of 1.5 g DM/min. A lamb eating this at a rate of 1 kg DM/day would have a discomfort due to lack of ME of $(20 - 1.0 \times 10) = 10$ MJ/day, giving a relative error of $10/20 = 0.5$ and a relative discomfort of $0.5^2 = 0.25$. Similar calculations for CP, NDF and time spent eating give discomforts of 0.36, 0.25 and 0.012, respectively and a total discomfort of 0.93 units (square root of the sum of squares of each of the individual discomforts).

Repeating the calculations with a daily intake of 1.2 kg/day we find that total discomfort has risen to 1.09. Reducing intake to 0.8 kg DM/day gives a total discomfort of 0.93; further iterations show that total discomfort is minimized at 0.91 when daily intake is 0.90 kg DM. This is plotted in Fig. 10.4, with discomfort on the y-axis and intake on the x-axis (note that the MTD model run with similar parameters (Forbes, 1999a) gave different results because a different weighting was applied to each factor, but this is not now considered justifiable at our present state of understanding).

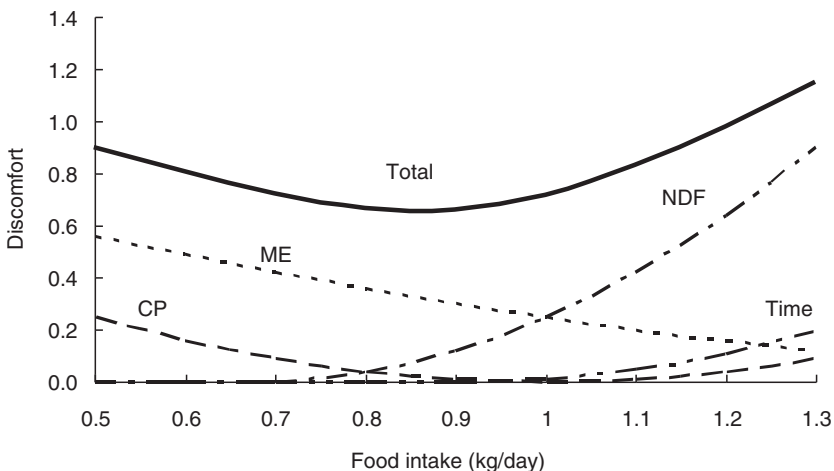


Fig. 10.4. Calculations of discomfort due to deviations in supply of ME, CP, NDF and time spent eating from optimum, and total discomfort (see text for details).

The example given here is simple – in reality, changes in the quantity and rumen degradable fraction of the CP are likely to affect yield of ME and rate of digestion of NDF; excess CP can be used as a source of energy. A model of rumen and animal metabolism should be used in conjunction with the MTD model if it is to be tested more realistically for its adequacy in predicting food intake of ruminants.

Further, the function relating the deviation in supply of a food property from that required to the discomfort generated – the unweighted square of the proportional deviation from the ‘requirement’ – is not likely to be optimal. It is unrealistic to expect that an intake of a mineral at half the required rate will generate as much discomfort as ME supplying half the requirement, so the question of whether and how to place a relative weighting on each factor will have to be resolved before this approach can be expected to generate quantitatively appropriate predictions.

There are other factors that can generate discomfort under some conditions: (i) social pressures – whether to follow the flock or to stay eating the rich patch of herbage; (ii) heat production – the problem of heat dissipation in a hot environment and/or with a heavy covering of insulation; while (iii) other constituents to be considered include individual essential amino acids, minerals, vitamins and toxins.

Note the shallow nature of the total discomfort curve: intake can change quite a lot around the optimum with little change in TD. Emmans and Kyriazakis (1995) criticized the theory of optimization of energy yield per unit of oxygen consumption (Ketelaars and Tolkamp, 1992b) for this very feature but, of course, it's what happens in reality – similar animals eat different amounts from each other and the same animal eats different amounts on different days. This is a major obstacle to the short-term predictions of intake at the level of the individual animals (see ‘day-to-day variation’, below).

MTD in action

The example above describes how the MTD hypothesis is quantified. It will work with inputs from one factor (i.e. just ME, as a trivial example) upwards to as many factors as required for the situation under review. One or more of the food properties and/or animal requirements can be systematically altered to investigate how MTD holds up under a variety of conditions. Examples are presented in the following publications: (i) effect of dietary protein level and selection for protein in sheep (Forbes and Provenza, 2000); (ii) rate of harvesting by sheep (Forbes, 2001); (iii) choice between two types of herbage by sheep (Forbes and Mayes, 2002); (iv) dietary NDF in sheep (Forbes, 2005a); (v) effect of food CP on diet selection by growing chickens (Forbes, 2005b); and (vi) food quality (energy, protein and NDF covarying), food protein, supplementation and substitution, selection for protein in sheep (Forbes, 2007). In each case the model performed in a similar manner to animals subjected to the same treatments, but it cannot be claimed that predictions are precise – the model is semi-quantitative in its current state.

EFFECT OF ME CONTENT ON INTAKE BY LACTATING COWS As a further example of the use of the MTD model, we here investigate its performance for dairy cows over a range of foods of different qualities. ME was varied from 8 to 13 MJ ME/kg, in parallel with which NFD decreased progressively from 700 to 300 g/kg; CP was maintained at 140 g CP/kg.

Figure 10.5 shows the predictions of intake plotted against food quality (expressed here as ME concentration) of the food for the lactating cow with optimal intakes of 219 MJ ME/day, 1.60 kg CP/day and 8.60 kg NDF/day. It can be seen that intake increases with improvements in energy yield up to about 9 MJ ME/kg, but then decreases with the highest-quality foods. When the ME requirements of the animal were increased to 250 MJ ME/day (but the NDF threshold stayed the same), the maximum DM intake was predicted to be achieved at an ME content of about 10 MJ ME/kg. An increased productive energy output was thus predicted to increase food intake with diets of high ME content; despite no change in the ‘capacity’ to handle fibre, the intake of forages was predicted to be increased by increased nutrient demand, as observed by Tulloh (1966).

The predicted change-over from a positive to a negative relationship is not abrupt, as suggested by Conrad *et al.* (1964) but, as envisaged by Owen *et al.* (1969) and observed in practice (Bines, 1979; NRC, 1987, p. 57), occurs gradually in a manner that is more biologically credible than a sudden change in slope.

APPLICATION OF MTD TO LAYING HENS In this example, the laying hen has optimal intakes (‘requirements’) of 1.25 MJ ME, 3 g calcium and 25 g protein/day and is offered a single food containing 11.5 MJ ME, 17 g crude protein (CP) and 2.5 g calcium (Ca)/kg. Figure 10.6 shows the predictions that discomfort due to ME is minimal at an intake of 110 g/day, that due to Ca at an intake of 120

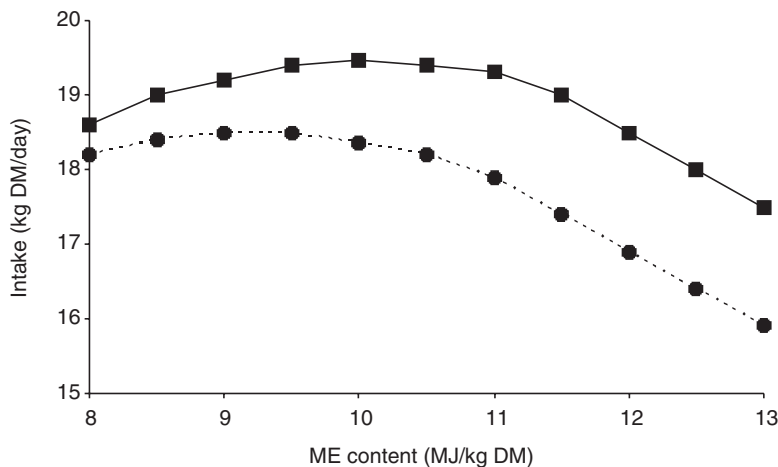


Fig. 10.5. Predicted intake of foods of a range of nutrient values (see text) for a lactating cow with ME requirement of 219 MJ/day (●) and another with ME requirement of 250 MJ/day (■).

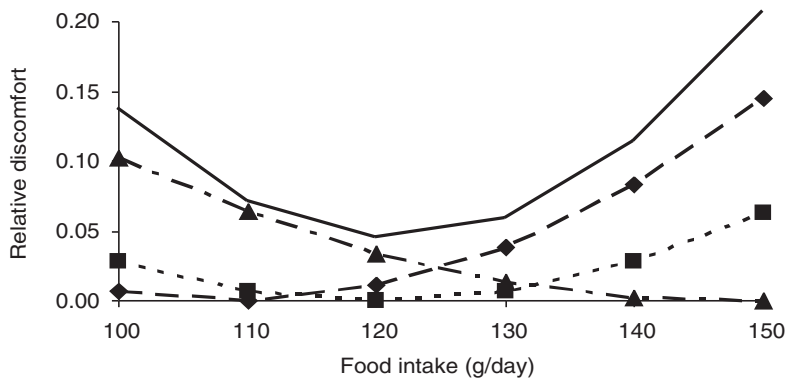


Fig. 10.6. Relative discomfort due to ME (♦), Ca (■), CP (▲) and total discomfort (—) for laying hens at food intakes of 100–150 g/day (from Forbes, 2006b).

g/day while discomfort due to CP is minimal up to an intake of 150 g/day. Summation of the squared discomforts gives a total discomfort curve whose minimum is at an intake of 120 g/day, at which point discomfort is not zero as the animal is suffering a moderate excess of ME and a deficiency of CP.

To simulate a bird with access to two or more foods, the model is given the bird's 'requirements' and the composition of the foods and 'experiments' with different combinations of food until it arrives at that mixture which gives minimal total discomfort. A hen with the same requirements as above is offered two foods with different protein:energy ratios and ground limestone, i.e. a choice between three foods. High-protein food has an ME content of 11.5 MJ/kg, a CP content of 0.25 kg/kg and a calcium content of 0.010 kg/kg; low-protein food contains 12.5 MJ ME, 0.15 kg CP and 0.01 kg Ca/kg, while limestone includes 0.35 kg Ca/kg with no energy or protein.

It is not always possible to achieve optimal intakes of three nutrients when choosing between three foods but, in this case, there is a mixture of the three that provides optimal intakes of ME, CP and Ca and this is shown in Table 10.1, which also includes the results of simulations with each pair of foods and each single food. Comments on the right of the table indicate how the hen is predicted to cope in each situation. As long as limestone is available Ca intake can be maintained but, in the absence of either the high- or low-protein foods, then ME or CP, respectively, is under-consumed. The model appears to behave as hens are expected to behave, but no attempt is made here to compare the predictions with real observations.

Validation

It is not the intention to screen numerous published sets of results searching for a few that match the outputs of the model, but rather to see that a model believed by the author to be based on physiological principles behaves in a

Table 10.1. Outcome of running the MTD model for laying hens with either three, two or one food available, in terms of intake (g/day) and total discomfort (TD, arbitrary units) (see text for details of hens' requirements and composition of foods). HP, high-protein food; LP, low-protein food; LS, limestone (from Forbes, 2006b).

Food(s) available	HP intake	LP intake	LS intake	Total intake	TD	Comments
HP, LP and LS	89	18	6	113	0	Perfect match
HP and LP	74	50		124	0.378	Overeats both ME and CP, but very short of Ca
LP and LS		118	5	123	0.118	Overeats ME and undereats CP, marginally; normal for Ca
HP and LS	104		6	110	0.003	Undereats ME and overeats CP, marginally; normal for Ca
HP	115			115	0.410	Overeats a little to try to acquire Ca
LP		131		131	0.460	Overeats a lot to try to get Ca and CP; excessive ME intake
LS			9	9	2	Eats only to acquire exactly right Ca; dies of starvation

rational manner. It is not a predictive model but a research tool designed to be used to explore the usefulness of the MTD approach to understanding how intake and selection might be controlled. There is a long way to go, especially in discovering relative weighting factors for each food resource and determining the shape of the relationships between food intake and discomfort generated by each of the nutrients of interest.

In addition, many other factors than those mentioned above can be incorporated, such as: (i) infusion of metabolites and inflation of a balloon in the stomach; (ii) social influences, as long as they can be quantified; and (iii) environmental factors (see Chapter 18). As far as the author can see, this flexibility is unique amongst models of food intake and selection and is one reason why it seems to be a path worth following.

Day-to-day Variation in Intake in the Context of the MTD Hypothesis

If the MTD hypothesis has any bearing on the way in which animals control the intake and choice of foods, then it must surely depend on them experiencing the effects of straying from the optimum in order to know whether their current intake and/or choice is still the most appropriate. To what extent is there day-to-day variation in intake?

It is usual for mean intakes to be calculated over several days and several animals, but it is a matter of common observation that there are large day-to-day variations in intake both between and within animals. In terms of the MTD hypothesis (and indeed of some other hypotheses) this is not surprising, as the control of daily intake is not expected to be closely controlled.

Some of this variation is likely to be due to external factors such as short-term changes in the composition of the food, climatic variables and changes in management procedures. However, there is individual variation over-and-above that induced by external factors, which would be similar for all animals in a group (A.O. Jolaosho and J.M. Forbes, unpublished observations), and it may be that such variation serves some useful evolutionary purpose.

An animal that eats exactly the same amount of food each day has no opportunity to find out whether its overall comfort would be better served by eating a little more, or a little less, than on the previous days. An animal can only know whether it should be eating more (or less) than at present in order to minimize its discomfort if intake varies from time to time. Even when it has arrived at the optimal state it can only know whether it should maintain the same level of intake if it tries out the effects of different rates of intake. The concept that animals find an optimum intake by 'experimenting' with a range of intakes, which implies that learning is involved, is supported by clear demonstrations that ruminants, like other animals, learn to associate the sensory properties of the food with the consequences of eating that food (Forbes and Provenza, 2000; Chapter 6).

Poultry

An example of day-to-day variation of intake in a laying hen can be seen in Fig. 16.8. In a study of the daily variation in intake by broiler chickens (S. Wahl and J.M. Forbes, unpublished observations), residuals from the regression of intake on age tended to be positively correlated with intakes 1 and 2 days later, but negatively with the third and subsequent days. This suggests that intake is being controlled to meet requirements over a period of several days; higher than average intake might persist for 2 or 3 days but is followed by lower than average intake for the next few days. This behaviour can be interpreted as the birds 'experimenting' by increasing or decreasing their daily intake in order to determine whether they feel more or less comfortable, and then following the line of least discomfort.

Pigs

Figure 15.3 illustrates an example of the extreme day-to-day variation in intake of an individual growing pig. Each of a large number of pigs showed similar amounts of variability, some of it synchronized but much of it unique to individuals.

Cattle

Graphs of day-to-day fluctuations of intake of forages by cattle (Forbes and Provenza, 2000; Forbes, 2001, 2003a) show the large and irregular variations which, when smoothed over increasing numbers of days, become more stable. Ingvarsten *et al.* (1992) studied random day-to-day variation in DMI and reported an average CV of 19.6 within animals. It has been suggested that a cyclic food intake pattern reflected repeated bouts of acidosis, and a fourfold increase in the odds of a health incident (calving, metabolic or digestive disorder) associated with a 1% increase in the CV of DMI in the first 21 days after calving has been reported.

More consistent food consumption could help minimize the incidence of ketosis and displaced abomasum, and it can be suggested that it is in the cow's interests to maintain stable intakes, day by day. The fact that they do not might mean that there is some advantage in variable daily intake, and this advantage might be to allow them better to judge whether their current intake is optimal.

Sheep

Figure 6.5 shows the daily intakes of two sheep selected at random from data of 32 sheep provided by J. Hills (unpublished observations). Examination of data from the previous 15 days, by which time intake had become relatively stable, again showed large day-to-day fluctuations in intake by individuals, in

comparison with fluctuations in the mean for all animals. The mean standard deviation of the residuals was 82, with a range of 31–162 g/day for individuals. Only in 15 out of the 32 individual sheep was daily intake in the last 15 days significantly ($P < 0.05$) correlated with the daily mean intake of all 32 sheep.

This is clear evidence for large variations in daily intake that are unrelated to external factors such as food quality or climatic variables. Even if this day-to-day variation is not purposeful, it still serves the animals' intake control system by providing information about whether a small increase or decrease in intake improves metabolic comfort.

Conclusions

It is proposed that animals eat according to an integration of negative and positive signals from myriad sources, including gut and liver receptors, metabolites and adipose tissue. These signals are speculated to generate discomforts in proportion to the square of the deviation from optimal intakes of each food resource, and the discomforts are added together to provide the integrated signal that the animal can learn to associate with the sensory properties of the food in question.

The advantage of the MTD hypothesis is that it can take into account any factors that affect food intake, although it is necessary for them to be quantifiable. The weaknesses include the fact that many such factors are not properly capable of being quantified and, even for those that are, we do not often have reliable relationships between their strength and the response, nor do we know the relative weighting to be put on each factor. The theory can, therefore, be called semi-quantitative, at best. Nevertheless, the author hopes that it will stimulate discussion, experimentation and modelling.

The MTD hypothesis incorporates and emphasizes the role of learning, not only in determining what choice between foods should be made, but also what total amount of food should be eaten. The large day-to-day variation in food intake shown by most animals when fed *ad libitum* provides the wherewithal for this learning process; an animal taking exactly the same amount of food each day does not know whether that amount is optimum for its current physiological state or for the food currently available. MTD provides a very flexible tool for integrating thinking on many aspects of the control of food intake and diet selection.

11

Diet Digestibility, Energy Concentration and Supplementation of Forages

'Animals eat for calories.' While not true under all circumstances this statement provides a good starting point for consideration of the effects of digestible or metabolizable energy concentration in the diet on the intake of DM. Perfect compensation for changes in DE¹ or ME² content (i.e. 'useful energy') or digestibility (which is closely related to energy yield) would entail animals regulating their DM intake in order to maintain a constant energy intake under conditions of changing concentrations of available energy. Similarly, changes in energy requirements, as in animals in lactation, should lead to changes in DM intake exactly sufficient to match the new requirements.

Such perfection is, however, rarely achieved. First, the measured or estimated concentrations of DE or ME in their diet may not reflect exactly the yield of useable energy per kg of food. Secondly, animals might not be seeking to achieve simply constancy of useful energy. Thirdly, there are frequently limiting factors preventing increases in intake large enough to compensate for reductions in useful energy concentration of foods, or increases in animals' energy requirements. Management of the energy concentration of foods for farm animals is probably the most important task for animal nutritionists and managers; in view of this importance, a great deal of information is available on the effects of useful energy concentration on voluntary intake and animals' performance, hence a whole chapter is devoted to this subject.

Voluntary food intake is dependent to a considerable extent on the chemical and physical characteristics of the food(s) being eaten. It is essential, therefore, to incorporate some measure(s) of food quality in multiple regression

¹ DE is the amount of energy in the diet that does not appear in faeces, expressed as MJ/kg DM. This is the common method of expressing energy value of foods for pigs.

² ME is the amount of energy in the diet that does not appear in faeces, urine or gas, expressed as MJ/kg DM. This is a common method of expressing energy value of foods for poultry and ruminants.

equations for predicting food intake. Parameters such as digestibility and rate of passage of food are functions of both the animal and the food and should, in theory at least, be capable of being predicted from primary measurements made separately on the animal and the food. However, digestibility and rate of passage are to some extent dependent on the level of food intake, so direct measurement is preferable to prediction until we have a better understanding of the causal relationships between all of these factors.

The amount and type of fibre in a food influences the extent and rate of digestion and thus the yield of absorbable energy and nutrients. There are, therefore, relationships between the yield of energy and nutrients per kg of food and such parameters as the content of fibre (crude, acid detergent, neutral detergent), degradation rate in nylon bags, rate of gas production during incubation with ruminal microbes *in vivo* and NIR spectra. Because of the high fibre content of many ruminant foods, the relationships between fibre content and food intake have been explored predominantly with this class of animal. In the section of this chapter on ruminants, therefore, there are subsections dealing with the relationships of each of the above-listed parameters with voluntary intake.

Poultry

There is a negative relationship between the concentration of ME in the diet and voluntary intake. However, the compensation is not usually complete, so that increasing the ME content of the diet by adding fat can be used to increase ME intake and thus weight gain or egg production. Conversely, fibrous ingredients can be included in the diet where high levels of performance are not required, e.g. growing pullets.

Growing birds

Fat incorporation in the diet tends to reduce DM intake. In general, it is thought that fats depress intake by a general energy-related effect because injection of small amounts of individual long-chain fatty acids (the major constituents of fat) intraperitoneally or their inclusion in the food does not depress intake to a significant extent. Some short- and medium-chain fatty acids do depress intake, however, whether given intraperitoneally or in the diet (Cave, 1982). In the latter case propionic, but not acetic, acid was effective; caprylic and lauric acids gave a 5–6 g depression in daily food intake by 2–3-week-old broilers for each gram of the acid included per kg of diet.

However, the modern broiler actually increases its intake when maize oil or tallow is incorporated in the food, presumably due to the lack of complete control over ME intake in young birds. Fats high in polyunsaturated fatty acids, such as cod liver oil and olive oil, depress intake by broilers, possibly due to deterioration or to toxic effects. It is clearly inappropriate to refer to 'fat' in this context without specifying the type of triglycerides involved.

Dilution of the food with 100 or 200 g kaolin/kg increased the total food intake of growing Leghorn (layer strain) cockerels to regain the same intake of digestible DM and maintain the same weight gain as controls (Savory, 1984). When 300 g kaolin/kg was included they stopped gaining weight, while with 400 g/kg they lost weight because, although total food intake increased, it did not immediately do so sufficiently to maintain intake of digestible nutrients. Eventually, however, intake did increase but weight gains were still depressed, presumably because of the high cost of eating the greater amount of food. Physical limitation of intake, although usually considered in the context of ruminants, can exert an effect on the voluntary intake of simple-stomached animals but has not been well characterized.

With a fast-growing broiler strain, however, dilution of a standard finisher food with up to 50% sand and oats resulted in a 100% increase in food intake and thus a maintenance of weight gain (Leeson *et al.*, 1996). Broilers have much greater growth potential than layer chicks and, according to the MTD theory (see Chapter 10), this will make them less prone to physical limitation, analogous to the effect of lactation in cows.

Laying hens

Laying hens adjust their food intake to satisfy their energy requirements when the energy concentration of the food is changed. Compensation is not perfect, however, de Groot (1972) gave foods with ME concentrations ranging from 10.5–13.4 MJ/kg and observed a significant negative relationship between ME concentration and food intake (see Fig. 11.1a). The reduction in food intake caused by increasing ME concentration was not sufficient to prevent an increase in ME intake (see Fig. 11.1b) and egg weight and body weight gain were significantly increased by increasing ME concentration of the food.

Heavier eggs can thus be obtained by feeding more energy-dense diets, but such diets are invariably more expensive than less dense foods. Given the value of eggs and cost of foods at the time of de Groot's work, the economic optimum food ME concentration was around 11.7 MJ/kg under the conditions of this experiment.

Morris (1968) surveyed the available literature and found the following overall relationship between the voluntary intake (MEI, kJ/day) by laying hens and the metabolizable energy concentration of the food (MEC, kJ/g):

$$\text{MEI} = \text{SMEI} + ((2.28 * \text{SMEI}) - 612.7) * (\text{MEC} - 11.3) \quad (11.1)$$

where SMEI is the intake of a standard food with a metabolizable energy concentration of 11.3 kJ/g DM. The compensation in voluntary intake is not usually sufficient to prevent changes in ME intake, especially when intakes are low, e.g. associated with low egg production at high temperatures.

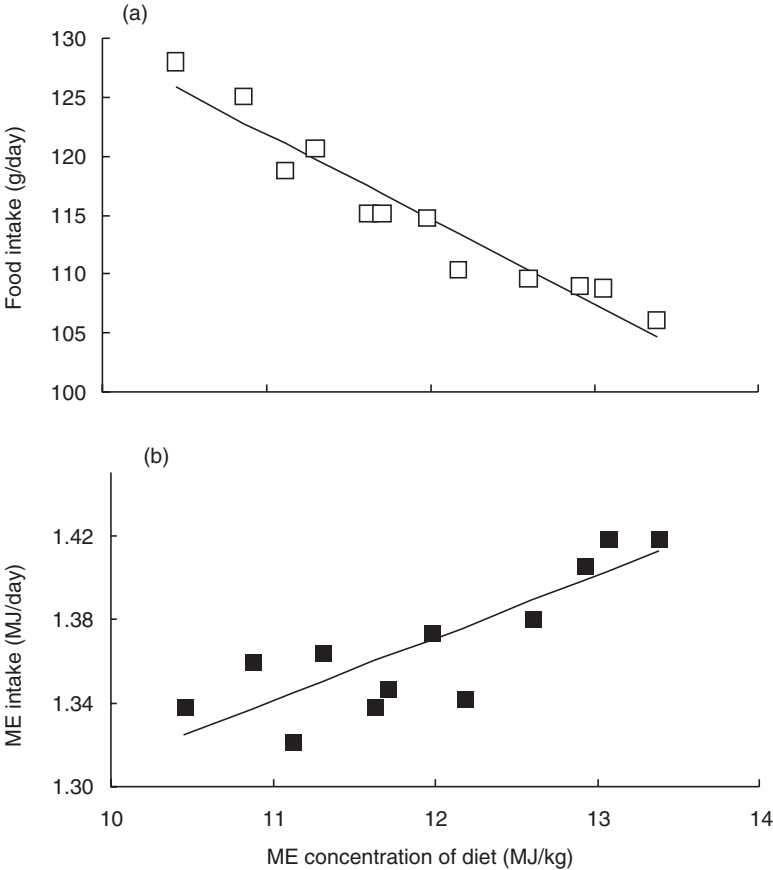


Fig. 11.1. Effect of dietary concentration of metabolizable energy (ME) on (a) food intake (g/day) and (b) ME intake (MJ/day) by laying hens (from de Groot, 1972).

Whole cereals

Although choice-feeding of whole barley and a balancer food has been reported to improve or have no effect on egg production, including whole barley in a single, balanced food has met with mixed results (see Chapter 8). In a carefully balanced experiment, Bennett and Classen (2003) compared foods with either 60% ground or 60% whole barley, with or without insoluble grit provided at 4 g/bird/week. The latter was studied as it was thought it might improve the breakdown of the whole grains and improve performance of hens on the whole-grain food. Feeding whole barley reduced egg production, food efficiency and egg specific gravity and increased food intake, egg weight and body weight gain (see Fig. 11.2). Access to insoluble grit had no effect on any of the production variables measured and there were no interactions between the physical form of the cereal and the provision of grit.

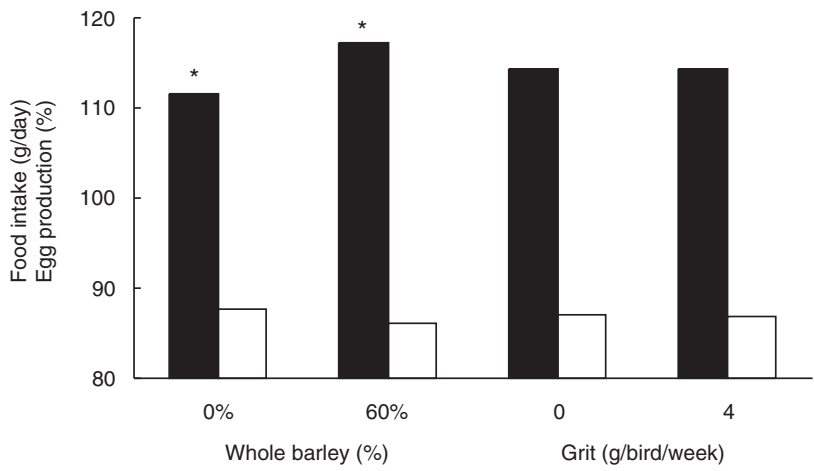


Fig. 11.2. Effect of whole barley and insoluble grit on food intake (solid bars) and egg production (open bars) of hens from 19 to 43 weeks of age. *, significant effect of level of barley, $P < 0.05$ (from Bennett and Classen, 2003).

Pigs

As noted in Chapter 1, pigs tend to overeat and attempts to manipulate voluntary intake have concentrated on limiting the digestible energy (DE) intake while feeding *ad libitum* to save labour (as detailed in Chapter 15, modern pig genotypes have much less propensity to fatten and *ad libitum* feeding of conventional foods to growing pigs is now widely practised in the UK).

In many studies with growing pigs, energy density of the diet has not been shown to affect DE intake, i.e. there is complete compensation. However, compensation is not complete with foods below about 14.5 MJ DE/kg, although the exact DE content below which failure to compensate completely depends on the age of the pig (NRC, 1987). Henry (1985) concluded, from a broad review of the literature, that as DE concentration increases DE intake also increases, while DMI is reduced, resulting in pigs becoming fatter on more concentrated diets. Whether energy concentration was increased by adding fat or starch, the effect on intake was similar (Cole and Chadd, 1989).

However, growth was slower on high-fat diets compared with high-starch foods, even though intakes were the same. This may be due to a poorer efficiency of utilization of the energy from high levels of fat for protein synthesis. Inclusion of fat is useful at higher environmental temperatures as it has a lower heat increment than carbohydrate or protein and therefore depresses intake less in hot climates.

An experiment was carried out in which growing pigs were given foods with different TDN³ concentrations (Owen and Ridgman, 1967). From the results

³ Total Digestible Nutrients: this approximates to the proportion of energy-yielding nutrients in the diet.

shown in Fig. 11.3, it can be seen that food intake was greater in the older animals; in addition to their greater maintenance requirements, they were also depositing fat at a much greater rate than the younger animals although protein deposition would be little changed (Whittemore, 1987). It will also be noted that intake of indigestible material was considerably greater in the older animals, especially with foods low in TDN, indicating their greater capacity to handle bulk.

During the early stage of growth, from 27 to 50 kg, food intake was relatively unaffected by the nutrient content of the diet, which meant that TDN intake increased and indigestible matter intake decreased with the more digestible diets (see Fig. 11.3a). When the same pigs were approaching slaughter weight, however, intake of both food and indigestibles declined with increasing nutrient density, while TDN intake was relatively constant (see Fig. 11.3b). In this experiment, the foods were formulated to have a constant ratio

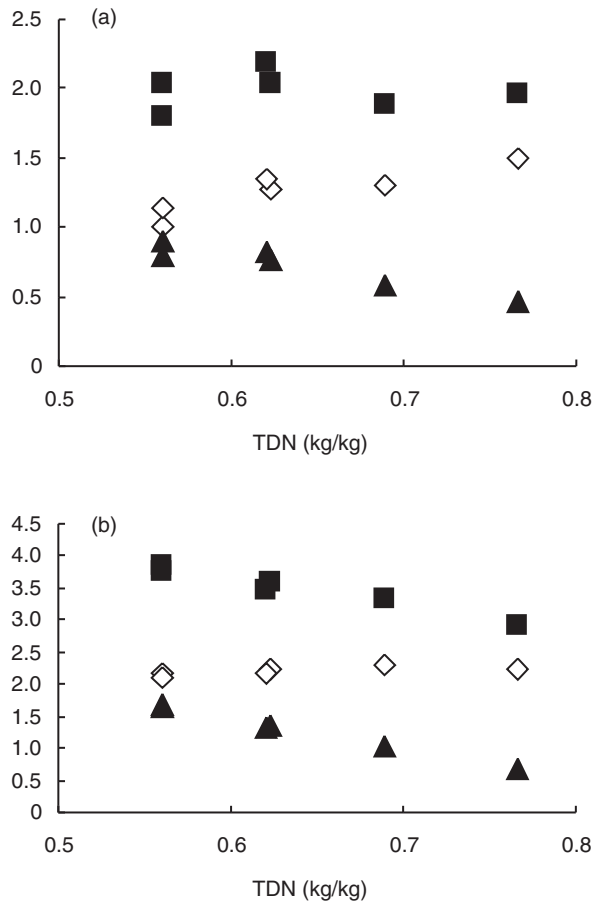


Fig. 11.3. Intakes of dry matter (■), TDN (◇) and indigestible matter (▲) by growing pigs fed diets with different TDN contents from (a) 27–50; (b) 95–118 kg live weight (from Owen and Ridgman, 1967).

of protein:TDN, so protein intake also increased with TDN concentration in young pigs and remained more or less constant in the older animals.

Although it has been shown that inclusion of inert fillers in the food of growing pigs reduces the intake of digestible energy, substantial dilution has to be made in order to depress DE intake sufficiently to affect fattening significantly. Fillers such as sawdust are easy to obtain in small amounts, for experimental purposes, but if they were to be included in commercial rations the demand created would soon result in an increase in price. Lower grades of food, such as oat hulls, have been used to depress DE intake but compensation for such dilution occurs in older pigs, i.e. when the depression in DE intake is most required to prevent over-fatness.

Figure 11.4 summarizes the proposals of a model of the effects of energy concentration of the food on intake of pigs at different stages of growth (Tybirk, 1989). This agrees with the observations reported above, that in young pigs there is a positive relationship between the DE concentration of the food and the amount of DE eaten, but as the pig grows the intake-depressing effect of low-energy diets becomes less.

These results demonstrate that the importance of different factors controlling intake changes as the animal grows; presumably the older animal has a greater gut capacity, relative to its nutrient requirements, and this allows it to eat more high-fibre material and maintain its intake of nutrients to meet its metabolic demands. Even so, the intake of DE increases slightly with increasing nutrient concentration – there appears to be some interaction between physical and metabolic controls, as envisaged by the MTD hypothesis (see Chapter 10).

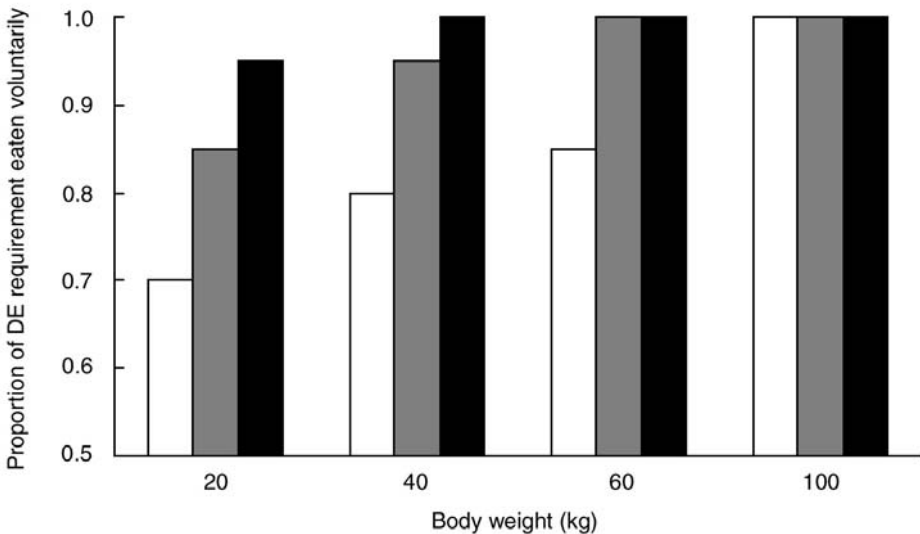


Fig. 11.4. Effect of body weight of growing pigs on the intake of DE, expressed as a proportion of energy capacity as influenced by the energy concentration of the diet: 11 MJ/kg, open bars; 12 MJ/kg, grey bars; 13 MJ/kg, solid bars (from Tybirk, 1989).

Capacity for bulk

The question of the capacity of the digestive system of the growing pig for bulk has been addressed in detail by Whittemore *et al.* (2001a), who present several equations for predicting the effects of bulk, expressed either as fibre content or water-holding capacity (WHC) of the food. They draw particular attention to an experiment that included a range of values for WHC of less than 2 to greater than 6 (g/g) and show a one unit (g/g) increase in WHC as being associated with a decrease in food intake of about 6 g food DM/kg body weight (Kyriazakis and Emmans, 1995). From their considerations, Whittemore *et al.* (2001a) proposed:

Food intake (kg/day) = (0.111W^{0.803}) – (0.006(WHC – 4)W) (11.2)

where W = body weight (kg) and WHC = water-holding capacity of the diet (g/g) for foods of 0.9 DM.

The WHC of foods is mainly related to the NSP⁴ content (Tsaras *et al.*, 1998). Figure 11.5 shows the relationship between the water-holding capacity of a range of foods with different NSP contents and voluntary intake by growing pigs. With bulky foods such as these it was noted that intake is proportional to body weight rather than to metabolic body weight, suggestive of physical limitation of intake.

Pigs adapt to bulky foods more quickly if they have had previous experience of bulky foods, being able to consume up to 1.4 times as much of a high-bulk

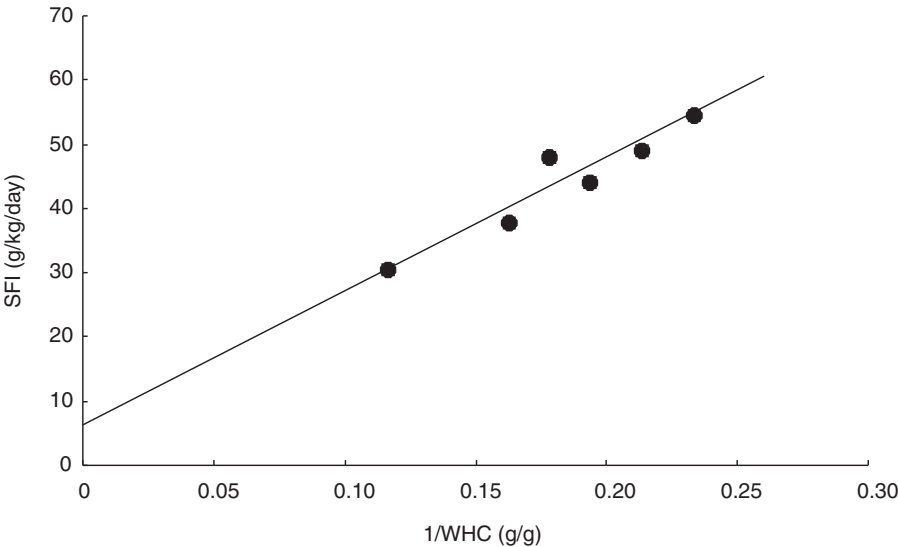


Fig. 11.5. Intake (SFI) of six bulky foods by growing pigs plotted against the reciprocal of the water-holding capacity (WHC) of the foods (from Tsaras *et al.*, 1998).

⁴ NSP, non-starch polysaccharides – polysaccharide component of dietary fibre.

food than pigs that had previously been fed a low-bulk food (Whittemore *et al.*, 2001c).

To investigate further the relationship between live weight and the intake of bulky foods in pigs, Whittemore *et al.* (2001c) offered bulky foods – intended to limit growth – for 21 days to pigs of 12, 36 and 108 kg live weight. The high-bulk foods reduced weight gain and caused significant increases in the weights of the stomach, large intestine, caecum and gut fill. The pigs' capacity for bulk (Cap, kg water-holding capacity/day) was related to live weight (W, kg):

$$\text{Cap} = (0.192 \times W) - (0.000299 \times W^2) \quad (11.3)$$

The weights of the large intestine plus caecum (WLIC) changed with W in parallel with Cap, and the ratio of Cap to WLIC was close to constant. It was considered, therefore, that the capacity of the large intestine and caecum may determine the capacity for food bulk in pigs.

Selection for efficiency of lean growth has led to a marked reduction in voluntary food intake of modern genotypes, and there is concern that lean growth rate is being limited. It has been found that modern Large White \times Landrace pigs have poorer ability to compensate for diluted foods than do pigs with 1/8 Meishan blood (Gill *et al.*, 1999). The conditions under which the Meishan breed has developed, where there is a need to utilize low-nutrient density by-products, might have led to greater ability to accommodate bulky foods.

As discussed in Chapter 10, the idea of a fixed limit to gut capacity does not sit well with physiological concepts, although the intake of bulky foods by pigs appeared limited to around 50 g daily food intake/kg body weight (Whittemore *et al.*, 2000). It seems as if the modern pig has been changed genotypically in a similar way to the broiler, where physiological control of intake seems to have given way to some extent to eating for bulk. The younger the animal, the greater its nutrient requirements per unit of body weight and the more important is stomach distension as a limit to food intake.

It can be concluded, therefore, that when the concentration of digestible energy in the diet changes then pigs, like hens, vary the level of voluntary intake in the appropriate direction to maintain digestible energy intake, but that compensation is not complete, giving increased DE intake with increased DE concentration in the food. Maximum weight gains in weaner pigs, therefore, require a diet high in DE, which can be achieved by adding fat, while older pigs can be fed a diet with a lower nutrient specification.

The effects of dietary dilution on voluntary intake of pregnant sows and the potential for commercial application are discussed in Chapter 16. The whole question of predicting intake and performance on changes in food bulk is thoroughly discussed by Whittemore *et al.* (2003).

Ruminants

The pre-ruminant calf or lamb compensates for dilution of its milk although excessive dilution, necessitating high fluid intakes, causes loss of production (see Chapter 15).

Digestibility

It used to be thought that the response of the ruminant animal to changes in the digestibility of the food was entirely opposite to that of non-ruminants, a reasonable conclusion based on the evidence available up to the early 1960s, i.e. a positive correlation between intake of forages and their digestibility by ruminants (Baile and Forbes, 1974). There is a great deal of evidence that dilution of a forage-based diet depresses intake of ruminants, some of which will now be reviewed.

In contrast to dilution with inert solid material, sheep and cattle can compensate for dilution of forages with water because the free water is quickly absorbed. If, however, the water is trapped inside cells, as in fresh grass or silage, then intake is often negatively correlated with water content (see Chapter 14).

Crampton *et al.* (1960) realized the significance of intake in determining the nutritive value of forages whose value is proportional to the yield of digestible nutrients per unit weight multiplied by the weight eaten. Thus, nutritive value is proportional to the square of digestibility for foods whose intake is limited predominantly by physical factors and thus dependant on digestibility. For example, a food of 500 g/kg DM digestibility might be eaten by cattle at a rate of 10 kg/day; another food of 600 g/kg DM digestibility would be eaten by the same animal at about 12 kg/day, thus increasing the intake of digestible DM from 5.0 to 7.2 kg/day.

Crampton and colleagues also realized that between-animal variations in intake would obscure between-food variations. They therefore used a standard food of lucerne offered to each of their animals, against which the intake for the other forages could be compared. Unfortunately, since different batches of lucerne varied in composition between experiments, comparisons were difficult. Moreover, the use of wether sheep as the standard animal may not predict relative intakes for forages by dairy cows.

In the early 1960s, then, ruminants were thought to control their food intake by physical limitation. Then came several developments that suggested a role for metabolic control. With pelleted diets, ranging from lucerne alone to 40% hay:60% concentrates, it was found that sheep controlled their intake to a constant intake of digestible energy, i.e. DM intake falls as the concentration of DE increases. This implied metabolic rather than physical control of intake. Also around this time came a series of experiments in which it was shown that infusion of short-chain fatty acids depressed intake (see Chapter 3), which indicated the possible mechanisms of such metabolic control.

Conrad *et al.* (1964) then published their analysis of a large volume of data obtained from routine digestion trials at the Ohio Research and Development Station, USA. They described the voluntary intakes of lactating cows for a wide range of foods. Despite the flawed nature of their analysis (Grovmum, 1987; Tolkamp, 1999), the concept that the intake of forages is limited physically while that of highly digestible foods was controlled metabolically had a great impact at the time of its publication.

This has been called the two-phase hypothesis (TPH) for the control of intake by ruminants (Pittroff and Kothmann, 2001b), which states that animals

eat that amount of food which meets their energy requirements unless prevented from doing so by the physical bulk of the food (see Chapter 9). The inverted V-shaped relationship between the DE content of the food and voluntary intake can be seen in the large amount of data collated by Baumgardt (1970; Fig. 11.6). In general, up to a DE concentration of about 12.5 MJ DE/kg DM, DE intake is positively related, while above this there are negative relationships. Note, however, the extreme variability between DE intakes in different experiments at any one DE content.

Where the food is of moderate digestibility but the forage part is ground, a negative effect on intake may be seen, as passage of particles is not a limiting factor to intake as it would be if the forage was in its long form. Thus, in the results of Montgomery and Baumgardt (1965) with beef cattle, it will be seen that DM intake decreases in a linear manner with increasing DE concentration (see Fig. 11.7a); this is the direction expected if the animals were compensating in order to maintain their DE intake. There is, nevertheless, a small but consistent *reduction* in DE intake as DE concentration increases (see Fig. 11.7b); although compensation in DM intake has been in the right direction it has not been such as to maintain a constant intake of DE.

This is in contrast to observations with simple-stomached animals, in which increased availability of energy in the food results in slight but persistent *increases* in DE intake. It is also in contrast to many other studies with

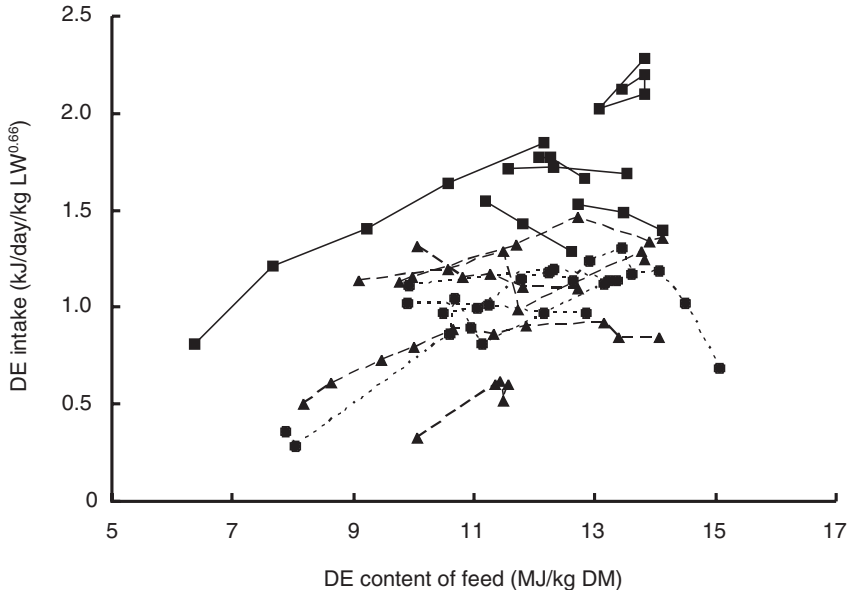


Fig. 11.6. Voluntary intake of digestible energy (DE) by sheep (■), growing cattle (●) and lactating cows (▲) (MJ/kg^{0.66}/day) against concentration of DE in the feeds (MJ/kg DM); treatments within each experiment are joined by a line (plotted from data included in Baumgardt, 1970).

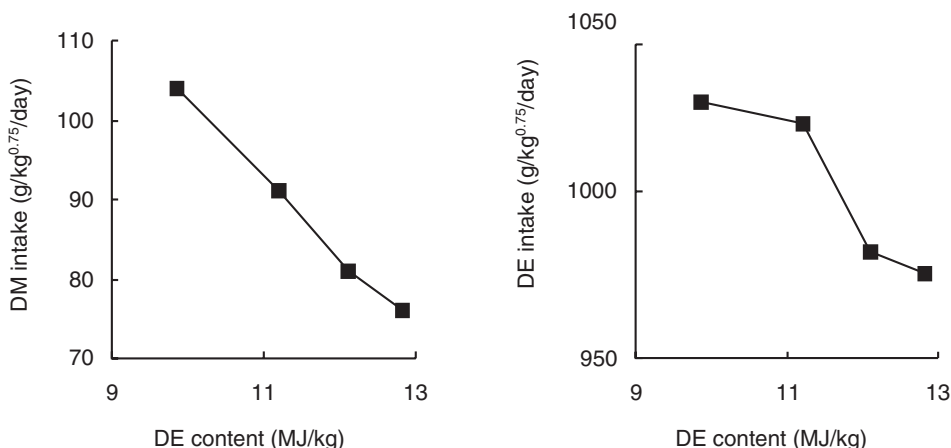


Fig.11.7. Intake of pelleted feeds of different digestible energy (DE) concentrations by growing beef cattle: (a) DM intake; (b) DE intake (from Montgomery and Baumgardt, 1965).

ruminants, in which there is a similar slight increase in DE intake with increasing DE concentration (Grovm, 1987).

Another example of a negative relationship between ME concentration of food (as low as 8.5 MJ ME/kg DM) and DM intake is to be found in Chapter 17 (Webster *et al.*, 2000; Fig. 17.6).

Digestible and metabolizable energy

With the increasing agricultural use of cereal-based rations for ruminants in the early 1960s, experiments were carried out that included foods with a wider range of digestibilities than had previously been used.

When sheep were fed on pellets containing various proportions of cereals and inert fillers (Dinius and Baumgardt, 1970), intake (g/day) was positively related to DE concentration (proportional to DM digestibility) for diets < 10.5 kJ DE/g DM:

$$\text{Intake} = 619\text{DEC} - 660 \quad (11.4)$$

where intake is kJ DE/kg BW^{0.66} and DEC is DE concentration in kJ/g. Above 10.5 kJ DE/g intake of DE was almost constant:

$$\text{Intake} = 1007 - 50\text{DEC}$$

suggesting that intake was controlled to match energy requirements when physical constraints were not important. The tendency for a negative slope on the latter relationship and in other published work indicates again that intake is not perfectly controlled by metabolic mechanisms.

Net energy

From a particularly large data set (1102 dairy cows) with a wide range of forages with concentrate supplementation, the following equation was derived:

$$FI = 0.009LW + 2.21NEL^{0.67} - 0.07CI^{1.63} \quad (11.5)$$

where FI is forage intake (kg DM/day), LW is live weight (kg), NEL is net energy concentration of the forage (MJ NEL/kg DM) and CI is concentrate intake (kg DM/day) (Schwarz *et al.*, 1996). This shows that increasing energy concentration increases the forage intake, but at a declining rate, in agreement with previous observations, although it does not show the decline in intake with very high-quality ground foods seen in some cases. Increasing the rate of concentrate supplementation results in an increased depression in forage intake, i.e. substitution rate increases with high rates of supplementation.

Fibre

There are many examples of negative relationships between the fibre content of food and its intake by ruminants. However, variations in the rate of digestion of fibre, as well as its extent, are likely to cause variations in the intake of forages, as rapid digestion releases digestive capacity quickly to allow more food to be accepted.

Earlier reliance on chemical measures of fibre, especially neutral detergent fibre (NDF), has been replaced by measures with more biological meaning, including: (i) rates of disappearance of food material from nylon bags suspended in the rumen; (ii) gas production by samples incubated *in vitro* with ruminal inocula; or (iii) methods giving a much greater number of physicochemical measures, such as NIR.

There are several types of fibre in most forages. Lignin is indigestible and so its content is inversely related to digestibility, but it has no consistent relationship with voluntary intake. Cellulose and hemicellulose are degradable by the ruminal microorganisms, but the rate of digestion is variable and the time spent by a particle in the rumen also varies, so there is no close relationship between a forage's content of these and the level of voluntary intake.

NDF

Van Soest (1967) has pioneered the cell-wall constituents (CWC) fraction of forages, as measured by the neutral detergent fibre (NDF) method, for predicting the physical fill created by food in the rumen. For a wide range of grasses, including many tropical species, there is an almost constant intake of NDF:

$$I = 110 - 1716/(1 - CWC) \quad (11.6)$$

where I is the voluntary intake (g DM/kg LW^{0.75}) by sheep and CWC is the proportion of CWC in the dry matter over a range of CWC contents from 350–750 g/kg. Rumination time is well correlated with the intake of NDF but

not with the weight of food eaten. There is, however, a very large amount of variation between intakes of forages with similar contents of NDF, which shows either that NDF is not a suitable descriptor for the prediction of intake or that other factors in addition to physical limitation are involved in the control of voluntary intake (see Chapter 10).

Although highly fibrous forages are eaten in lower amounts than those with low NDF content, there is a danger of feeding too little fibre that results in the lack of a 'mat' to trap particles in the rumen, so that faecal particles are bigger! Sometimes, grinding and pelleting *increases* faecal particle size because of this. There is also the risk of low milk-fat concentration if the food is too low in fibre and the optimal NDF content of the whole ration for milk production is 360 g/kg, irrespective of the type of forage on offer.

Indigestible organic matter (IOM)

Hopkins (1985) used IOM to develop a practical system for predicting intake by dairy cows under UK conditions. He accepted that, with high-energy diets, the metabolic controls of intake are of prime importance, but argued that this is of academic interest in view of the need to feed as much forage as possible in order to reduce concentrate requirements. From a review of the literature, Hopkins calculated that a mature cow can eat 6 g/kg body weight/day of forage IOM whilst growing heifers and beef cattle only eat 4.5 g/kg of their body weight. When compound foods are offered, the substitution rate resulting is appropriate to an IOM concentration of 110 g/kg of concentrate dry matter. Comparison of observed and predicted substitution rates showed that agreement is moderately good.

Predicting food intake in ruminants

In situ degradability

Digestibility is relatively easy to measure, but is probably not the most useful animal/food measurement for predicting intake. This is because some foods may be poorly digested but pass through the digestive tract relatively quickly, thereby occupying space for less time than a more digestible food with a slower rate of passage. For example, grinding a poor-quality forage increases its rate of passage and intake but, because particles spend less time in the tract, they are less well digested. Rate of passage through the whole tract is not a good predictor of intake, however, but a more useful measurement is the rate of degradation of food in the rumen, carried out by suspension of nylon bags containing food samples in the rumen of fistulated animals. The use of degradation of samples of food suspended in the rumen in nylon bags has been reviewed by Ørskov (2000).

For example, Carro *et al.* (1991) monitored the intakes of hays by sheep and the degradation characteristics, both for DM and for NDF. Disappearance from the bag was fitted to the equation of Ørskov and McDonald (1979):

$$y = a + b(1 - e^{-ct}) \quad (11.7)$$

where y is the DM or NDF disappearance (g/kg) from the bag after time t , a represents the immediately soluble material, b is the insoluble but potentially degradable material and c is the rate of degradation. Carro *et al.* (1991) found significant relationships between voluntary intake and the soluble fraction of the DM, the rate of degradation of DM and the rate of degradation of NDF. The best fit, however, was:

$$\text{DMI} = 21.3 + 0.073\text{PSOL} + 138\text{DINSOL} \quad (11.8)$$

where DMI is voluntary DM intake (g/kg^{0.75}/day), PSOL is the proportion of solubles in the DM and DINSOL is the rate of degradation of the insoluble potentially degradable fraction of the DM. Although NDF degradation characteristics were not as closely related to intake as those for DM degradation characteristics in this set of forages, the simple correlation between intake and NDF content was highly significant ($r = -0.84$), which reinforces the importance of routinely measuring NDF in forage evaluation programmes.

Another example of the many studies done on the relationship between degradability in the rumen and voluntary intake of roughages is that of Fonseca *et al.* (1998). Mature, non-pregnant, non-lactating ewes were fed five untreated cereal straws, two cereal straws treated with urea and five grass hays in different periods for the measurement of voluntary intake. To avoid protein deficiency, soybean meal was given in addition in amounts calculated to provide for the degradable nitrogen needs of the ruminal microbes. Male sheep were used to measure the digestibility of each diet and the kinetics of dry matter (DM) degradation in the rumen of the roughages. The best prediction of food intake, which ranged from 9.6 to 17.9 g/kg live weight, was given by the proportion degraded in the first 3 h of incubation ($r^2 = 0.68$) and the ADF content of the forage ($r^2 = 0.67$). However, digestible DM intake was best predicted by a multiple regression equation including the soluble fraction and rate of degradation, accounting for 89% of the variation observed.

A wider range of forages was included in the study of Blummel and Becker (1997), who found 82% of the variation in DMI to be accounted for by the parameters for the degradation of NDF. A combination of determination of NDF-D after many hours (≥ 24 h) and gas volume measurements after a short period of incubation (4–8 h) gives good prediction with a shorter analysis time (24 h) than used by many others. Eighty per cent of the variation in DMI was accounted for by degradation parameters obtained from the incubation of 500 mg whole roughage, when incubation was terminated after 24 h and the residual undegraded substrate quantified.

While these correlations suggest that the *in situ* degradation method – especially when coupled with gas production methodology (see below) – provides accurate prediction of intake, great care must be taken before using this methodology in practice. First, the parameters that give best prediction are often different in different studies. For example, the optimum time of incubation varies widely between studies, some suggesting that a few hours are sufficient, others insisting that several days are necessary.

Secondly, the way in which the samples are prepared for incubation can have marked effects on the results. For example, it has been found that more

finely ground samples of dried maize silage appeared to have faster degradation and, importantly, a greater proportion of degradable material, than unground samples (Valentin *et al.*, 1999). Even simply drying the silage increases its apparent degradability, compared with incubation of fresh samples.

Gas production

Studies of rate of degradation of materials in the rumen by the nylon bag method are time consuming and do not lend themselves to automation. Fermentation produces gas in amounts and at rates proportional to the degradation of materials, and gas production *in vitro* is much easier to measure than degradation. Close correlations between total gas produced during incubation of forage samples and food intake by ruminant animals have been observed (Blummel and Becker, 1997). The subject has been reviewed by Getachew *et al.* (1998).

Khazaal *et al.* (1995) compared many laboratory methods for predicting voluntary intake of forages: CP, NDF, ADF and ADL *in vitro* digestibility, *in situ* (nylon bag) DM degradation and gas production of 10 graminaceous hays fed *ad libitum* to four sheep; they also measured *in vivo* digestibility. Intake and DMD of the hays were variable and poorly related ($r = 0.52$). *In situ* DM degradation to 96 h of incubation was significantly related to intake ($r = 0.75$). Accurate prediction of intake ($r = 0.90$) was achieved using NDF, ADF, ADL and CP in a multiple regression or by using the (a + b) and c of gas production ($r = 0.87$).

When data of the graminaceous and other data from leguminous hays were combined, the most accurate prediction of intake was by using characteristics of *in situ* DM degradation followed by those of gas production, the latter in turn being more accurate than using chemical components or the *in vitro* digestibility. It was concluded that accurate prediction of intake can be achieved simply from the degradation characteristics of foods. However, these impressive correlation coefficients do not necessarily mean accurate prediction, and the relatively narrow data set (ten hays and four sheep) are not conducive to widespread application of the results.

Artificial mastication

Smaller food particles disappear from the rumen faster than larger ones, so that the ease with which a food can be masticated will affect rate of passage and thus food intake. Troelson and Bigsby (1964) developed a method of artificial mastication involving gentle passage of the wetted food between gears followed by drying and estimation of particle size index (P). The close relationship ($r = 0.94$) with intake by sheep (DMI, g/day) was:

$$\text{DMI} = 353\text{P} - 14 \quad (11.9)$$

which predicted forage intake by a 45 kg sheep to within 127 g/day. Bear in mind, however, that the hay intakes were by similar sheep kept under standard conditions.

Blummel *et al.* (1996) studied relationships between the extent and rate of *in vitro* gas production and the energy required to grind through a 1 mm screen, of 40 Syrian barley straws and their dry matter intakes by sheep and steers. *In vitro* gas-production parameters were closely correlated with the logarithm of grinding energy, and both measures were equally good in predicting intake ($r^2 = 0.84$ and 0.83 , respectively). Thus, as grinding energy is a much quicker and cheaper measure than gas production, the former could be used to predict intake quite accurately in this data set. Importantly, in the context of this review, forages should be selected for low grinding energy in order to have a chance of high levels of intake when fed to dairy cows.

NIRS

The measurement of *in situ* degradation is time consuming and requires fistulated animals; gas production methods also take several days in the laboratory and there is a need for better methods of food analysis, both to give results more quickly – preferably on the farm – and to give results that are better predictors of nutritive value and voluntary food intake than the laboratory methods currently in use. Near infrared spectroscopy (NIRS) is a promising tool for this purpose, as it quickly and cheaply provides information on the whole chemistry of a food rather than the few specific moieties normally monitored. However, a large databank of NIR spectra for foods with known intake characteristics must be built up and this is occurring only slowly.

NIRS gives a complex spectrum from which can be deduced a great deal about the chemical linkages in the material being analysed. Features of the spectrum are related to protein, fibre and other factors of nutritional interest. Initially, correlations of NIRS spectra with intake were found for dry forages (Givens *et al.*, 1997), but it has subsequently been found that intake of grass silage by sheep and cattle can be predicted well by NIRS and that wet samples can give similar accuracy of prediction ($r^2 = 0.88$) to dried samples (Park *et al.*, 1996). This paves the way for rapid assessment of nutritive value and prediction of intake on-farm once the cost of NIRS equipment comes within range of a small group of users.

In an attempt to simplify the indirect measurement of intake, Garnsworthy and Unal (2004) used NIRS of faeces to predict intake and digestibility in dairy cows in which DM intake had also been measured directly. The standard error of prediction of DMI directly from NIRS was 0.48 kg/day ($r^2 = 0.97$), but prediction of dry matter digestibility was much less accurate ($r^2 = 0.68$), probably because of the limited variation in digestibility values within the data set. The estimates of DMI are of similar accuracy to those derived from the traditional alkane technique.

Dilution with low-quality food

Cattle

Reduction of digestibility by inclusion of up to 30% of straw in a compound food for growing cattle may be compensated for by an increase in intake, but not always sufficiently to maintain the same growth rate.

Sheep

When lambs that had passed their stage of maximum growth were offered pelleted foods in which a barley/oats food was diluted with oat husks, to give a range of dry matter digestibilities of 600–780 g/kg, intake of digestible organic matter was constant and growth was unaffected. Because of the relatively low nutrient requirements of the sheep and the fast rate of passage of the residues of the ground, pelleted food, the point of inflexion of the intake/digestibility curve was < 600 g/kg.

Owen (1969) fed lambs on coarse or ground oat husks at 200, 400 or 600 g/kg in meal or pelleted form with a barley-based concentrate. From 15 to 27 kg live weight, intakes were constant or increased with increasing digestibility. From 28 to 40 kg, intakes of foods containing ground straw decreased with increasing digestibility, providing evidence for metabolic control in older lambs when there was a fast rate of passage. In several other experiments in which ground straw was used to dilute concentrate foods to give a range of digestibilities from 540–800 g/kg, there was complete compensation of voluntary intake by growing lambs.

Food Processing

Pigs

Pelleting appears to reduce food intake by weaners by about 10% but, at later stages of growth, the effect is much less. However, it is difficult to know how much of this apparent reduction in intake is really a reduction in wastage.

Cattle

NRC (1984a) provide a comprehensive coverage of effects of food processing on intake and digestibility in ruminants. Increases in intake caused by grinding and pelleting are generally negatively related to forage quality. Chopping increases intake of high-fibre, but not of better-quality, hay by cows; whether this is due to a limit imposed by chewing or ruminal capacity is not clear.

Particle size

It has been found that, the faster the rate of disappearance of food from the digestive tract, the lower is the digestibility above which intake declines. One way to reduce the time spent by food particles in the rumen is to offer forages in ground form. Inclusion of ground forages in complete foods for lactating cows allows digestible energy intake to be maintained, even at up to 60% forage, because the small particles of ground forage leave the rumen more quickly. Although digestibility is usually depressed, as there is faster rate of passage and thus less time for digestion, the yield of absorbable nutrients (intake \times digestibility) is normally increased and animal performance is improved. The benefits of grinding are greatest with forages of low digestibility.

Sheep

Sheep are much more sensitive to particle size than cattle. For cattle, unmilled and milled foods were eaten in similar amounts while, for sheep, the intakes were 57 and 91 g/kg body weight^{0.75}, respectively.

When dried grass was ground to different degrees of fineness, voluntary intake by cattle and sheep increased with decreasing particle size but the digestibility of organic matter was depressed, resulting in unchanged intake of digestible organic matter. With the finer particle size it is necessary to incorporate a binding agent to reduce dust.

Complete Foods for Ruminants

Knowledge of the relationships between intake and food characteristics can be utilized to manipulate the intake of metabolizable energy and thus the level of growth or milk production. When nutrient requirements are relatively low, a food of lower ME concentration can be offered, thus reducing the cost of feeding. A food consisting of concentrates and chopped or ground forage and presented in a form in which it is not possible for the animals to select one ingredient is often termed a *complete diet* (or *feed* or *food*) or a *Total Mixed Ration* (TMR). For any given level of animal performance there is a ME concentration which can be reflected in a forage:concentrate ratio that allows the ruminant animal to voluntarily eat the amount of food containing ME appropriate to its requirements. Ad libitum feeding of a complete food may encourage a higher intake than conventional restricted feeding of concentrates with forage ad libitum, and therefore gives the potential for better use of forages.

Owen (1979) has presented a detailed account of the principles and practice of complete diet systems for cattle and sheep. Within a herd of dairy cows there is usually a wide range of milk yields and nutrient requirements, from the high-yielding cow at the peak of lactation – which Owen suggests requires at least 50% concentrates – to the dry cow whose requirements can be met by good forage alone. It is implicit, therefore, that the herd must be grouped according to requirements, and it is the complication of feeding and milking several groups of cows that has largely been responsible for the delay in the widespread adoption of the complete diet system for winter feeding on dairy farms in the UK.

In the USA, however, herds are often larger and fed on conserved foods at all times of the year, justifying expenditure on machinery for handling and mixing the diets. Everson *et al.* (1976) compared the production of cows fed on a complete food consisting of 60% forage:40% grain compared with others on a 50:50 diet during the first 21 weeks of lactation, a 65:35 food for the remainder of lactation and an 85:15 food during the dry period. There was no difference between groups in milk yields or composition, although the fat content was higher in the cows on the complete diet of constant composition. The variable-composition system was closer to the animals' nutrient requirements and resulted in more rapid return to calving body weight, lower blood ketone values and

earlier post-calving oestrus. A high-concentrate diet in early lactation seems to be a good way of encouraging high intake.

Inclusion of a high-energy ingredient such as fat has been used in an attempt to increase energy intake in dairy cows. However, dietary fat seems to interfere with ruminal fermentation and voluntary food intake is usually depressed, so that often its inclusion does not result in any increase in metabolizable energy intake.

Modification of Ruminal Fermentation

Monensin is a commercially used food additive that modifies fermentation patterns in the rumen, giving increased propionate production and less methane. In beef cattle there is either no increase in weight gain and a reduction in voluntary food intake or increased weight gain with no effect on food intake, but in either case the efficiency of conversion is improved. Weight gains were improved and milk yields of beef cows were not affected, even though the amount of time spent grazing was decreased by the inclusion of monensin in the concentrate supplement (Lemenager *et al.*, 1978). It has been suggested that the decrease in intake that usually occurs when monensin is included in concentrate foods for cattle is due to an aversion to some sensory cue associated with malaise resulting from the changes in ruminal fermentation.

Replacement of One Food with Another

A major practical and theoretical problem for ruminant nutritionists is to be able to predict the effect, on the intake of one food available in unlimited quantities, of changing the quantity and/or quality of another food, given in restricted amounts. Although numerous empirical approaches have been made, the underlying theory is not often considered, perhaps due to lack of hypotheses to test, but more likely due to the great expense of performing the necessary research with cattle, which is where the main interest lies.

The reduction in forage intake for a unit increase in supplement allowance is termed the *substitution rate*. For dairy cows this is usually in the range 0.4–0.8, i.e. despite the reduction in forage consumption the intake of digestible nutrients increases with supplementation. The ability to predict the substitution rate is of great commercial significance as the increase in the value of the output (milk) should more than compensate for the increase in the cost of feeding.

Cattle

It is common practice to feed dairy cows forage *ad libitum* supplemented with predetermined amounts of compound food. The concentrate allowance is increased if forage intake is insufficient to meet the required level of production. Most experience shows increasing effects of higher levels of supplementation

(Ostergaard, 1979; Chapter 15); substitution rate also increases as lactation progresses, even at fixed levels of concentrate feeding.

A review of the literature (Bines, 1985) strongly supports a positive relationship between forage quality and substitution rate. With growing heifers it was found that with poor forages the substitution rate increased to 0.64 as forage digestibility increased but then remained steady with better forages (Leaver, 1973), suggesting that physical constraints controlled substitution rate with poor- to medium-quality forages but that with good forages the control was primarily metabolic.

Increasing the level of supplementation with concentrates often causes a decline in the rate of digestion of forages in the rumen. It may be better, therefore, to use slowly fermenting concentrates high in cellulose, such as sugar-beet pulp, rather than ones based on starchy materials such as barley, in order to avoid the adverse effects of rapidly fermentable starch on fibre digestion.

In a comprehensive piece of research, involving a total of eight trials at three centres, Faverdin *et al.* (1991) gave combinations of three levels of concentrate supplementation (L, M and H, with approximately 2 kg DM between each level), three types of forage (maize silage, grass silage, hay) and three types of concentrates (high starch, high digestible fibre, low digestible fibre). Each trial was of 3×3 Latin Square design, replicated three or four times, each period lasting 1 month. Substitution rates increased with increasing supplement level (see Fig. 11.8) and, on average, were 0.47 between L and M and 0.67 between M and H.

For a given forage, the increase in the energy concentration of the concentrate gave an increase in substitution rate, mainly between L and M. The

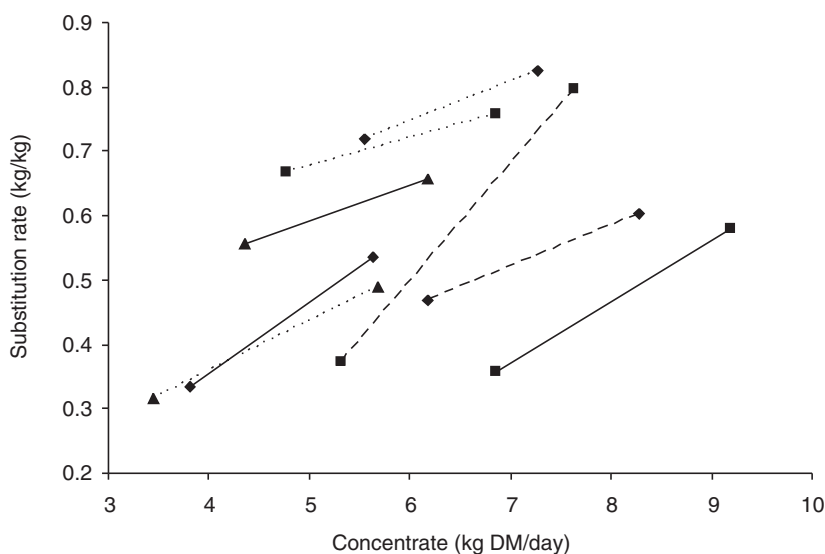


Fig. 11.8. Substitution rate at different levels of concentrate supplementation of dairy cows; each line is for a different forage/concentrate combination (from Faverdin *et al.*, 1991).

average substitution rate with maize silage was 0.7, with grass silage, 0.53 and for hay, 0.44. In mid-lactation, the higher the energy balance, the greater the substitution rate. There were highly significant relationships between substitution rate and milk production and energy balance:

$$\text{Substitution rate} = 0.7 - 0.11\text{dMP} \quad (11.10)$$

$$\text{Substitution rate} = 0.50 + 0.14\text{EB} \quad (11.11)$$

where dMP is the change in milk production between levels H and L; EB is the energy balance in UFL (energy value for milk production).

Where the quality of the forage is high, the mean decrease in hay DM intake/kg of concentrates can be as high as 0.8. In contrast, where the forage quality is very poor, there may be no effect of supplementation on forage intake with low levels of concentrate supplementation, and low substitution rates (0.2–0.4) with high levels. With lactating dairy cows, therefore, the mean substitution rate is around 0.5, but there is a positive relationship with the level of concentrates fed and the quality of the forage.

For growing cattle fed silage, as with dairy cows, substitution rate is greater with higher levels of supplementation. For example, adding barley incrementally to silage so that it formed 0–90% of the diet increased total DM intake, up to 40% inclusion, above which it decreased (Petchey and Broadbent, 1980). When the barley was mixed with the forage in a complete food:

$$\text{DM intake (kg/day)} = 6.63 + 6.91\text{PB} - 6.08\text{PB}^2 \quad (11.12)$$

while for barley fed as a discrete meal once per day:

$$\text{DM intake (kg/day)} = 6.00 + 9.26\text{PB} - 10.57\text{PB}^2 \quad (11.13)$$

where PB is the percentage of barley in the mixture. The substitution rate was very low at low levels of incorporation of barley but then increased to very high levels when barley became the predominant component of the ration. The situation is complicated by the fact that the intake of barley varied with total intake, which declined at high levels of inclusion so that, between the 78 and 90% inclusion rates, total intake fell and, in that situation, the concept of substitution is not very meaningful.

Sheep

Clearly, there is a large influence on the intake of lactating ewes of both the type of forage offered and the amount of concentrate supplement (see Chapter 16). The results of a series of experiments (Orr and Treacher, 1994) showed very different substitution rates between experiments, as well as between forage types. Ewes rearing twins and fed ad libitum on forage were given three levels of supplement: 300, 650 or 1000 g of a barley-based concentrate per day. In one experiment in which hay (OMD 0.59) and silage (OMD 0.65) were compared, OM intakes and performance were similar but, while the substitution rate was 0.09 for silage, it was 0.62 for hay; the former is a very low replacement rate while the latter is similar to that expected from similar work with dairy cows.

In another experiment with three silages (OMD 0.56, 0.60, 0.67), substitution rates were not so low (0.29), and there was no significant difference between silages. In a third experiment with three hays (OMD 0.51, 0.59, 0.72), substitution rates were very similar to those for silages (0.30), again independent of hay quality. The lack of effect of forage quality on the decline in intake with increasing supplement level in the second and third experiments in this series is surprising in view of the findings with dairy cows.

INRA model for substitution

The extent to which a unit of concentrate food will replace forage depends on the ingestibilities (see Chapter 9) of both foods. A summary of 30 sets of data showed that substitution rates in dairy cows (S) were related ($r = 0.87$) to the bulk value of the forage as follows:

$$S = 1 - (\text{BUC} - 0.975)^{0.33} \quad (11.14)$$

Substitution rates are low (0.2–0.4) for forages of poor to medium ingestibility, but approach unity with high-quality forages; this is similar to the range of substitution rates normally encountered (see below).

Substitution is negatively related to the difference between the energy of the forage fed alone and the animal's energy requirements – the wider this gap, the lower the substitution rate. It is lower for high- than low-producing animals.

$$S = 0.673 + 1.134\text{OMD} - 0.665\text{FFV} + 126.2\text{PC} - 118.2\text{PC}^2 \quad (11.15)$$

where S is substitution rate, OMD is digestibility of OM (g/g DM), FFV is fill value of forage (g/g DM) and PC is proportion of concentrates in ration (g/g).

Methods of supplementation

At high levels of concentrate feeding, many cows cannot consume their allowance in the milking parlour within the time it takes them to be milked, which means that extra compound food may be offered outside the parlour and this must be rationed to prevent over-consumption. Automatic out-of-parlour feeders are now widely used on dairy farms; simple versions dispense a fixed weight of compound food to any cow wearing a metal chain around her neck. More sophisticated equipment automatically identifies each animal from a collar-borne tag that transmits a unique signal, and the equipment is programmed to allocate the amount of compound food appropriate to the milk yield and stage of lactation.

Efforts can be made to speed up the rate of eating in the parlour. Pelleting of the compound food increases the rate of eating, while mixing with water to form a slurry causes an even greater acceleration. In one case, lactating cows ate loose meal at 323 g/min, pellets at 455 g/min and slurry at 1670 g/min (Clough, 1972). The use of wet concentrates for slow-eating cows, or unpalatable food, could be beneficial if it takes longer to eat the food allowance

than to be milked but the potential problems, such as moulding of residues, prevent its routine use.

Flavouring agents, such as aniseed, are often incorporated in dairy compound foods. These may encourage a faster rate of eating but the main reason for using them is to ensure that cows don't reject a new food when it is first offered.

Restricted intake

For ruminants, restriction of forage intake is not usually intentional but often occurs as, in an effort to reduce wastage, more is not given until the previous allocation has been completely eaten. In other cases silage is available, but in the tightly packed face of a clamp silo from which cows are unwilling to pull it, especially when they are expecting some to be cut down for them to eat more easily. Maximum intake of forage cannot be expected if animals have to work for it for all or part of the day.

Conclusions

The content of digestible or metabolizable energy is probably the most important factor affecting voluntary intake in farm animals, from a commercial point of view. The cost of the food varies generally in relation to the energy content, and providing the most economical diet demands a knowledge of the way in which dietary energy affects food intake.

Although there is compensation in the voluntary intake of poultry and pigs for changes in the digestible energy content of foods, this is not sufficient to achieve an absolutely constant intake of digestible energy; given high-energy diets, poultry and pigs gain more weight than when given low-energy foods.

With ruminants there is a positive relationship between the digestibility of forages and the level of voluntary intake, due to physical limitation. Increasing the rate of degradation and/or outflow from the rumen increases the voluntary intake. With high-energy diets that are digested quickly, this physical limit is not reached and the animal controls its intake to meet approximately its energy requirements. In order to achieve the required level of production it is often necessary to supplement the forage with concentrates, but this depresses forage intake to an extent that varies with the level of concentrate feeding and the quality of both foods.

12 Protein and Other Nutrients

While the energy content of food and the energy required by animals for their maintenance and productive processes are the major determinants of food intake in many situations (see Chapter 11), the food's complement of nutrients (energy is not a nutrient) can have an important impact on the amount eaten. In terms of quantities, the most important nutrient is protein, although it is the constituent amino acids that should really be thought of as nutrients in their own right. Minerals, vitamins and water are other constituents of the diet and many of these have effects on food intake if present in the diet in amounts insufficient or in excess of animals' needs.

Animals can usually tolerate mild over-provision of a nutrient but a deficiency leads to disruption of normal metabolism causing ill-defined feelings of malaise (discomfort). It seems that there are direct inhibitory effects of impaired metabolic pathways on intake, and that the animal learns that by eating more of the unbalanced food its condition deteriorates.

Protein

Within the normal range of dietary protein contents voluntary intake is not affected by protein content. Intake is, however, depressed by diets of low or very high protein concentration. The lower critical content of protein in a food can be defined as that level below which voluntary intake is depressed, for any given class of livestock. Note that part of the dietary 'protein' in this context can be replaced by non-protein nitrogen in the diet of ruminants, where the ruminal microflora can use it for protein synthesis.

The decline in intake with very low protein foods leads eventually to death but, if a greater demand for energy is created (e.g. by a reduction in environmental temperature to below the lower critical temperature), then intake increases and the total amount of protein consumed may once again be

adequate for life. An excessive protein content in food, leading to increased heat production from deamination of the excess amino acids, may depress intake if heat dissipation becomes limiting and body temperature rises or if the products of deamination (i.e. ammonia and urea) become marginally toxic.

Poultry

Morris and Njuru (1990) gave foods with a range of protein contents from 167–251 g CP/kg to growing broilers and layer chickens. Broilers grew three times faster than layer cockerels and optimal growth was attained on a food containing 251 g CP/kg, while layers needed only 188 g/kg to achieve maximum growth rate. Broilers ate about twice as much as layers (see Fig. 12.1) and, in both strains, optimum conversion efficiency was attained with a food of 230 g CP/kg. Carcass fat decreased from 87 to 29 g/kg of the whole body for layers and from 167 to 81 g/kg in broilers as dietary protein increased. The question of optimum protein content of a food therefore depends on the potential of the birds to grow and fatten and also on the criterion used – maximum growth or maximum efficiency.

Shariatmadari and Forbes (1993) offered growing broiler and layer cockerels foods containing a wide range of protein content (65, 115, 172, 225 or 280 g CP/kg) and found that food intake, while lower in all cases in layers than broilers, was unaffected by diet except the one with the lowest protein content, on which it was greatly depressed in both strains. Live weight gain was maximal for foods with 172 g/kg or more, i.e. the critical protein content for growth was higher than for food intake. Thus, the carcasses of those birds given the 115 and 172 g/kg foods were fatter than those whose food was higher in protein content.

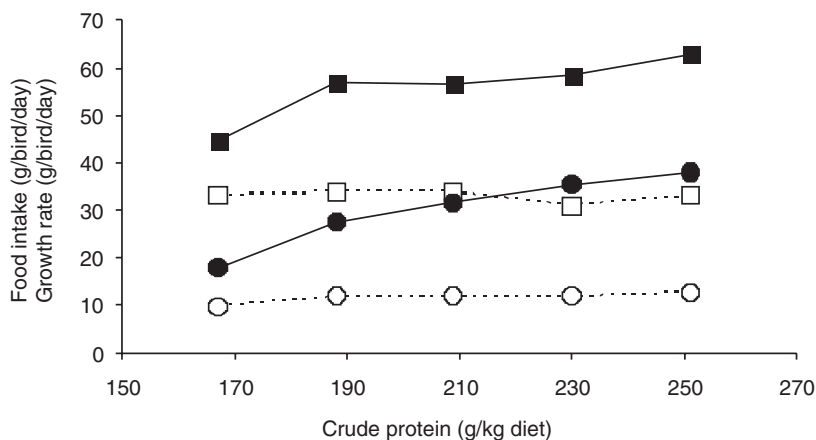


Fig. 12.1. Food intake (■,□) and growth rate (●,○) from 0–21 days of male broiler (solid symbols) and layer strain (open symbols) chicks fed on diets of five different protein concentrations (from Morris and Njuru, 1990).

It should be possible to reduce gradually the protein content of the diet as the broiler grows and its amino acid requirements per gram of food decline. In practice, a single change of diet is often applied, at about 4 weeks after hatching, when the protein content is reduced from 220 to 190 g/kg.

A review of the literature on the effects of protein content on the voluntary food intake of laying hens found that there is some compensation for differences in protein concentration, but that this is not enough to maintain a constant protein intake (Boorman, 1979). The situation is complicated by the fact that low protein intake leads to low growth rate and/or egg production leading to a decreased protein requirement.

When hens were given a high-fat diet they showed signs of becoming protein-deficient and egg weight declined but, during a spell of very cold weather when the temperature of the poultry house fell, food intake and egg quality returned to normal showing that sufficient protein was now being eaten (G.H. Smith, personal communication). This example indicates that intake of a single food is primarily controlled so as to regulate energy intake rather than protein intake.

Pigs

Very low or very high protein content of a food reduces intake, and the maximum DM intake is with a food whose protein and amino acid composition is close to that which gives maximum efficiency of growth when given at a restricted level. The amino acid composition of the dietary protein is of particular importance in controlling the level of voluntary intake (see below).

Reduction of the protein content of the food to somewhat below the optimum for growth causes increased food intake, but this is not seen when the food is of low energy content. Henry (1985) concluded that protein and energy intake are regulated separately and that the mechanisms for both interact to determine the level of voluntary food intake.

It is likely that pigs offered *ad libitum* a food inadequate in protein still feel hungry as they increase their general activity, walking and rooting in straw in much the same way as they do when fed restricted amounts of a balanced diet. Rooting for straw declines with time, perhaps as pigs learn that it does not provide much nutrition.

Ruminants

As with other animals, low protein content of the food depresses voluntary intake, but the critical level is lower than in monogastric species because the ruminant animal supplements the dietary protein supply with urea recycled in the saliva, which can be used for protein synthesis by the ruminal microorganisms. Mature sheep and cattle eat less when the crude protein (CP¹) content is lower than about

¹ Crude protein is the nitrogen content multiplied by 6.25; this incorporates non-protein nitrogen but, as this can be utilized by microorganisms in the rumen, it is a useful expression of protein equivalent for the ruminant animal.

80–100 g/kg DM while lactating cows, where protein requirements are higher, need at least 120 g CP/kg of food. A low-protein food can be supplemented with a high-protein concentrate or with non-protein nitrogen in order to alleviate the nitrogen deficiency in the rumen and stimulate microbial activity. The intake of low-protein forages is usually increased by such supplementation, i.e. a negative substitution rate, due to either the improvement in ruminal fermentation and resultant increase in rates of digestion and passage (see Chapter 3), the amelioration of amino acid deficiency in the animal itself (see below) or both.

As well as providing nitrogen for the ruminal microorganisms (rumen degradable protein, RDP), the diet should also provide sufficient protein that escapes degradation in the rumen, to ensure that those amino acids not produced in sufficient quantities by the microorganisms are available to the host animal; such protein is called undegradable dietary protein (UDP), or 'by-pass' protein.

Cattle

Supplementation of a low-protein hay with low-protein concentrates depresses hay intake, while high-protein concentrates stimulate hay intake. Straw intake by 13-month-old beef steers was significantly higher when 1.37 kg of a concentrate food containing 136 g CP/kg was given than with the same amount of a supplement containing 89 g CP/kg (Lyons *et al.*, 1970). There was no further increase with concentrates > 136 g CP/kg.

A comparison was made between the benefits of infusing 400 g/day of sodium caseinate into the rumen or into the abomasum of beef steers given a very poor-quality hay (34 g CP, 766 g NDF/kg) (Bandyk *et al.*, 2001). Ruminal infusion gave a greater increase than post-ruminal infusion, but the effect of both treatments increased with time on experiment. Organic matter (OM) digestion improved with supplementation but there was no effect on NDF digestion. Supplementation via either route increased plasma urea N, relative to controls, and ammonia N concentrations in ruminal fluid were also increased by supplementation, with a much greater effect of ruminal infusion. In this case, therefore, where the rumen itself was grossly deficient in N, there was no further benefit of post-ruminal protein supply than the increase in ruminal ammonia N, via the saliva.

In arid countries leguminous trees and shrubs are a useful source of supplementary protein, and it was found that intake of hay by lactating cows increased from 7.8 to 9.3 and to 10.4 kg/day due to giving supplements of 4 or 8 kg fresh weight of *Leucaena*, respectively; live weight loss was reduced and milk yield was increased (Muinga *et al.*, 1992).

Supplementation of low-protein forage with high-protein concentrates is not always effective in increasing intake. If the primary cause of the low-forage intake is not protein deficiency, then no benefit of supplementation with protein may be evident.

RUMEN DEGRADABLE NITROGEN The frequently advanced explanation for the positive relationship between food protein content and voluntary intake is the effect of the crude protein on microbial activity and the digestion of N in the

rumen (Faverdin, 1999). Food digestibility and microbial activity are improved when crude protein that is degradable in the rumen is added to the diet. Faster and more complete digestion apparently reduces rumen fill and thus enables an increase in food intake.

While this hypothesis is plausible with very poor roughage, it is not convincing for other diets. High-carbohydrate foods seem to benefit more, in terms of voluntary intake, than high-forage diets from the addition of crude protein, despite bulk being less important with the concentrated foods. Ruminants rapidly learn to prefer diets that improve the functioning of the rumen. For example, after a conditioning period, lambs always prefer diets associated with the presence of casein in the rumen, whereas this is not always the case with high doses of urea, which may result in excess NH_3 (see Chapter 6).

A significant positive relationship was found between the amount of RDP given to pregnant beef cows, with an increase in forage intake of 3.5 g/day/g RDP; during lactation the increase in intake was 5.9 g/day/g of RDP (Alawa *et al.*, 1987).

Tied up with the amount of RDP available from the diet is the rate of degradation of dietary protein. Slowing down of degradation by such methods as heating has usually not affected voluntary intake. Protection of proteins from degradation in the rumen by formaldehyde tanning has been seen to increase food intake.

UNDEGRADED DIGESTIBLE PROTEIN (UDP) Adding protein directly to the abomasum or to the duodenum by continuous infusion generally has no significant effect on food intake (Faverdin, 1999), except in a few cases with very poor roughage, grass or grass silage. In a comparison with lactating cows of supplements containing either 74 or 45 g/kg DM of UDP, it was observed that the higher level of UDP resulted in lower hay intake in thin animals but had no effect on intake in fatter animals, whose milk yield was increased (Garnsworthy and Jones, 1987).

Sheep and goats

With tropical forages of < 70 g CP/kg, there is a positive relationship between the crude protein content of the diet and intake by mature sheep, while above this level there is little effect of protein content on intake (Milford and Minson, 1966).

Urea supplementation of straw increases its intake. In practice, the basal food is often poor forage in which it is impossible to incorporate a supplement. Under these conditions, urea is given in the form of a block in which it is mixed with cereals and molasses or in liquid form with molasses and salt. Although it is claimed that the continuous availability of this type of supplement ensures that all animals have a good chance to eat some, it has been found that a significant minority of hill ewes did not eat any.

Mechanisms for the effect of protein content on intake by ruminants

Protein deficiency in the ruminant reduces the activity of the ruminal microflora and thus the rate of digestion of cellulose. It was therefore suspected that

protein deficiency depresses voluntary intake by physical means but this is only part of the reason, as clearly demonstrated by the experiments of Egan and Moir (1964). They compared the effects of duodenal infusion of casein, isonitrogenous amounts of urea or phosphate (as control) into sheep on a low-protein (41 g CP/kg) forage. Casein had a rapid effect, and within a few hours intake was increased. The effect of urea was delayed for 24 h, during which time there was an increase in ruminal cellulolytic activity. Urea increased the digestibility of DM and accelerated the rate of digestion of cotton threads in the rumen, while casein had very small effects on digestibility and cellulose disappearance.

It was concluded that casein alleviated a protein deficiency and thereby increased the rate of removal of metabolites by tissues, and thus stimulated intake while urea acted primarily by increasing rates of digestion and passage after absorption from the intestines and secretion in saliva. Longer periods of casein infusion gave persistent increases in intake, even though digestibility decreased and the volume of rumen contents increased. Summarizing his work, Egan (1965) concluded that: '... differences in the level of ad libitum energy intake should be examined in relation to changes in the ability to utilise energy'. According to the MTD hypothesis (see Chapter 10), an increase in the rate at which body tissues can utilize metabolites – such as induced by the alleviation of protein deficiency – will allow a greater degree of rumen fill before the total discomfort reaches a critical level, hence the increase in volume of ruminal contents seen in this example.

Amino Acid Deficiency and Imbalance

A food in which the essential amino acids are available in a ratio that is widely different from the animal's requirements for amino acids is as effective in depressing intake as a low-protein food. Such an imbalance can be alleviated by supplementing the food with the deficient amino acid (or by infusion of this amino acid into the digestive tract or circulation). The way in which the protein content of the diet is monitored by the animal is not fully understood, but there are some clues as to the mechanisms of action of severe imbalance or deficiency of amino acids. It is likely that the primary effect of imbalance is on voluntary intake, with a secondary effect on growth. Studies in the rat have shown that the imbalance is sensed in the brain, in a site(s) other than the ventromedial hypothalamus – probably the anterior prepyriform cortex and medial amygdala, which have connections with the lateral hypothalamus. It is likely that animals learn to associate eating an imbalanced food with the consequent feeling of malaise (see Chapter 6).

Animals' ability to store amino acids in excess of immediate requirements is very limited, so not only must the correct amounts of amino acids become available from the food, but they must also be available at the same time. Provision of an imbalanced mixture of amino acids slows growth and increases the oxidation of all but the most limiting amino acid, thereby causing inefficient utilization of dietary protein as well as lower voluntary intake.

Poultry

Amino acid imbalance depresses voluntary intake in poultry. If the imbalance is severe there is a large fall in growth and intake. This can be induced by adding small amounts of one or a few amino acids to a balanced, low-protein diet (see Fig. 12.2). Compared to a balanced food, a low-protein food (deficiency of all amino acids) did not depress daily food intake by chicks, while deficiencies of individual amino acids caused a marked reduction in intake. Not only does a deficiency of an amino acid depress intake and performance, but an excess can also have this effect as, with diets containing above about 12 g lysine/kg, there is reduced performance due to a proportion of birds developing leg problems, the reason being unknown.

To resolve the site of action of amino acid imbalances, Tobin and Boorman (1979) prepared young cockerels with indwelling catheters in the carotid artery and jugular vein. The birds were fed on a low-protein diet (100 g/kg) that was imbalanced by the addition of a mixture of all the essential amino acids except histidine. Infusion of histidine into the carotid artery significantly increased intake, while infusion into the jugular vein had no effect; this is direct evidence for an area of the brain being sensitive to the amino acid imbalance. In order to induce lysine imbalance, cockerels were offered a diet with a low level of balanced protein (100 g/kg) and infused with lysine into the carotid artery or jugular vein at 100 mg/h. In both cases voluntary intake was severely depressed, from 40.4 to 11.6 g/day with carotid infusion and from 48.4 to 26.6 g with jugular infusion. The greater effect of the carotid infusion again strongly suggests that the sensitive area is in the brain.

The fact that imbalances of amino acids affect intake rapidly suggests that it is the primary way in which amino acid imbalance affects growth. Force-

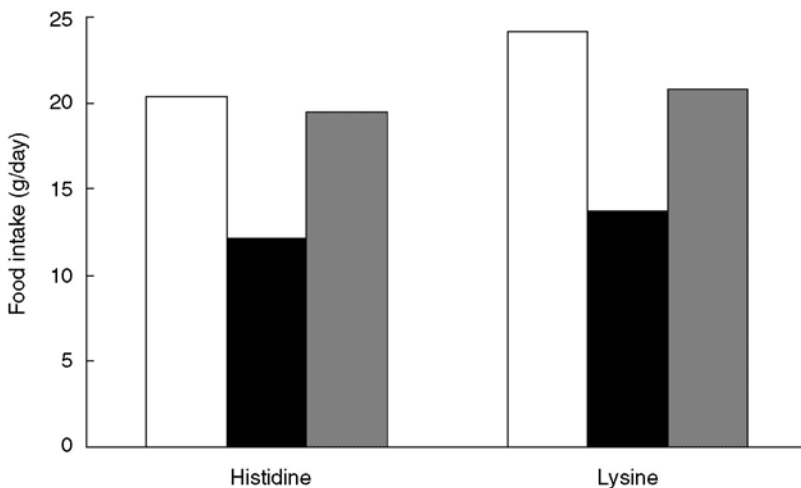


Fig. 12.2. Effect on food intake of young chicks of supplementation of a low-protein food (open bars) with either a mixture of amino acids deficient in histidine or lysine (solid bars) or a similar mixture of amino acids designed to provide a balance (grey bars) (from Boorman, 1979).

feeding of chicks eating an imbalanced diet to the same level of intake as controls gave normal growth, demonstrating that the major effect of imbalance is on voluntary food intake. However, others have noticed a deceleration of growth before a decrease in intake and put forward the idea that the drop in food intake seen under such circumstances is secondary to the reduction in growth rate.

The results referred to above have been obtained using severe imbalances. If the imbalance is mild there may be a compensatory increase in food intake. Thus, G. Tobin and K.N. Boorman (cited by Boorman, 1979) showed increased intake by chickens when a supplement lacking histidine was added to a low-protein food; this was, however, only a transitory effect. With growing birds there is some evidence of increased intake when the lysine content is slightly suboptimal; the lysine content that gives maximum weight gain is higher than that giving maximum food intake, again pointing to increased intake in mild lysine deficiency (see Boorman, 1979).

In another study in which lysine was included in the diet of broilers at levels of 9.1–14.4 g apparent faecal digestible lysine/kg, there was no significant effect on food intake although weight gain, and thus conversion efficiency, were increased and carcass fat content was decreased, by increasing lysine concentration in the diet (Wijtten *et al.*, 2004). A similar phenomenon also appears in the laying hen. One practical consequence is that the dietary amino acid concentration required for optimum food conversion efficiency is higher than that for maximum production.

Pigs

Lysine is the first limiting amino acid for growing pigs. Increasing lysine supplementation from 4.3 to 9.1 g/kg of the food increased intake from 1000 to 1400 g/day, with smaller increments at higher levels of supplementation (Baker *et al.*, 1975). Sparkes *et al.* (1981) included ten levels of lysine, from 5.5 to 12.7 g/kg, balanced for non-essential amino acids and isocaloric, in foods offered to boars, castrated male and female pigs. Voluntary intake was increased up to lysine contents of 9.1, 8.4 and 9.4 g/kg DM, respectively, for the three 'sexes'. Modern, lean pigs require higher concentrations of digestible lysine in their diet than do fatter pigs, because of the lower daily food intake of the former. Growing Pietrain-cross intact pigs have an optimal lysine content of > 11 g/kg.

When lysine was included in foods for growing pigs at levels of 6–30 g/kg, the maximum voluntary intake was with the food containing about 10 g/kg, which is close to the optimum for growth according to work with restricted-fed pigs (Cole and Chadd, 1989). It was concluded that: 'Changing the level of a single amino acid to alter amino acid balance has a more drastic effect [on voluntary intake] than altering total protein'. Figure 12.3 shows the food intake response by growing boars to different levels of dietary lysine (G.M. Sparkes, D.J.A. Cole and D. Lewis, unpublished observations), and it can be seen that the highest intake is with a food containing just over 10 g lysine/kg, which is just below the optimum. At higher levels of lysine there is approximately

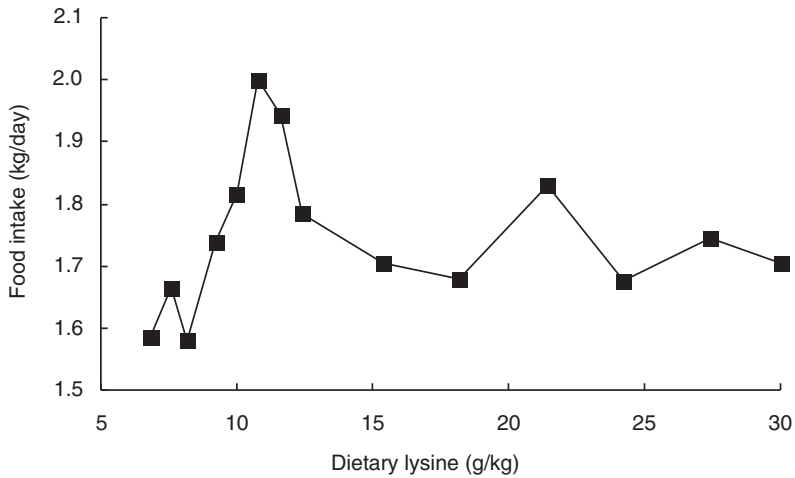


Fig. 12.3. Food intake of boars growing from 25 to 55 kg and given foods with different lysine contents (from G.M. Sparkes, D.J.A. Cole and D. Lewis, unpublished observations).

constant food intake (apart from the anomalous point at 22 g lysine/kg) but, when a toxic excess of an amino acid is included in the food, there is a sharp reduction in intake (not shown on this graph).

When pigs are given foods slightly deficient in lysine, as in the instance above, or threonine, there is a slight increase in voluntary food intake. However, if the amino acid in question is present at below about 90% of requirements, food intake is depressed showing that the pig's ability to compensate for amino acid deficiency is quite limited, presumably by the consequences of eating more of the other components of the diet, especially energy. As with protein deficiency, pigs offered a diet deficient in tryptophan increase their explorative behaviour compared with similar animals on a balanced diet.

Henry *et al.* (1992) varied lysine and protein contents of food for growing pigs independently by offering foods with either 5.5 or 6.5 g/kg lysine in foods containing either: (i) 130 g CP/kg; (ii) 156 g CP/kg with the same amino acid pattern as food 1; or (iii) 152 g CP/kg with glutamic acid added to food 1 as a source of non-essential amino acids. At the same lysine content, increasing the protein content did not affect voluntary intake but reduced growth due to the increased load of catabolizing the excess protein. Increasing the protein supply with non-essential amino acids caused a fall in intake, probably due to an inadequate supply of methionine and threonine in the basal food, as evidenced by the plasma amino acid pattern.

Methionine supplementation can also stimulate food intake additively with the effects of lysine. If the environmental temperature is reduced to below the critical temperature and food intake is thereby stimulated to meet the increased requirements for energy, then the intake of a deficient amino acid is also increased and the deficiency is alleviated.

Valine is more likely to be limiting in lactating sows than lysine, and sows fed a valine-deficient but otherwise balanced diet responded to additions of

valine by increasing their food intake (Paulicks *et al.*, 2003). The basal food contained 3.5 g apparent ileal digestible valine/kg, and L-valine was added to give concentrations of 5.5, 6.5, 8.5, 10.5 and 14.5 g/kg. Food intake of the sows during lactation averaged 2.9, 4.3, 4.6, 4.6, 4.9 and 5.1 kg/day for the six treatments, respectively. Although the treatment containing 5.5 g valine/kg increased food intake almost as much as the higher rates, sow weight losses, milk production and piglet growth rate did not plateau until that containing 6.5 g valine/kg, so this is the recommendation for the valine content of a diet for lactating sows.

Cattle

High-quality protein or single amino acids of dietary origin are degraded in the rumen so that it is necessary to infuse amino acids post-uminally, or to feed them in a form in which they are protected from degradation in the rumen, to discover those that are limiting intake, growth or milk production. The specific effects of amino acids on food intake in ruminants are much fewer than those in single-stomached animals. Variation in the composition of intestinal amino acids is less than that in single-stomached animals, due to the large proportion of microbial protein in intestinal protein flows. However, the availability of protected methionine and lysine now makes it easy to increase the intake of these two amino acids but, at the levels at which they are usually used (i.e. 6–30 g/day for a lactating dairy cow), there is generally no significant effect on food intake (Faverdin, 1999).

Sheep

In a survey of the results of ten experiments in which post-uminal amino acid supplementation was given to sheep on various types of food (Barry, 1976), voluntary intake was seen to be increased in seven cases and nitrogen retention or wool growth was increased in almost all instances.

Intravenous infusion of methionine at 1 g/day into sheep significantly increased the intake of a low-protein straw (J. Twigg and J.M. Forbes, unpublished observations). Removal of threonine or isoleucine from a milk substitute containing 80 g protein/kg halved voluntary intake by lambs. There is thus some evidence that amino acid imbalance affects intake in sheep in a way similar to that in other species.

Minerals

A deficiency of any of the essential minerals results in reduced food intake, while an excess of many of the minerals has toxic effects, including reduced intake. In most cases the role of each mineral in one or more metabolic pathways is known, but the way in which a mineral deficiency or toxicity depresses voluntary

intake is unclear. In Chapter 6 we discussed learned associations between the sensory properties of foods and their metabolic consequences, and presumably animals learn to adjust their intake of a food to minimize the discomfort induced by that food (see Chapter 10). Chapter 13 includes a discussion of appetites for minerals. References to support the statements made in the following section can be found in the first edition of this book (Forbes, 1995).

Calcium

There is an optimum content of dietary calcium below or above which intake is depressed. When the contents of calcium and phosphorus in food for sows were increased from 6 and 5 g/kg to 8 and 6 g/kg, respectively, there was an increase in voluntary food intake, but this then decreased again when they were raised further to 9 and 7 g/kg, respectively. Calcium deficiency causes depressed food intake in calves.

Copper

Copper sulphate is used as a growth stimulant for pigs as it improves the efficiency of food conversion and has no effect on food intake up to an inclusion rate of about 1 g/kg. At 2 g/kg or above, intake is depressed. In adult ruminants, deficiencies of copper cause inappetence while an excess results in a haemolytic crisis and death.

Iodine

Excess iodine in the diet of both growing chickens and laying hens depresses food intake.

Magnesium

Voluntary intake of cattle introduced to a magnesium-free food fell to 32% of control by the fourth day; this was alleviated by inclusion of 10 mg magnesium/kg live weight/day in the food. Cellulose digestibility was depressed by the magnesium deficiency, but not enough to account for the large decrease in voluntary intake.

Phosphorus

Phosphorus is an essential mineral, both as a structural component of bone and as a participant in many metabolic processes. Dietary deficiency depresses voluntary food intake and results in severe economic losses in range animals where soils are deficient in phosphorus.

The requirements for dietary phosphorus are particularly high in the laying hen, to support the secretion of the shell around the egg. Even relatively mild deficiency of phosphorus depresses food intake and reduces egg production (Barkley *et al.*, 2004), and the effects become more severe as time progresses, as bone reserves of phosphorus and calcium become exhausted.

Sheep

Phosphorus deficiency depresses food intake in sheep. This could be due to a lack of P for ruminal microbial activity, thereby slowing fermentation and applying a greater physical constraint to intake, or to P deficiency in the animal's body, interfering with normal metabolism, or both. In a cleverly designed experiment, Milton and Ternouth (1985) set out to determine what was the limiting factor by correcting the P deficiency in both rumen and animal, or just in the animal.

Sheep were prepared with parotid duct catheters to allow depletion of body P, ruminal fistulae to allow sampling of rumen contents and abomasal catheters to allow diversion of parotid saliva around the rumen; they were fed on a P-deficient diet. The three treatments were: (i) low-rumen, low-body P (LRLB) by diverting saliva away from the body; (ii) high-rumen, high-body P (HRHB) by infusing 1.3 g/day of P into the abomasum and returning saliva to the mouth; and (iii) low-rumen, high-body P (LRHB) by draining saliva, abomasal infusion of 4.7 g/day of P and P-free saliva infused into the mouth.

The results are shown in Table 12.1, and it can be seen that correcting just the body P level, leaving the ruminal P deficient, had as large an ameliorating effect on intake as did the treatment that corrected both ruminal and body deficiencies. This demonstrates that it was the shortage of P in the body that was depressing intake in the LRLB treatment. The lack of difference in the digestibility of OM between treatments also shows that the activity of the ruminal microbes was not inhibited by the level of ruminal P achieved in the rumen-deficient treatments.

Further evidence of the importance of P supply to the body of the ruminant, as distinct from its rumen, is provided by experiments in which low-P and low-Ca diets depressed food intake of sheep, the extent of which was directly related to the resultant levels of P in the blood rather than in the rumen (Ternouth and Sevilla, 1990).

Table 12.1. Effect of ruminal and blood P levels of sheep fed a low-P diet on food intake and digestibility; see text for explanation (from Milton and Ternouth, 1985).

	LRLB	HRHB	LRHB
Rumen inorganic P (mg/l)	148*	314	70*
Plasma inorganic P (mg/l)	2.8*	4.7	4.4
Food intake (g OM/day)	592**	906	892
Apparent digestibility of OM	0.65	0.65	0.64

Significance of differences from HRHB: *, $P < 0.05$; **, $P < 0.01$.

Selenium

Selenium deficiency in chickens depressed voluntary intake and, when selenium was added to the food, the birds started to eat more within 3 h. Toxic excesses of selenium depress intake in ruminants.

Sodium

Sodium deficiency depresses intake by poultry: chicks offered a sodium-deficient food ate 11.7 g/day compared with a daily intake of 15.7 g/day in those on a normal food containing 2.5 g sodium chloride/kg. Diets high in salt can lead to sodium toxicity in pigs; these do not reduce their intake sufficiently to prevent this, suggesting that the excessive salt is not aversive.

Deficiencies of sodium cause inappetence in adult ruminants. Excessive salt also leads to reduced intake; addition of 30 g sodium/kg to a sodium-adequate diet depressed the food intake of sheep without affecting plasma sodium concentrations. However, plasma calcium and magnesium concentrations were depressed while calcium retention was increased, so it is not clear as to what actually depresses intake. There was no decrease in voluntary intake of Merino sheep until the sodium chloride content of the diet exceeded 100 g/kg, and sheep can tolerate up to 13 g/l in their drinking water without serious effects on food intake.

Zinc

Food intake is reduced within 1 h when adult hens are given 8 mg/kg or more of dietary zinc. In adult ruminants, deficiencies of zinc and toxic excesses have been reported to cause inappetence.

Other minerals

Toxic excesses of arsenic, fluoride or molybdenum depress food intake in ruminants, while deficiencies of cobalt, manganese or potassium have been reported to cause inappetence.

Vitamins

As with minerals, much is known about the metabolic roles of the vitamins, and it is likely that animals learn to eat that amount of a food with a deficiency or excess of a nutrient which minimizes their overall feelings of discomfort (see Chapter 10).

There is a decrease in food intake and growth when chicks are heat stressed, and this is partly alleviated by supplementing the diet with about 200 ppm ascorbic acid (Kutlu and Forbes, 1993a). Supplementation of non-stressed chicks tends to reduce intake, and the optimum level of supplementation can be assessed by appropriate choice-feeding experiments (see Chapter 8).

In adult ruminants, deficiencies of vitamin A or vitamin D cause inappetence. Riboflavin deficiency causes depressed intake in calves.

Further information about animals' ability to select for vitamins is provided in Chapter 13.

Toxins in Food

The effects of toxins on food choice are discussed in Chapter 7.

Oilseed rape (canola) meal is available in Europe in large quantities and is a good source of vegetable protein. However, it contains several substances, including glucosinolates, sinapines and tannins, which are mildly toxic and which usually reduce the intake of foods into which they are incorporated.

Poultry

Inclusion of 100 or 200 g/kg of rapeseed meal in a food for broiler chickens caused reduced food intake, even though the variety of rape used was one low in glucosinolates and erucic acid (McNeill *et al.*, 2004).

Pigs

Intakes and weight gains of growing pigs closely follow the acceptabilities established in an experiment in which they were not allowed to become accustomed to the effects of each food. Intake seemed to be more closely related to glucosinolate content than to contents of sinapines or tannins. However, glucosinolate level alone cannot be used as a predictor of intake and performance.

Cattle

Heat/moisture treatment of rapeseed meal reduces its glucosinolate level and can increase the intake of silage given alongside the rapeseed-containing concentrate food. The improved performance could not be explained solely by the reduced ruminal degradability, so is likely to have been due to the increased intake. No close relationship has been found between glucosinolate content and intake of rapeseed-containing foods by calves and lambs. Modern varieties of rape have greatly reduced levels of toxins and are not likely to cause problems of low intake as long as they are not included in diets at excessive levels.

Sheep

Fungal infestation of herbage has a negative effect on its intake. While part of this effect might be due to the effects on the taste or smell of the grass, it was shown that a more important factor is the feeling of nausea generated in sheep after eating contaminated grass (Aldrich *et al.*, 1993), which would lead to learned aversion. Daily treatment of these sheep with an anti-emetic (metoclopramide) increased intake of endophyte-infected tall fescue but had no effect on the intake of uninfected grass.

Water Deprivation

Water is an essential nutrient and the most indispensable of all. In the early stages of water deficiency there is the discomfort of a dry mouth, and later there is reduced secretion of digestive juices and ultimately a comprehensive disruption of bodily function. Not surprisingly, lack of water results in reduced food intake and eventually in complete anorexia. The voluntary intake of water is covered as 'water appetite' in Chapter 13.

Poultry

Effects of water deprivation on food intake by poultry have been reviewed by Bailey (1999). When daily water allowance is restricted, the reductions in voluntary food intake and growth rate that follow are proportional to the degree of restriction; in one case, as water supply for broilers was reduced from ad libitum to 50% of that level, the daily food intake fell from 111 to 75 g/day.

Cattle

In addition to ensuring free access to food, there should be no restriction of water intake if forage intake by cattle is to be maximized. Reducing the water allowance for dairy cows to 40% below ad libitum depressed food intake by only 16% (Little *et al.*, 1976), which might suggest that cows are quite resistant to water shortage. However, if the ad libitum intake of these cows was excessive due to boredom, as they were individually tethered, it is possible that this result underestimates the magnitude of the real effect of water shortage.

By the fourth day of water deprivation the hay intake of cattle falls to less than one-quarter of control. Cattle that normally ate 7.6 kg of food/day ate 4.2, 2.2, 0.9 and 0.5 kg on four successive days when water was removed.

Although cows fed on silage took only a few drinks per day, most of these were large and associated with meals, often occurring in the middle of a meal (Forbes *et al.*, 1991). In this case the water trough was adjacent to the silage and it was convenient for cows to mix eating and drinking. If they had to walk some distance in order to drink they might either have forgone a drink and continued

eating, but eaten less due to increased osmolality of ruminal contents, or else gone to drink but not taken the trouble to walk all the way back to continue eating, as they were already partly satiated.

Sheep

The food intake of sheep declines noticeably by the second day without water. This can be attributed to the difficulty of transporting the more viscous digesta through the digestive tract, but must also be due to the general feeling of malaise accompanying dehydration of the body. A moderate reduction in water allowance (to 0.75 of ad libitum) does not affect the dry matter intake by sheep, as urinary volume can be reduced to some extent without harm to the animal.

Ruminants in extensive agricultural systems sometimes have to walk extremely long distances to water. Squires and Wilson (1971) studied the effect on Border Leicester wether sheep of placing water and food pellets containing 15% sodium chloride different distances apart. As the distance increased from 1.6 to 5.6 km, the number of drinks per day decreased and the food intake fell from around 70 to 45 g/kg^{0.75}/day. The maximum distance walked by the wethers was 17.6 km/day.

Wet feeding

Wet mashes of food mixed with water were commonly given to backyard poultry and it is now common practice in Europe to feed growing pigs on wet foods. Some work with rats has shown improved dry matter intake and weight gain when the food is mixed with water.

Poultry

Foods with more water than is conventionally found in cereal-based mixtures have been examined for poultry feeding for two reasons: the utilization of wet by-products and the alleviation of heat stress. An example of the former is the incorporation of lucerne juice when chicks compensated for the added water and there was no effect on DM intake. Egg production decreased when hens were fed diets > 300 g moisture/kg by the addition of methane digester effluent; the suppression in performance was attributed to fungal growth. Laying hens fed a diet containing methane digester effluent to give 400 g moisture/kg had egg production and food efficiency similar to those hens fed an air-dried control diet. An automated feeding system to deliver high-moisture by-product diets with 50% added water to laying hens has been developed; improvements in egg production, egg weight and food efficiency have been found.

Wet food can be useful in partially alleviating the reduction in food intake and performance under very hot climatic conditions. Giving hens food with 50% water added stimulated dry matter intake by 38% under environmental temperatures of 33.3°C. Offering broiler chickens a food with the addition of 33

or 50% water increased both food intake and body weight in the hot season (37°C); however, food intake and body weight were reduced significantly by wet feeding under normal temperatures (20°C).

There is, however, a significant body of evidence that the use of wet foods can be beneficial for the performance and/or efficiency of both broiler and laying chickens kept under temperate conditions (see review by Forbes, 2003b). The optimal rate of addition of water is between 1 and about 2.5 l/kg of air-dry food. With an insufficient rate the improvements are not seen, probably because there is inadequate penetration of water into the food particles to allow rapid diffusion of digestive chemicals in the stomach, but excess water, whereby there is a layer of free water over the wet food, inhibits feeding as poultry do not like to put their beaks under the water. The amount of water absorbed by different foods varies considerably, and it would be necessary to make some preliminary tests to discover the optimum rate of water addition for foods intended for offering in the wet form.

If the primary effect of wet feeding is to increase food intake then it would be expected that there would be a large increase in fat deposition. However, the composition of the carcass, in terms of its fat:protein ratio, is not affected by wet feeding. The suggestion is that the rapidly growing broiler, or the high-yielding laying hen, is limited in its productivity by the amount of nutrients it can obtain and that improved digestion due to pre-wetting of the food can improve efficiency and/or intake.

Pigs

It has become very common in intensive pig production throughout the world to feed growing pigs on liquid foods, the main advantage being that delivery can be automated. However, wet feeding can also have benefits for biological efficiency, as indicated by a large-scale survey in Denmark (Danish National Committee for Pig Breeding and Production, 1986, quoted by Riley, 1989), which showed that on wet-feeding systems pigs ate 2.27 Scandinavian Feed Units (SFU)/day and gained 717 g/day compared with dry-fed pigs that ate 2.03 SFU and gained 643 g. Weaner pigs given food with approximately equal weights of water and dry food had higher DM intakes than dry-fed, significantly so in most weeks and, as growth rate was improved, there were no differences in conversion ratios. Sows may also benefit from wet feeding as they ate more when fed from a trough with a water nipple in it, i.e. wet food.

With very wet foods (< 75% water), further increasing the water content to as much as 85% has no effect on DM intake as the extra water is readily excreted. Presumably there is a threshold above which very high water content does begin to affect DM intake. However, in order to avoid an undue increase in effluent output, it is recommended that the water content of liquid diets should not exceed 80% (equivalent to a 3.5:1 water:food ratio, bearing in mind that normal 'dry' food contains about 10% water). Care must be taken that trough design is not such as to encourage food wastage. When wastage is minimized, wet feeding increases efficiency of conversion of food into growth.

Conclusions

Foods containing a significantly lower concentration of an essential nutrient than required by the animal to which they are fed are eaten in smaller amounts than foods with an adequate content. This shows that when offered a single food, animals are generally not able to respond to a deficiency by increasing their daily intake. A common feature of all deficiencies is that they interfere with normal metabolism and lead to feelings of metabolic unease, and it seems likely that it is an innate response of animals to reduce their intake of a food that makes them feel unwell. In nature the animal could turn its attention to other sources of food, but in intensive husbandry no such opportunity is available so the only option is for the animal to eat less in an attempt to relieve the metabolic discomfort.

A toxic excess of a substance in food causes reduced intake as does an imbalance, such as when a low-protein food is supplemented with an individual amino acid, even with amounts that only bring its concentration in the food to what would be normal for a high-protein food.

Figure 12.4 is a general diagram of responses to changes in the content of an essential nutrient. For foods with a content of the nutrient just below the 'requirement', there is sometimes a modest increase in intake as the animal tries to maintain its intake of the nutrient in question. Below this metabolic illness occurs with consequent depression in intake. For foods with a content above the 'requirement', there is little or no effect on intake until such a high content is reached that intake is depressed due to the toxic effects of the excess.

Water deprivation reduces the intake of food. Initially this is due to the unpleasantness of a dry mouth but, ultimately, the disturbance of metabolism will reduce feeding, which is a major determinant of the need for water.

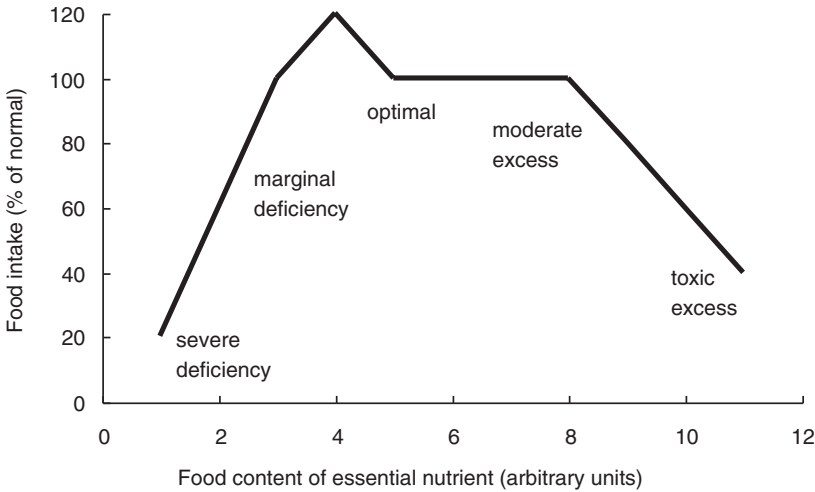


Fig. 12.4. Generalized diagram of the effects of a nutrient in food on voluntary intake of excesses and deficiencies.

13

Appetites for Specific Nutrients

In Chapters 7 and 8 the principles and practice of diet selection in farm animals have been discussed, i.e. the ability to choose from two or more imbalanced foods a diet of adequate composition to meet the animals' nutrient requirements. It has been demonstrated that there needs to be learning of the metabolic effects of each food and association with some sensory property or properties of each food (see Chapter 6). It has also been shown in Chapter 12 that a dietary deficiency or excess of one or more essential nutrients causes a reduction in intake when a single food is offered. In this chapter we examine evidence for appetites for many nutrients, including water. As we have used protein and energy to illustrate the principles of diet selection in Chapters 7 and 8, the following section should be read in conjunction with that earlier discussion.

Regulation of Protein Intake

Interest in choice feeding has centred on animals offered two foods: one with a protein content higher than that required for optimum performance, the other with lower than optimal content of protein (HP and LP, respectively). There is a very wide range of protein content in readily available foodstuffs, from around 40 g/kg for straw to 600 g/kg for fishmeal, while the range of usable energy contents is quite small, from 9–13 MJ ME/kg. Also, protein is an expensive dietary constituent and there is considerable interest in optimizing its dietary concentration in commercial practice.

It must be acknowledged that, in most cases, it is only an assumption that protein is the target of the animals' selection between HP and LP, as details of the content of minerals and vitamins are not always published. Thus, where whole grain is given in choice with a compound pellet, the latter will be higher in many minerals and vitamins as well as protein, and it is possible that the

results are clouded by an appetite for one or more of the trace constituents as well as, or instead of, an appetite for protein.

Growing chickens

If a claim is made that birds are selecting an optimum diet from a choice of foods, it is necessary to demonstrate this by feeding other groups of birds on single-food mixtures of the two foods used in the choice-feeding situation. Shariatmadari and Forbes (1993) have done this for broilers and layer cockerels, and the results have been discussed in Chapter 8.

Four foods of 195, 210, 227 and 242 g protein/kg were offered simultaneously to male and female broilers from 2–8 weeks of age by Kaminska (1979). They ate most of the lowest-protein food and this preference increased in the last 2 weeks; the mean protein content selected was 214 g/kg up to week 6, but then it decreased to 210 and 207 in the final 2 weeks, results similar to those from broilers given only two foods by Shariatmadari and Forbes (1993).

In a further experiment (B. Kaminska, personal communication), broilers were offered foods with ME contents of 11.6, 12.2, 13.0 and 13.8 MJ/kg. In this case they ate more of the higher energy diets, progressively as the experiment progressed. With a higher protein content there was even more preference for the high-energy foods. It is clear from these experiments that broilers use diet selection to achieve their 'ideal' dietary energy:protein ratio. Thus, an appetite for protein has been clearly demonstrated in growing chickens.

As the bird grows, its requirement for energy relative to protein increases, so that the concentration of protein required in the food declines with age. It would be expected that the ratio of HP:total would fall with age in choice-fed birds – and this is often the case. For example, the proportion of HP taken by chicks fell from 0.25 at 15 days of age to 0.15 at 50 days, a decline in the protein content of the selected diet from 250 to 140 g/kg (review by Forbes and Shariatmadari, 1994).

Rapeseed meal is an economically attractive source of protein, but it is claimed that poor palatability prevents its use as more than a small proportion of the diet. Rapeseed meal, even the modern genotypes with low levels of glucosinolates, contains toxins, however, so the taste of rapeseed could be used as a cue to aversion even if the substance(s) being tasted was not itself toxic. However, broilers offered a choice between the standard food and one containing rapeseed meal over a period of 28 days ate similar amounts of each (McNeill *et al.*, 2004), suggesting neither sensory nor metabolic problems with the latter.

When HP and LP offered as a choice to broilers could provide a balanced diet there were significant decreases in the HP:total ratio as the birds grew, in line with the decrease in protein:energy requirements during this phase of growth (Shariatmadari and Forbes, 1993); this applies to the choices between HP and VLP and between AP and L (see Fig. 13.1). However, when the two foods could not provide a balanced diet (LP+VLP, AP+VLP, VHP+HP), the most unbalanced pair was largely avoided and this avoidance became more

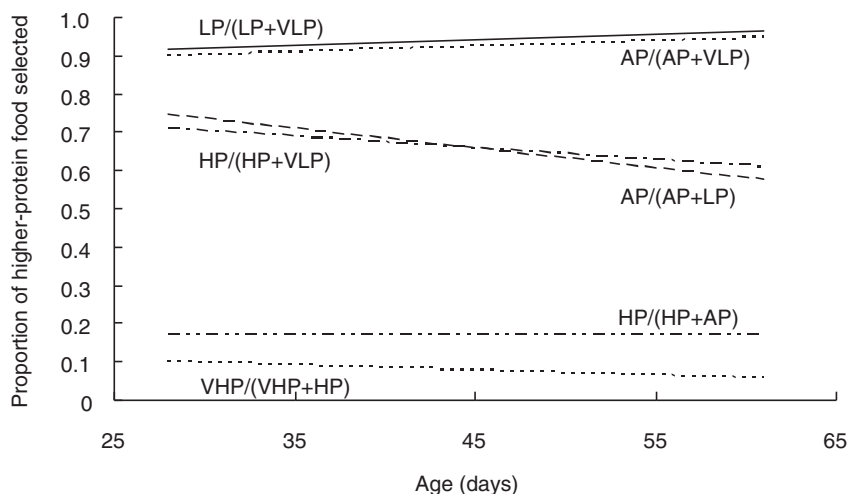


Fig. 13.1. Proportions of two foods with different protein contents selected by broiler chickens from 28–61 days. VLP, very low protein (65 g CP/kg); LP, low protein (116 g CP/kg); AP, adequate protein (225 g CP/kg); HP, high protein (280 g CP/kg); VHP, very high protein (320 g CP/kg) (from Shariatmadari and Forbes, 1993).

extreme as time passed – as the birds' conviction of its harmfulness strengthened as they gained more experience.

As observed in Chapter 7, animals almost always continue to sample aversive foods from time to time, as if to check that they are still as unbalanced as before. The sixth choice, between HP and AP, declined slightly from about 0.18 HP through the observation period, suggesting that AP was not quite 'adequate' for the birds in question. Overall, therefore, these results confirm the decline in preferred dietary protein content as the optimum protein:energy ratio declines with stage of growth.

There is, after several decades of intensive selection, a very large difference in the potential for growth between chicks of layer and broiler strains. Because of the requirements of energy for maintenance, slower-growing birds require a lower protein:energy ratio in their food so would be expected to choose a lower HP:total than faster-growing birds. In choice-feeding comparisons of broiler and layer chicks, significantly higher intakes of HP than of LP by broilers were observed, giving an overall protein content in the diet selected of 205 g/kg, whereas layers ate similar amounts of HP and LP to give an overall content of 184 g protein/kg.

Mature birds from a strain of broiler selected for high body weight ate more protein than a low-weight strain when given the choice of HP and LP foods (Brody *et al.*, 1984), and birds of both strains ate less protein when given a choice of HP (467 g/kg) and LP (82 g/kg) than when given a complete food with a protein content of 188 g/kg. Low-weight birds increased their energy intake by 38–53% when given a choice of foods compared with a single complete food, suggesting that the latter placed a considerable constraint on

intake in birds of the low-weight strain, probably by having too high a protein content. These birds took considerable amounts of glucose solution when given the single, complete food, but much less when given a choice of HP and LP, showing that the complete food was providing too little energy (relative to its protein content) and that this imbalance depressed food intake.

Males have a higher growth potential and seem to be capable of responding to this by eating a higher proportion of the HP food than females. While growing turkeys select similar energy concentrations irrespective of gender, the males – which have a higher growth potential – select a higher concentration of protein than females; similar results have been obtained with growing broilers.

Laying hens

Up to about 14 weeks of age, the growing pullet requires protein only for feather development and a relatively slow rate of muscle deposition but, around 15 weeks of age, there is rapid development of the ovaries and oviduct that would be expected to increase protein demand and, thus, protein intake in a choice-feeding situation. This has been observed as a marked increase in the protein content of their diet about 2 weeks before the onset of lay in choice-fed pullets.

Laying hens are capable of choosing an appropriate protein intake when given the opportunity, and showed a preference for HP that increased steadily during a 26-day observation period.

Emmans (1977) gave laying hens from 41–56 weeks of age a conventional food with a crude protein content of 173 g CP/kg, either as the sole food or with a choice of ground barley. There were no differences in egg production or total food intake. The choice-fed birds ate, on average, 84% of their intake as the compound food, but this was affected by output: those with higher than average egg production ate more food, but this extra was all from the compound food. Emmans was careful to point out that there were differences other than in protein content and quality between the layer mash and the barley, especially calcium, and that his results were not absolute proof of a protein appetite.

Pairs of foods containing 80/170, 110/170, 80/230 or 110/230 g protein/kg were offered as choices to laying hens by Steinruck and Kirchgessner (1992). There were no differences in egg output between any of the choice-fed groups compared with those on single foods of 170 or 230 g CP/kg, nor any significant differences in body weight gain. The dietary protein concentrations selected on the four choice treatments were 153, 152, 188 and 179 g/kg, respectively, and this was claimed to demonstrate the ability of laying hens to select a protein intake corresponding to their requirements for optimal egg production, but this ability was not very accurate.

These results provide clear evidence that poultry demonstrate an appetite for protein.

Pigs

As described in Chapter 8, growing pigs choose between high- and low-protein foods in such a way as to meet their supposed requirements for growth, without over-consuming protein.

As a further test of the theory that growing pigs can select for a protein intake meeting their growth requirements, Bradford and Gous (1991) offered pigs choices between pairs of foods containing 220/180, 220/140, 220/100, 180/100 or 140/100 g CP/kg. Compared to controls on a single 160 g/kg food, choice-fed pigs grew leaner and more efficiently from 30 to 90 kg. The proportion of HP eaten fell as the pigs grew, except in the 140/100 choice, where they ate almost all from the 140 g/kg food.

Of course, the intake of protein might be controlled in order to obtain the appropriate amount of the first limiting amino acid, and it was observed that the isoleucine content chosen was almost exactly what would be predicted, whereas lysine intake was higher than predicted, suggesting that isoleucine is the first limiting amino acid under the conditions used in that experiment. It will, therefore, be difficult to tell whether an appetite is for protein or for the most limiting amino acid.

There is variability in protein choice between batches of pigs reared in the same facilities, as shown when maize and a protein supplement were fed to growing pigs in complete and free-choice diets (Engelke *et al.*, 1984). In the first experiment, the pigs grew well and the proportion of protein supplement chosen declined as the pigs grew, so that over the entire experiment the protein content of the chosen food was 136 g/kg compared with 146 g/kg for the complete food given to controls. In a second experiment, however, the choice-fed pigs ate a lot of supplement and consumed more protein than complete-diet-fed animals. Variability, both between and within batches of animals, is a feature of choice feeding and the extent to which this is related to differences in growth potential, and therefore nutrient requirements, is not yet clear.

Synthetic foods with extremes of protein have been used for growing gilts offered a protein-free food and one fortified with casein (Robinson, 1974). Each successive week the protein content of the fortified food was increased, from 200 to 800 g/kg in steps of 100. There was significant selection for the food containing protein up to a protein content of 600 g/kg, resulting in protein consumption greatly in excess of requirements. Foods containing 700 or 800 g protein/kg were rejected. Even though the protein-free food was highly unpalatable and was avoided to a great extent, it was preferable to a very high-protein food which would exert considerable metabolic costs of deamination.

Female growing pigs were offered 122, 206 or 240 g CP/kg fresh food or a choice between 122 and 240, and free access to straw (Jensen *et al.*, 1993). Those on the lowest-protein food alone had lower live weight gain and food conversion efficiency and stood for longer, walked and rooted in straw more. It was suggested that: 'specific nutritional needs can increase the foraging motivation of growing pigs'. The choice-fed group did not select an adequate diet and grew a bit more slowly than those on the medium- or high-protein foods (this was thought to be due to positional, social and urination effects).

As pigs grow, the ratio of protein:energy required in the diet declines and there is evidence that they select decreasing protein contents when offered HP and LP. Kyriazakis *et al.* (1990) noted that the protein content selected fell from about 250 to 180 g/kg over an 18-day period starting at 15 kg live weight. Similarly, when growing pigs were given a choice between two foods made from the cereal and protein components of a standard control food, the protein content of the chosen diet fell with age from 254 to 191 g protein/kg over a 3-week period from 18 kg live weight (Healy *et al.*, 1993).

Nutrient requirements for growth are influenced by previous nutritional history, and Kyriazakis and Emmans (1991) have demonstrated that this is reflected in the choice pigs make for foods with different protein contents. Those previously given a single, low-protein food chose a diet containing 233 g CP/kg when given a choice of HP and LP, while those previously given a high-protein food chose only 175 g CP/kg. By 33 kg body weight the two groups did not differ in carcass composition, showing that the changes in composition induced by restriction in the first phase were compensated for by choice feeding in the second phase of the experiment. Males, with a higher growth potential, chose a diet higher in protein than did females (228 versus 181 g CP/kg).

Chinese Meishan pigs, of particular interest because of their great prolificacy but having low growth potential and a high rate of fat deposition, when given free choice between HP and LP chose 144 g protein/kg while Large White-cross animals, with a high potential for growth but low fat deposition, chose 194 g protein/kg (Kyriazakis *et al.*, 1993a). The growth rates achieved by the choice-fed animals were not significantly different from the highest achieved on a single food (130 and 220 g protein/kg for Meishan and Large White, respectively). This is another example of animals compiling a diet that avoids either an excess or deficiency of protein in relation to energy.

It is clear, therefore, that growing pigs have a well-developed appetite for protein.

Cattle

Appetite for protein was investigated by Tolkamp *et al.* (1998a), who gave lactating cows either LP (131 g CP/kg DM) or HP (185 g/kg) or a choice between the two. That LP was deficient in protein was demonstrated by the fact that the milk yield was significantly lower than for the other two treatments. Cows in the choice treatment chose a mean of 683 g HP/kg of food DM, significantly different from a 'random' choice of 500 g/kg, but any suggestion that they were selecting to meet their protein requirements was denied by the lack of change in the proportions of the two foods taken between the 2nd and 22nd weeks of lactation, a period during which milk yield and protein output declined markedly. Also, there was no relationship between milk protein output and the choice made by individual cows, in contrast to the results of Lawson *et al.* (2000) (Chapter 8).

In addition, it was calculated that even LP provided sufficient MP to meet the needs of the average cow, despite the low daily intakes of this food. It appears,

therefore, that the cows in this experiment were not selecting for protein, whether crude or metabolizable, to meet their requirements.

If selection is not for CP or MP then maybe it is for ruminally degradable protein (see Chapter 7). In a further experiment, Tolkamp *et al.* (1998b) gave cows a choice between a low-protein food (128 g CP/kg) and a high-protein food (185 g /kg) and also these same two foods to both of which was added urea at 7.5 g/kg food DM to give 161 and 225 g CP/kg, respectively. Urea is utilized by the ruminal microbes for protein synthesis and therefore provides ruminally degradable protein ($N \times 6.25$). By raising the CP content of both foods with the addition of the same amount of urea, any effect of the latter on 'palatability' was avoided, as the flavour of both foods would be affected in the same way.

Figure 13.2 summarizes the results and shows the effect of adding and then removing urea in the first half of the experiment (solid symbols). It can clearly be seen that the addition of urea causes a change in selection; whereas before urea addition cows chose about 800 g of HP/kg of total intake, this rapidly changed to around 300 g/kg, stabilizing at this lower level after about 3 days. Conversely, when the urea was removed, choice quickly reverted to around 800 g/kg.

In the second half of the experiment (open symbols), choice of HP was around 200 g/kg when both foods contained urea, increased to around 600 g/kg when it was removed from both foods and fell back to around 200 g/kg when the urea was reintroduced. It is possible that choice of the lower CP mixtures in the second half, compared with the first half, of the experiment was due to the

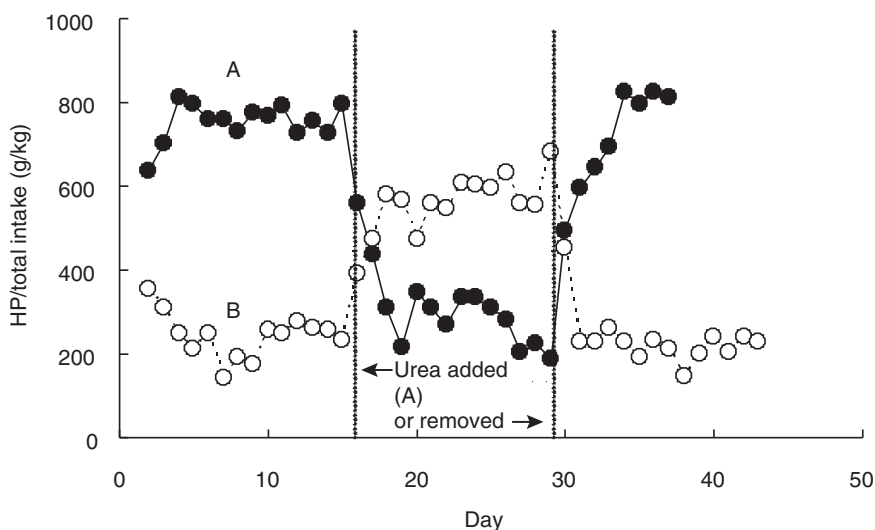


Fig. 13.2. Effect of adding and removing urea from both HP and LP foods on the choice made between them by lactating cows. A, solid circles, first half of experiment; B, open circles, second half (from Tolkamp *et al.*, 1998b).

cows being later in lactation and thus having lower protein requirements. These results are startling in both the magnitude and the speed of changes in food choice by cows, and suggest a substantial effect of the content of ruminally degradable protein (RDP) in foods on diet selection.

While the compensation in choice during periods with or without urea supplementation of both foods is not exact, the accumulated evidence supports the likelihood that cows can demonstrate an appetite for protein. It seems that cows can also select a diet adequate in protein when a choice between a high- and a low-protein concentrate is given as a supplement to silage (Lawson *et al.*, 2000; Figs 7.5 and 7.6).

Sheep

When growing sheep were given choices between two foods, one with a protein content above and the other below their presumed requirements, they made apparently nutritionally directed choices to achieve a dietary protein content of 131–133 g CP/kg, which was close to the protein content of a single food giving optimal tissue protein deposition (Kyriazakis and Oldham, 1993; Fig. 7.7). When two foods with protein contents above requirements were offered, the sheep consistently ate more of that with the lower content. However, when the choice was between a high-protein food and one supplemented with urea, the HP food was preferred, giving an overall protein content of the diet of 173 g CP/kg, i.e. greater than required. The sheep preferred to eat excess protein than excess urea, presumably because of the more toxic effects of the latter.

It seems that lambs are able to differentiate between foods with different protein contents and to select between them according to their protein and energy requirements. The choices made are not always such as to provide a constant intake of protein, however, as the sheep always ate some of both foods, even when to do so produced an imbalanced diet. The propensity to sample available foods from time to time has been noted in Chapter 7.

Environmental temperature

Increasing the environmental temperature to above the thermoneutral range depresses food intake in animals given a single, complete food. If given a choice between HP and LP it might be expected that protein intake could be maintained while energy intake was reduced to relieve the heat stress. However, protein metabolism and growth are heat-producing processes and it is difficult to predict the outcome of choice-feeding at high temperatures. The experimental evidence is conflicting.

Full discussion of effects of environmental temperature on food intake appears in Chapter 17.

Poultry

Several experiments have shown that increasing the environmental temperature tends to increase the protein concentration of the selected diet as energy intake falls, but this is not sufficient to prevent all of the temperature-induced reduction in performance, in either growing birds or laying hens. However, some other studies have found no difference in the proportion of HP selected by broilers whether they were kept in a thermoneutral or heat-stressing environment while one study, with mature birds from high- and low-weight strains, found increasing temperature to have a proportionately greater depressing effect on protein intake than on energy intake, against expectations.

Broilers given a choice of protein concentrate and whole sorghum grains ate 30% more grain during the day under constant 20°C than in a cyclical temperature of 20°C during the night and 33°C in the day with continuous illumination (Mastika and Cumming, 1985), i.e. the latter increased their proportion of HP in their diet during the hot period. Similar results were obtained in a second experiment, in which the lights were on for 16 h/day and choice-fed birds were more efficient than those on the complete food in the hot environment.

Under cold conditions (10°C), choice-fed broilers ate as much protein but more energy than at 20°C (Mastika and Cumming, 1987), a further demonstration of the ability of the broiler to independently control its energy and protein intakes according to changes in requirement.

Sheep

Cropper and Poppi (1992) kept growing lambs in thermoneutral (12–20°C), cold (3–6°C) or hot (27–30°C) environments for 7 weeks and gave a choice of two foods containing 67 and 251 g protein/kg. There were no differences between those in the thermoneutral and cold environments, whose consumption of protein and energy was at rates close to NRC recommendations, giving very high growth rates. Those in the hot environment increased their HP:LP ratio but reduced their total intake and growth rate. It was concluded that lambs change their selection in the appropriate direction when the environment is changed.

Regulation of Amino Acid Intake

Diets that are imbalanced in the amino acids absorbed from the digestive tract lead to metabolic disturbances and a reduction in food intake, which is directly proportional to the degree of amino acid deficiency or imbalance. The effect on intake may be due to the metabolic cost of deaminating the excess of those amino acids that cannot be utilized because of the deficiency – relative or absolute – of others. Appetites for individual amino acids can therefore be envisaged if the animal learns that one food contains too little of an amino acid for its requirements and another too much, as long as there are discernible sensory differences between the two foods to act as cues.

Poultry

Newly hatched layer chicks offered a choice between a low-lysine food and one with an excess of lysine ate some of the supplemented food but not enough to maintain a growth rate as high as those given a single, adequate food (Newman and Sands, 1983). The two food containers were kept in the same place through the 21-day experiment, but no colour cues were given and no separate training period was provided. In a second experiment, a low-lysine food was given in choice with L-lysine HCl but, although the birds ate some lysine, it was not enough to support normal growth. In this case, presumably the birds had no difficulty in differentiating the food from the pure lysine. When D-lysine HCl was offered as a choice with low-lysine food, the birds ate some of the former, suggesting that D-lysine triggers some receptor mechanism even though D-lysine was unavailable for metabolism. Given a choice between L- and D-lysine, birds ate more of the L form. Thus, there is some evidence of nutritional wisdom but not sufficient to give a properly balanced diet.

Broilers rendered methionine deficient by prior feeding on the low-methionine food and then given a choice between a complete food and one with 50% of the recommended methionine chose predominantly the former. In laying hens, a methionine-deficient diet depressed egg production from 85 to 67%, while a choice between deficient and adequate diets resulted in a 58% choice of the adequate diet and egg production of 80% (Hughes, 1979). Selection for methionine therefore occurred, but not quite enough to prevent a small decline in egg production.

Pigs

Growing pigs select a food with protein containing a balanced mixture of amino acids in strong preference to one with an imbalanced amino acid composition, whereas the preference for a balanced food paired with a protein-free food is not so marked: clearly, the imbalanced diet is aversive. It takes approximately 24 h for pigs to recognize an imbalanced diet, which is consistent with a learned aversion to a food causing malaise.

Pigs preferred a protein-free food to a threonine-imbalanced one (Robinson, 1975), and the imbalanced food was clearly aversive. Growing pigs selected a methionine-supplemented food in preference to an unsupplemented diet containing 90 g casein/kg, but this may have been due to the strong taste of the methionine rather than to a specific appetite. In the same report, there was no lasting selection for lysine-supplemented foods.

Addition of 4% of methionine, tryptophan, arginine, lysine or threonine to the food for growing pigs led to reductions in weight gain of 52, 31, 28, 16 and 5%, respectively and, when given a choice of one of the imbalanced foods and the control food, there were strong preferences for the balanced food (Edmonds *et al.*, 1987). When choices were offered between different excesses of amino acids, those with excess threonine, lysine or arginine were preferred to those with an equal excess of methionine or tryptophan. When given a

choice between a protein-free food and one with an excess of tryptophan, they initially preferred the protein-free one, but by 12 days were eating more of the tryptophan-supplemented food.

In research in which growing pigs were offered pairs of foods containing two different levels of lysine or two different levels of threonine, there was no consistent selection, probably due to the only cue being the position of the food. However, even when the cues were strengthened by flavouring either the lysine-supplemented or unsupplemented food for choice-fed weaner pigs, there was still no evidence for selection for lysine (Dalby *et al.*, 1994).

Bradford and Gous (1992) also studied lysine appetite. In their first experiment, foods containing 8.6, 11.7 or 17.4 g lysine/kg food were given singly, and the first and last of these were given as a choice to another group. The results supported the conclusion that the pigs chose for lysine but, as lysine was confounded with protein content, this could be only a tentative conclusion.

In a second experiment, foods containing 14.7 g lysine/kg were made, using either fish meal, soybean oil cake or sunflower/cottonseed/groundnut oil cake. These were fed alone or in choice with each other or with a low-protein food (8.3 g lysine/kg). When they were offered as single foods, there were no significant differences in growth, but when given as choice the pigs preferred not to eat much of the plant protein mixture. However, there was still no difference in daily food intake or growth.

The question then arises as to whether the plant protein-containing food contained an antinutritive factor or it was just unpalatable. The levels of the toxin gossypol were not high. With most of the food combinations in this second experiment, the lysine content chosen was 14.7 g/kg or very close, except when the choice was between the food containing plant protein and one with a low protein content, in which case only about 13% was eaten of the former, giving a lysine content of only 9.0 g/kg. Even though the three types of food had the same protein content, they were not eaten in equal amounts or at random, but for a remarkably constant lysine content, except where the plant protein was concerned.

On the other hand, Nam *et al.* (1995) concluded from their research that growing pigs are unable to control their protein and lysine intake to meet their requirement for growth when given a choice of two isoenergetic diets differing in protein and lysine content. However, the foods they offered to investigate protein selection contained 100 and 180 g/kg, so knowing that such pigs have an optimum of around 210 g/kg, falling as they grow to perhaps 180 g/kg, it is not surprising that they ate predominantly HP throughout. Also, the foods offered in the study of a possible lysine appetite both contained 140 g/kg CP with 5.3 or 9.0 g lysine/kg. Given the low CP content of the diet, whichever food they chose they would still be very deficient in many amino acids. This work, therefore, fails to meet some of the requirements necessary for demonstration of wise choices between foods (see Chapter 7).

There is clear evidence of an appetite for tryptophan (Trp) in newly weaned piglets (Ettle and Roth, 2004). In addition to Trp-adequate (2.0 g/kg) and Trp-deficient (1.1 g/kg) treatments, there were choices between the deficient and the adequate foods and between the deficient and a food mid-way between deficient and adequate (1.6 g/kg). In both choice-fed groups, the pigs ate predominately

the higher-Trip food, especially after the first week, during which time the preference was developing. Together with the results of growth performance, these results suggest that piglets are able to detect Trip deficiency-induced metabolic changes and respond with an aversion against the Trip-deficient diet.

Appetites for amino acids can be expressed in most cases as long as the experimental conditions are suitable.

Appetites for Minerals

In order to demonstrate a specific appetite for an individual nutrient rather than for a particular type of food, animals are offered a choice between two similar foods, one of which is supplemented with the nutrient in question while the other is not. A significant preference for the supplemented food may demonstrate a specific appetite for the nutrient. Such a conclusion can be strengthened by the demonstration that animals made deficient in the nutrient in question choose a higher proportion of the supplemented food than those not made deficient.

Calcium

The great demand for calcium (Ca) for the formation of the eggshell means that the laying hen has been the prime subject for studying Ca appetite.

Poultry

Perhaps the most widely recognized example of a specific appetite in farm species is the Ca appetite of the domestic chicken. Wood-Gush and Kare (1966) showed that Ca-deficient chickens preferred food containing Ca to a Ca-deficient food when the choice was given after 21 days of deprivation. Palatability is also involved, Ca lactate in food being selected for but Ca lactate in the water being avoided, even by deficient birds. Although this appetite for Ca develops slowly (2–4 days) in growing chickens, suggesting that it is learned, it develops very quickly (0.5 h) in laying hens where the Ca requirements are much higher. This has been used to support the suggestion that the Ca appetite in chickens is innate (Hughes, 1979), but it seems more likely that it is learned, given that most Ca salts are insoluble and therefore have little taste.

The higher food intake that is observed on days in which an egg is being formed might be due to the higher Ca requirement on those days, but might also be a response to amino acid or energy demand. Chah and Moran (1985) found differential intake of Ca and protein, however, as there was higher protein intake in the morning and higher Ca intake later in the day by hens producing at least 90% eggs and given choices of a high-energy food, a high-protein food and oyster shell flakes. Compared with controls given a complete food, there was no difference in egg production or body weight change, but eggshells were thicker and the efficiency of utilization of nutrients appeared to be better in the choice-fed birds.

Given foods containing 8.9 or 3.5 g Ca/kg and grit containing 380 g/kg, pullets chose diets containing 11.8, 20.8 and 35.0 g Ca/kg during the growing, pre-laying (medullary bone formation) and egg-laying phases, respectively, i.e. close to their requirements. Growing pullets have also been found to self-regulate their Ca intake well, but laying hens were not so efficient. When containers for pullets were switched between left and right sides, the birds gradually realized this and changed their selection appropriately within about 3 days. The fact that this change was not immediate suggests that the birds were using positional cues they had learnt to associate with the Ca levels of the two foods.

Clearly, the animal must be able to distinguish between high- and low-Ca foods by visual or taste cues, otherwise it cannot identify the appropriate diet (see Chapter 6). What is the reinforcement that leads to preference for a particular diet? It seems unlikely to be a learned aversion for the deficient food because birds tend to choose familiar foods even when they are deficient, as against novel diets that might supply the missing nutrient. It is more likely, therefore, that ingestion of Ca gives a feeling of well-being, which becomes associated with that particular food, i.e. preference for the Ca-supplemented food.

Although voluntary intake of food declines around the onset of laying in pullets, their intake of oyster shell increases during this period. Once in full lay, hens show a diurnal fluctuation in selection for Ca, eating more limestone grit or oyster shell just before dark (at a time when eggshell formation is proceeding) than earlier in the day (Mongin and Sauveur, 1979). To separate the effects of egg formation from those of photoperiod, hens were kept in continuous light; there was still a consistent peak in Ca selection 6–10 h after ovulation when Ca deposition in the shell was just about to start, which suggests an anticipation of need.

It had been found that hens ate more food in the first hour of the photoperiod (presumably because they were hungry after not eating all night) and again in the last hour or two before dusk (postulated to be in response to increased demand for Ca and phosphorus at that time). However, we have seen no evidence of such phenomena although we have confirmed that, when offered ground limestone separately from the main food, the hens ate limestone only between 20.00 h and midnight (lights off), i.e. at the beginning of shell deposition (S.H. Gordon, G.R. Barkley and J.M. Forbes, unpublished results).

Calcium deposition is not a direct stimulus to Ca intake, however, as preventing shell formation by placing a thread in the wall of the shell gland did not abolish the daily peak in Ca selection. Of the other events occurring during the egg-laying cycle of the hen, oestradiol secretion is the most likely to be involved in the diurnal changes in Ca selection. Oestradiol treatment of cockerels causes an increase in Ca intake, and plasma oestradiol concentrations closely parallel differences in Ca intake on different days.

Pigs

Growing pigs offered a choice between water and a 24 g/l solution of Ca lactate drank very little of the latter, even though they were on a low-Ca diet. Even after parathyroidectomy, when plasma Ca concentration was significantly

reduced, they did not choose Ca lactate and had to be revived with injections of Ca borogluconate (Pickard *et al.*, 1977). Intact pigs on a low-Ca diet did, however, eat solid Ca carbonate but did not reduce the intake of this when Ca carbonate was added to their food at the rate of 5 g/day. Thus, if there is a Ca appetite in pigs it is not very specific. As Ca absorption is regulated according to the animal's requirements, excess Ca in the gut is not absorbed, therefore a food containing an excess does not necessarily become aversive.

Ruminants

It is widespread practice to offer ruminants access to mineral licks (blocks containing multiple minerals) on the assumption that they will regulate their mineral intake, but this cannot be achieved when the block contains many minerals unless the composition is exactly in proportion to the animals' requirements, which is unlikely. It is inadvisable to offer Ca salts *ad libitum* because absorption of Ca from the gut is regulated in mammals: a high intake of Ca leads to a lower rate of absorption and no change in total uptake from the gut. Wide differences were observed in voluntary intake of dicalcium phosphate and calcium carbonate between pregnant cows fed a ration low in Ca and phosphate (Pickard *et al.*, 1978), and it must be concluded that there is no evidence for a specific Ca appetite in cattle. This conclusion can also be drawn from the compilation of experimental results by Pamp *et al.* (1976), although some of the results they quote are suggestive of a selective intake of bone meal by cows.

Phosphorus

Poultry

Phosphorus (P) is an essential nutrient, required for bone and eggshell formation in addition to many metabolic processes. Laying hens choose diets with intermediate P contents (5–10 g/kg) and reject those with low (2 g/kg) or high (24 g/kg) contents. When the Ca content was raised from 30 to 60 g/kg, the proportion eaten of a food containing 24 g P/kg rose from 20 to 37% when the other food contained 10 g P/kg, which suggests homeostatic control of P intake to maintain a constant ratio to Ca. However, Hughes (1979) reports a failure to demonstrate a P appetite in laying hens.

In addition to optimizing the nutrition of the hen, there is the increasingly important need to avoid excessive excretion into the environment. Much of the P in plant materials is in the form of phytate, which is resistant to digestion, hence the importance of the proportion of dietary P that is available for absorption (available P, AP). Phytase enzymes release P from phytate, and these are used as food additives to improve the availability of P from poultry diets. Nevertheless, it is not possible to predict with accuracy the optimal rate of inclusion of phytase in diets for birds in different physiological states. Some of the results presented in the previous paragraph suggest that diet selection methodology might offer a means of determining optimum provision of dietary P, including the use of phytase.

As described in Chapter 7, it is necessary to ensure that one food to be offered is deficient in the nutrient in question, in this case P. This has proved surprisingly difficult with the type of wheat-based food usually used in northern Europe, because of the relatively high activity of natural phytase in wheat. However, it is possible to produce P deficiency in hens by using maize/soy-based foods, and Barkley *et al.* (2004) confirmed that the low-AP (LAP, 1.1 g AP/kg) food they formulated was indeed deficient, as evidenced by significantly reduced egg weight compared with eggs from hens given a similar food formulated to be adequate in AP (normal AP, NAP, 2.2g AP/kg DM) by addition of dicalcium phosphate. Laying hens were then offered a choice between LAP and NAP foods to determine whether they would choose proportions of the two appropriate to their needs for AP.

At the peak of egg laying (25–28 weeks of age with a production of 0.98 eggs/bird/day), P-replete or P-deficient hens were fed either NAP or LAP alone, a choice of LAP and NAP or a choice of LAP and PAP (LAP with 400 FTU/kg microbial phytase). The P-deficient hens given a choice of NAP/LAP ate a significantly greater proportion of NAP (66%) than did P-replete hens fed NAP in phase 1 (28%), demonstrating that P deficiency influenced subsequent selection for AP, i.e. an appetite for P (see Fig. 13.3).

With a choice between LAP and the same deficient food with added phytase (PAP), there was no effect of previous diet on the proportions of food chosen, which were not significantly different from 50%. The recommended level of inclusion of phytase in the diet for laying hens is 200 ppm, and the diet taken included 0.5 of the food containing phytase at 400 FTU/kg; therefore, the

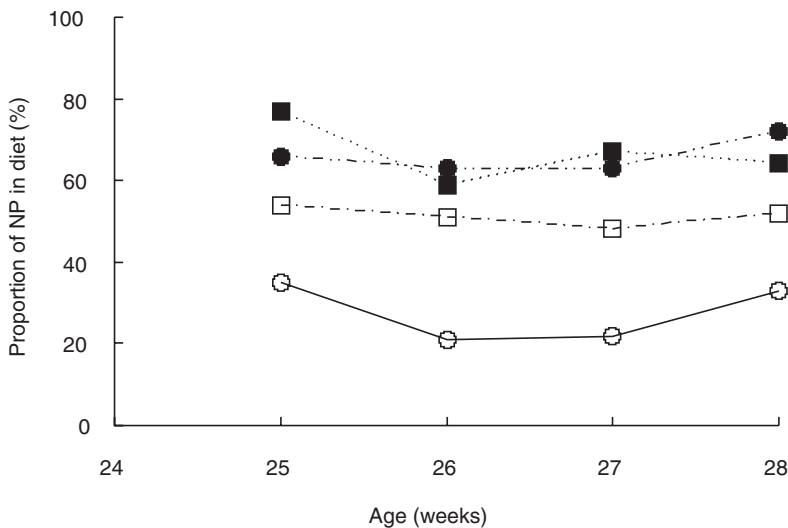


Fig 13.3. Proportion of NP or PP eaten by laying hens. Diets: ○, NP in phase 1, choice between NP and LP foods in phase 2; □, LP in phase 1, choice between LP and PP in phase 2; ●, NP in phase 1, choice between LP and PP in phase 2; ■, LP in phase 1, choice between NP and LP foods in phase 2 (from Barkley *et al.*, 2004).

concentration of exogenous phytase in their diet was diluted to approximately 200 FTU/kg, i.e. the recommended level. It may be, therefore, that the selection of close to 50% of each food was targeted at optimizing P nutrition rather than eating at random. Nevertheless, the P-depleted hens would have been expected to choose a higher proportion of PAP than did the P-replete birds, which they did not. This highlights the difficulty of interpreting results from diet selection experiments where the two foods used have an optimal mixture close to 50:50.

A factor limiting the birds' ability to choose wisely for AP might be the nature of the 'discomfort' induced by P deficiency. Mild deficiencies or toxicities whose effects on metabolism have a delayed onset, and/or which do not affect abdominal receptors, are less likely to induce sensory-paired aversions than are those inducing immediate nausea; P deficiency or excess is likely to fall into the former category and is therefore not a strong candidate for conditioned preference or aversion. Although the evidence supports an ability amongst hens to select their diet according to its P content, this has not been demonstrated as clearly as has been the case for protein.

Ruminants

Phosphorus-deficient sheep and cattle will eat bones but it is doubtful whether this is a true appetite for P, because they do not specifically select a supplement containing a high level of phosphate. However, cattle stop eating bones when their blood Pi (inorganic phosphate) levels have risen to normal or are excessive, providing circumstantial evidence for a P appetite.

Grazing cattle and sheep fail to select a P supplement to correct a P deficiency induced by low-P herbage. However, Merino sheep show preference for phosphorus-fertilized plots of grass in the dry season (but not in the wet season), even when the levels of P were higher than those giving maximum pasture growth (Ozanne and Howes, 1971). The major difference between the pastures was the P content but there was also a small but consistent fall in the phenol content as P increased, so perhaps they were using this as a cue, or even as the primary stimulus.

Selenium

Evidence for an appetite for selenium (Se) is provided by the results of an experiment in which Se-deficient hens preferred a food high in Se over a low-Se food during the first 3 weeks of choice but not thereafter, when presumably the deficiency had been alleviated (Zuberbuehler *et al.*, 2006).

Sodium

Poultry

Several attempts by Hughes and his colleagues (Hughes, 1979) failed to demonstrate anything more than a weak sodium (Na) appetite in laying hens;

even when a slight preference was shown for a higher-Na food, it was not enough to prevent a reduction in egg production. This is surprising, as Na is a major mineral in the body and many species of mammal have been shown clearly to have Na appetites.

Ruminants

A specific Na appetite has been demonstrated and studied by Denton and colleagues for many years. Housed sheep correct for Na deficits very accurately when given NaCl solutions (Denton, 1982), while on grazing they select plant species that are high in Na. The increase in intake of NaCl solution when sheep were Na-depleted by drainage of saliva via a parotid duct fistula is reversed by infusion of Na salts into a lateral ventricle of the brain, showing that the CNS is sensitive to Na ions.

Sodium depletion of calves led to reduced food intake and the development of a relatively specific appetite for the Na ion, calves responding more for Na bicarbonate in an operant situation when they were more severely Na depleted.

No increase has been found in the preference shown by ewes for salt when on low-salt diets during pregnancy or lactation, when salt requirements are known to be increased, but this increase in Na demand is likely to be small relative to that induced by saliva drainage.

Sulphur

There is good evidence for an appetite for sulphur (S) in sheep. Ewes offered foods with low (1.1 g/kg) and high (9.5 g/kg) contents of S after having been fed on a diet adequate in S initially ate at random but, within 2 days, increased the proportion of the low-S food so that their daily intake of S was very close to that required. Sheep previously made S-deficient initially ate a high proportion of the high-S food but later reduced the S content chosen until it had stabilized at close to the optimum level (Hills *et al.*, 1998). Moreover, ewes conditioned to associate different flavours of straw with different doses of S into the rumen preferred flavours associated with moderate doses but avoided flavours paired with high (mildly toxic) doses, as shown in Fig. 13.4 (Hills *et al.*, 1999). With the highest doses (9 or 12 g), preference for food of the flavours associated with these doses declined significantly in successive tests.

Zinc

Zinc (Zn)-deficient chicks will consume more of a food containing 65 mg Zn/kg than of one containing only 5 mg/kg (Hughes and Dewar, 1971). During the first 6 days after offering the Zn-supplemented food, it was consumed at greater than twice the level of the low-Zn food by Zn-deficient birds. Control birds ate about 40% of the high-Zn food for several days, but this proportion gradually increased as they apparently became marginally Zn-deficient themselves.

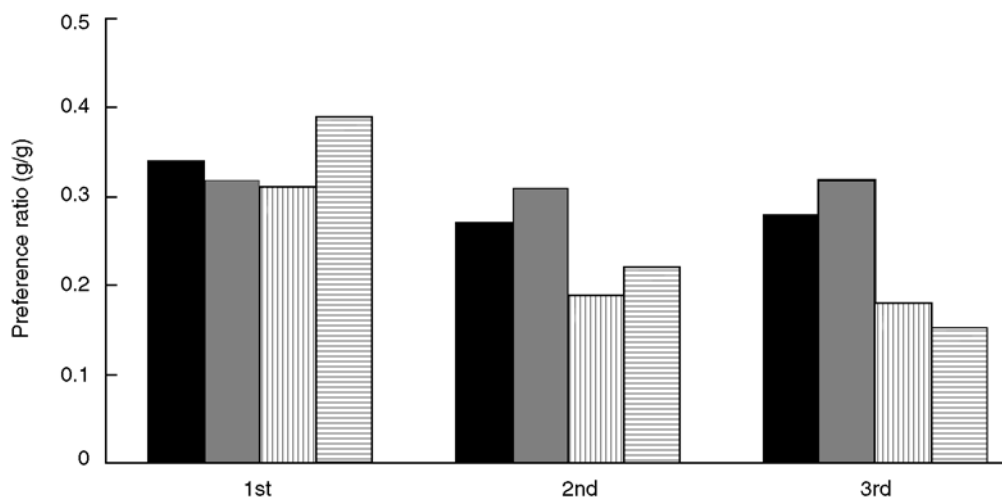


Fig. 13.4. Preference ratios of sheep for food of the flavour associated with doses of 3 g (solid bars), 6 g (shaded bars), 9 g (vertically striped bars) or 12 g (horizontally striped bars) sulphur given intra-ruminally during three conditioning periods (from Hills *et al.*, 1999).

Appetites for Vitamins

Thiamine (Vitamin B₁)

Thiamine selection has been studied in chickens by inducing a functional deficiency with injections of oxythiamine hydrochloride, a metabolic antagonist of thiamine (Hughes and Wood-Gush, 1971). When offered two foods, one deficient in thiamine, the other supplemented with 20 mg/kg, the depleted birds ate consistently more of the supplemented food than did control birds, demonstrating a specific appetite for thiamine.

Vitamin B₆

Broilers given a choice of vitamin B₆-sufficient and -deficient foods at first ate too little of the former and showed signs of deficiency of the vitamin (Steinruck *et al.*, 1991). They then increased their relative intake of the supplemented food to re-establish normal growth and continued to eat proportions of the two foods, which provided them with a balanced diet. Thus, they demonstrated a specific appetite for vitamin B₆ based on the learned consequences of eating the two foods.

Ascorbic acid (Vitamin C)

There have been several reports that the adverse effects of heat stress on food intake and performance are partially alleviated by supplementation of the diet

with ascorbic acid. This is somewhat unexpected, as it had been generally assumed that chickens could synthesize sufficient ascorbic acid and that dietary supplementation was unnecessary.

In order to see whether the different requirements for ascorbic acid under temperate and hot conditions would be expressed as an appetite for ascorbic acid, Kutlu and Forbes (1993c) trained young chicks to differentiate a supplemented food from an unsupplemented one by means of colour, and then gave them a choice of the two. Those birds kept in an non-stressful environment ate a significantly lower proportion of the supplemented food than those maintained under mildly heat-stressing conditions.

Figure 13.5 shows the ascorbic acid intakes chosen by broiler chicks under the two environmental conditions and the changes following reversal of the environments (Kutlu and Forbes, 1993b). It will be seen that, following a change in environmental temperature, the birds adjusted their ascorbic acid intake within 3 days; the voluntary intake of the vitamin in the thermoneutral environment was 5–6 mg/day, while under the hot conditions it was 9–10 mg/day. Clearly, the colour discrimination of the two foods had allowed the chicks to express their desire for an intake of ascorbic acid appropriate to their needs. If the two foods were offered without colour, the birds ate at random.

Appetite for Fibre

Given only a food whose ingredients have been finely ground, ruminants do not perform proper rumination and seem to crave a source of long fibre: provision of fibre restores normal rumination. To investigate whether this can be considered to be an appetite, in the true sense of the word, Campion and Leek

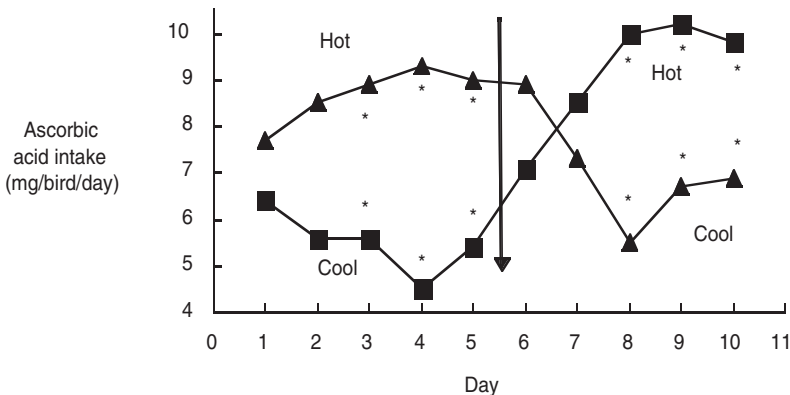


Fig. 13.5. Self-selected intakes of ascorbic acid by growing broiler chickens offered coloured foods that were unsupplemented or supplemented with ascorbic acid. \blacktriangle , birds in a heat-stressing environment for 5 days followed by a thermoneutral environment; \blacksquare , thermoneutral, followed by hot environment. The vertical arrow indicates the time of change of environments. *, selection between foods significantly different from 50:50 (from Kutlu and Forbes, 1993b).

(1997) offered polyethylene fibre to sheep on diets of long or ground hay. On switching from hay to the pelleted diet, the sheep commenced eating the fibre within 24 h. Further, tickling the anterior dorsal part of the rumen wall with polyethylene fibres – via the rumen fistula – reduced the voluntary intake of polyethylene fibres, suggesting that the intake of inert fibre may be a result of the reduction of ruminal sensory input to the brain normally provided by fibrous reticulo-ruminal contents.

However, when offered a choice between short (3 mm) and long (15 mm) polyethylene fibres, sheep on a finely ground food significantly preferred the 3 mm fibre, even though this did not permit proper rumination. Choice of fibre is therefore partly governed by ease of ingestion rather than by which substrate is more ideally suited to induction of rumination. This can be encompassed by the MTD theory (see Chapter 10), whereby the discomfort of eating too much fibre can be traded off against the problems of eating too little.

Toxins

While appetites for nutrients, and fibre, are directed towards providing sufficient food resources to allow the animal to achieve its programmed physiological activities, they also serve to prevent toxic excesses of these nutrients. The principle of conditioned preferences and aversions has been discussed in Chapter 7. The same principles apply to toxic substances, i.e. those for which the 'desired' intake is zero, or at least very low.

Tall larkspur is a rangeland herb that contains toxins and is frequently fatal if ingested. The hypothesis that cattle can generally limit intake of larkspur to sublethal levels was tested by feeding pelleted food containing 27% larkspur (Pfister *et al.*, 1997). The animals showed distinct cyclic patterns of intake, where increased larkspur consumption on one or two days was followed by significantly reduced consumption on the following day. The intake of larkspur provided just under the amount that would produce overt signs of toxicity.

Pfister *et al.* (1997) subsequently examined the response to doses of a toxin, in this case lithium chloride (LiCl), that varied with food intake. Increased consumption was followed by application of a stronger dose of LiCl, and this caused a reduction in food intake. According to the experimental protocol, this was followed by application of a lower dose of LiCl and therefore higher food intake, in a cyclical manner. Then they repeated this experiment but using oral administration of larkspur instead of LiCl and, again, there were clear cycles of intake, days of higher food consumption being followed by 1–3 days of reduced consumption. This might suggest that the fluctuations of daily intake commonly observed are due to toxins in the food, but there is no evidence for this in cases where the food appears to be free of obvious toxins (see Chapter 10).

Examples such as the one above and in Chapter 8 clearly show that animals can regulate their intake of toxins, in balance with their intakes of nutrients.

Water Intake

Water is the most important nutrient. If you doubt this statement then consider which nutrient, when removed from the diet, will cause illness and death most quickly. The fact that water is taken so much for granted in temperate countries is due to its ready availability and thus its very low cost.

Water is required for: (i) wetting food in the mouth and stomachs; (ii) as a medium for digestive reactions in stomachs and intestines; (iii) as the major component of the body; (iv) as a medium for the excretion of soluble material in the urine; and (v) for the secretion of sweat. Thus, its requirements are influenced by the amount and type of foods eaten and by the environmental temperature.

The voluntary intake of water is usually about twice the weight of dry matter eaten and, because many of the functions of water are related to the digestion and metabolism of food, water intake is closely related to food intake, both quantitatively and temporally. Simple-stomached animals usually drink before, during or after each meal of food whereas ruminants, with their great capacity for storing digesta with a high water content, often eat a meal without drinking and, when they do drink, take a very large volume of water.

In addition to the water drunk by the animal it is also present in foods, especially fresh grass, silage and root crops, so it is not always necessary to provide drinking water. However, fresh water should always be available because animals that are ill reduce their dry matter intake and will then require water, especially if they are suffering from diarrhoea – in which large amounts of water are lost in the faeces. In addition to ingested water, the metabolism of substrates in the body yields water, which provides a small but significant addition to the body's supply.

Water intake is depressed if water is difficult to obtain; a small degree of restriction is usually not harmful, but in many areas of the world water is not expensive and is usually offered *ad libitum*. Prediction of water requirements and intake has not, therefore, received as much attention as has the prediction of food intake.

Water intake is controlled by the hypothalamus, and an increase in the tonicity of cerebrospinal fluid is an important stimulus to drinking. The control of water intake is a complex subject dealt with in detail by Rolls and Rolls (1982), while Olsson and McKinley (1980) covered the subject for ruminants.

There is clearly a specific appetite for water and it is generally assumed that the animal takes in as much water as is needed to meet its requirements, although excessive water consumption can be induced under some conditions, such as the schedule-induced polydipsia seen in pigs. There is relatively little cost to the animal if it drinks too much water.

Poultry

Bailey (1999) has reviewed the control of water intake by poultry, factors affecting water intake and the effects of water restriction.

Chickens drink up to 40 times per day, but make fewer visits to drinkers as they mature. It is likely that poultry drink more than is strictly required because, when the water intake of chickens was restricted by adulteration with quinine to about 75% of normal, there was no effect on food intake and only a small reduction in growth rate.

Pigs

Brooks and Carpenter (1990) carefully considered the theoretical and practical aspects of the various requirements for water by growing and finishing pigs and the routes by which the animal gains and loses water, including a complete water balance sheet for a pig. They particularly considered wastage of water as introducing important errors in assessment of the true water requirements of pigs. Huge variation has been found between water intakes by pigs in different studies, and much of this may be due to inaccurate water meters. Also, there can be considerable wastage, especially if there are many pigs per drinker and/or if fighting occurs.

Flow rate is important in determining how much pigs drink. A low rate of delivery necessitates long drinking periods, and pigs seem unwilling to drink for more than a few seconds at a time. Barber *et al.* (1989) found pigs to have a significantly lower food intake during the 3 weeks following weaning from drinkers with a flow rate of 175 ml/min compared with that from those providing 450 ml/min.

Lactating sows have a very high requirement for water. They might be expected to drink up to 20 l/day, and even more in hot weather.

Cattle

Lactating cows fed a fixed amount of concentrates and silage *ad libitum* took about four drinks/day, even though silage was taken in 15 meals/day and concentrates in a further two to four allocations per day (J.M. Forbes, C.L. Johnson and D.A. Jackson, unpublished results). Figure 2.2 shows the feeding and drinking pattern over a 24 h period for a cow yielding 25 kg of milk/day and eating 14 kg of silage and 5.5 kg of concentrate DM. There were four drinks, ranging in size from 1–13 l, all in association with meals of silage.

As in other species, most drinks occur in close association with eating, even though many meals (of silage) are not accompanied by drinking. Figure 13.6 shows the distribution of the frequencies of different intervals between meals and subsequent drinks and between drinks and subsequent meals (Forbes *et al.*, 1991). Fifty-three per cent of drinks occurred within 10 min of eating.

Environmental temperature

Water intake by poultry is positively correlated with environmental temperature, but the initial increase that accompanies a sudden rise in temperature is not

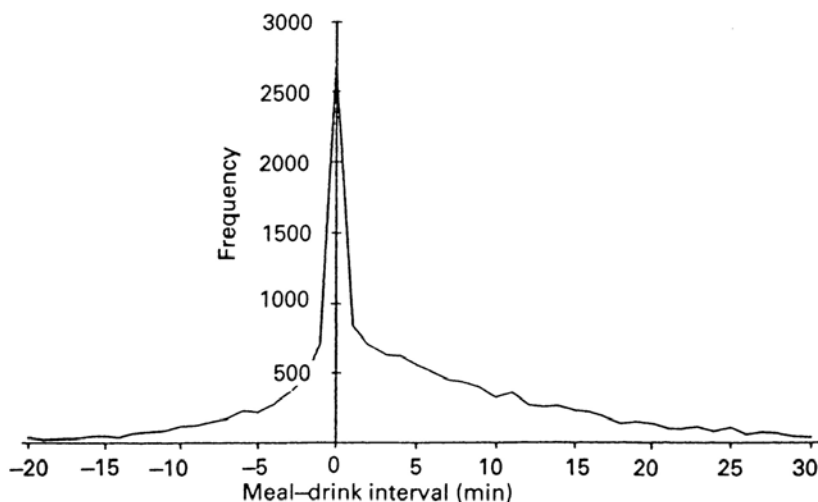


Fig. 13.6. Frequency distribution of drink-meal and meal-drink intervals in lactating dairy cows fed silage ad libitum (from Forbes *et al.*, 1991).

sustained as the birds become acclimatized. Cool water is preferred to warm water, even in a cool environment.

In pigs, there is a rise in the ratio of water intake to dry matter intake between 20 and 30°C from 2.7 to 4.3 kg/kg DM (Close *et al.*, 1971). Above 25°C this is mainly due to the decrease in food intake rather than to an increase in water intake. In cold weather, if the temperature of drinking water is warmer than that of the environment then pigs drink more while, in hot weather, they drink more if the water is cold.

Above 0°C there is a positive relationship between environmental temperature and water intake in cattle (Winchester and Morris, 1956). Below freezing, however, the water intake of lactating cows increases, probably due to the increased metabolic rate. Kadzerea *et al.* (2002) have reviewed the effects of heat stress on water intake by cattle and quote the following equation for lactating Holstein cows:

$$WI = 15.99 + 1.58DMI + 0.90MY + 0.05SODIN + 1.20 TMIN \quad (13.1)$$

where WI is water intake in l/day, DMI is total DM intake in kg/day, MY is milk production in kg/day and TMIN is the weekly mean minimum temperature in degrees Celsius; SODIN is sodium intake in grams/day (Murphy *et al.*, 1982). Note that if milk yield is omitted then the regression coefficient for DM intake becomes much larger and in line with other results, because of the high degree of correlation between milk yield and food intake.

Provision of cool water encourages a higher water intake by cattle in very hot environmental conditions. Sheep also drink more as temperatures increase but, like cattle, also increase water intake/unit of DM eaten when environmental temperatures fall below about 0°C (Forbes, 1968c).

Dry matter intake

The greater the dry matter intake, the greater the urinary excretion and the requirement for water. In addition, heat production is increased by increased food intake, which leads to greater evaporative heat loss and thus to greater water intake.

Water intake by poultry increases with increasing food intake; the best single predictor of water intake is dry matter intake, and drinking usually follows meals (Hill *et al.*, 1979). Fasted broilers drink about one-third of their normal daily intake of water.

There are two phases of drinking in growing pigs, one of which is closely associated with eating, the amount of water being about 89% of the weight of food eaten, while the other is drinking between meals, which is fairly constant at 2.2 l/day. The total weight of food and water intake comes to close to 12% of body weight/day in each case, and it might be speculated that there is a weight or volume limit to intake.

Restricting the food allowance for pigs to half the usual amount or complete fasting increases the volume of water consumed by up to sixfold. As discussed in Chapter 2, chronic hunger leads to oral activities such as bar chewing, and it is likely that the polydipsia of underfeeding is such a displacement activity. Care is needed before accepting very high water intakes as being valid, as much of that apparently drunk might be wasted. For example, stalled sows have been noted to stand with their snouts pressing nipple drinkers for up to 1 h/day but without drinking.

Water intake increases in direct proportion to the intake of food DM eaten by cows. Under UK conditions with cows fed grass silage, the following equation was one of several ridge regressions that gave a good fit ($R^2 = 0.89$) to data (Dewhurst *et al.*, 1998b):

$$WI = -73.7 + 2.19DMI + 2.21MY - 6.9VFAPROP + 16.3pH \quad (13.2)$$

where WI is water intake (l/day), DMI is total DM intake (kg/day), MY is milk yield (kg/day), VFAPROP is VFA proportion of total fermentation acids and pH is silage pH. Note that the coefficients that are common to equation 13.1 above are not similar, highlighting the specificity of such equations to the conditions under which they were derived.

Total water intake (free water plus water in the food) is correlated with dry matter intake in sheep and goats. In observations on non-pregnant ewes of two breeds of very different type fed on silage, hay or dried grass, the relationship was:

$$TWI = 3.86 DMI - 0.99 \quad (13.3)$$

where TWI is total water intake (l/day) and DMI is DM intake (kg/day) (Forbes, 1968c).

Silanikove (1989) found a close relationship between water turnover and digestible energy intake in desert and temperate goats:

$$WT = -5.4 + 0.22 DEI \quad (13.4)$$

where WT is water turnover (ml/kg body weight/day) and DEI is digestible energy intake (kJ/kg/day). This relationship holds good for a wide range of sizes and physiological states, including lactation.

Diet composition

Increasing the salt concentration or the protein level of the diet stimulates increased water intake in all species because of the increase in urine volume necessary for the excretion of the salt or urea.

Increases in the fat, protein or potassium content of the food all lead to an increase in water intake by poultry. Water intake in pigs is also increased by protein (especially unabsorbed protein), Na, potassium (K) and by some antibiotics.

Pregnant gilts and sows given restricted amounts of food with different levels of fibre show a significant reduction in the time spent drinking and in water intake with higher-fibre foods. This suggests that some drinking is a substitute for eating and that the longer time spent eating and chewing a high-fibre food reduces the desire for further oral stimulation by drinking.

Water drinking is induced by intra-cerebroventricular infusion of hypertonic solutions in cattle but without effect on the intakes of food or NaCl. The effect of NaCl infusion is greater than that of mannitol or sucrose, despite the fact that they all cause very similar increases in osmolality of cerebrospinal fluid. When given intravenously, NaCl and mannitol have equal effects, demonstrating that there are central NaCl receptors as well as osmoreceptors in cattle.

A dried grass diet was associated with a higher intake of water per unit of dry matter by sheep than hay, presumably because of the higher ash and protein contents (Forbes, 1968c). Increasing the intake of dry matter and/or crude protein increases water intake by sheep, and the diurnal distribution of water intake is directly related to feeding times.

In summer, when other grasses are available in addition to saltbush (a salt-tolerant orache plant), sheep in Australia drink only once per day but, in autumn, only saltbush is available and they must drink twice per day. They then spend about 3 h/day walking to and from water. Where there is no saltbush, they normally drink only once every 2–3 days, and only in very hot weather do they drink every day.

Physiological state

Inadequate water intake has sometimes been thought to be the reason for the post-weaning growth check in piglets, and flavouring the water has been found to be effective in overcoming this problem in some cases, but not all.

It has also been suggested that low water intake might be a cause of low food intake and loss of weight for a few days after weaning of lambs, and ways should be sought to increase water intake, perhaps by offering it before weaning when lambs can sometimes drink considerable amounts.

Water intake increases during pregnancy in the ewe in proportion to the number of fetuses carried. In contrast to the results with goats, quoted above, Forbes (1968c) found lactation to stimulate water intake in ewes by more than the volume of water in the milk, presumably because of the increased food intake and heat production of the lactating animal (see Fig. 13.7).

Conclusions

Poultry and pigs can select a diet containing a ratio of protein to energy that is close to that providing for optimal growth. Changes in the requirements for protein during growth are accompanied by reductions in the proportion taken of the high-protein food, and animals with a higher propensity to grow or produce eggs eat more protein than those with a greater potential to deposit fat.

There is considerable evidence that animals can select between foods according to their requirements for individual amino acids, although the balance of amino acids in a food can have a profound effect on its selection.

Many minerals and vitamins have been shown to be capable of being selected, as long as the animals are able to differentiate the deficient and sufficient foods by means of sight, taste or position.

Water intake is regulated largely by the intake of food and responds to such factors as environmental temperature, pregnancy and lactation. Overconsumption of water is a common problem of intensive housing, especially when restricted feeding is practised.

Overall, therefore, it has been clearly demonstrated that appetites for essential nutrients can be developed. This depends on animals sensing their metabolic ‘well-being’ and associating this with the sensory properties of the foods on offer. The possibility of any appetites being innate seems remote, although the salt appetite of sheep seems to be very accurate, even in untrained animals.

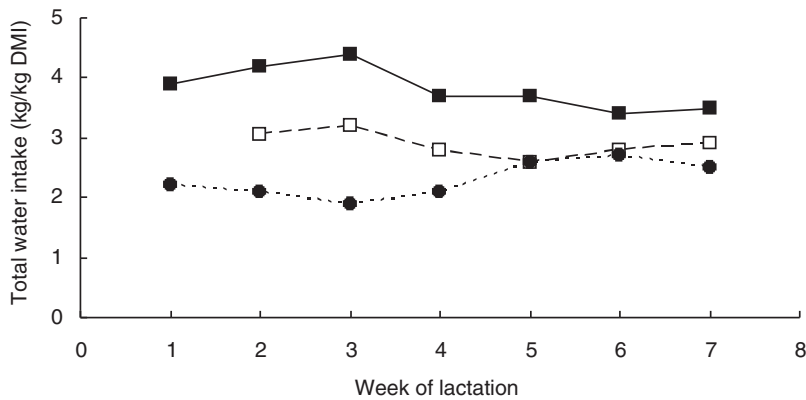


Fig. 13.7. Total water intake (free water and in food) per unit of food DM (kg/kg) by lactating (■) and non-lactating (●) ewes. □, total water intake minus water in milk (from Forbes, 1968c).

14 Silage

Conservation is necessary in much of the world where grass stops growing for part of the year due to coldness or drought. Traditionally, herbage has been made into hay, i.e. cut, left to lie in the field to dry and then stored under cover. The quality of the original grass is better retained if the drying is more rapid and one avoids rain falling on the cut grass.

Artificial grass-drying has therefore been used in rainy developed countries, but the cost of fuel for drying is very high. It is possible to preserve grass by pickling rather than by drying; grass preserved in this way is called silage and is produced by compressing the material within a day or so of cutting to exclude air and thereby encouraging the production of acids by naturally occurring anaerobic microorganisms. It is common to add acids at the time of ensiling, and the addition of a culture of particularly effective microorganisms is also now widely used. Approximately 85% of the grass conserved in the UK is in the form of silage, as the frequent rain makes hay-making a risky process.

The reason for particular interest in the voluntary intake of silage is that the voluntary intake of ensiled forage has been reported to be, on average, 27% (range 1–64%) lower than that of the corresponding fresh herbage, with sheep being more sensitive than cattle to ensiling. With partially fermented silages, the depression in intake is much less, suggesting that products of fermentation – particularly nitrogenous products – are largely responsible. However, grass is usually more mature when cut for silage than when grazed, and thus less digestible, which will result in lower intakes (see Chapter 11).

Even where intakes of grass silage are similar to intakes of the parent grass, milk yield and protein production are still significantly lower, the efficiency of utilization being reduced on average by 13% for dairy cows and by about 25% in growing heifers and finishing beef cattle; efficiency of utilization of energy in forages has been implicated in the control of food intake by ruminants (see Chapter 9).

In many parts of the world, the crop predominantly used for silage is maize. Cutting takes place before the cobs mature, and maize silage is characteristically lower in nitrogen and higher in soluble carbohydrate than grass silage. Maize silage has been made in increasing quantities in northern Europe in recent years, as varieties have been developed suitable for growing at higher latitudes. Many other plant materials can be made into silage, and some of these will be mentioned below.

Although the yield of grass for conservation is increased by cutting later in the summer, this is obtained at the expense of decreased digestibility. It is better to cut early and then take a second cut of the regrowth. The optimum strategy depends on the class of livestock to be fed on the conserved forage.

The products that depress intake appear to include ammonia and volatile fatty acids, particularly acetic acid (Tayler and Wilkins, 1976). Partial neutralization sometimes increases voluntary intake while addition of formic acid, which has sometimes been used as a preservative, depresses intake. Thomas and Chamberlain (1983) quote correlations between voluntary intake and several chemical components but point out that there are also intercorrelations between the various components: acid concentration and ammonia nitrogen are negatively related to intake, while the ratio of lactic acid:total acid is positively related. Poor ensilage conditions, which encourage a clostridial type of fermentation, yield a silage with particularly low intake characteristics.

Books by McDonald *et al.* (1991) and Wilkinson (2005) cover the basic and applied aspects of silage, respectively.

Dry Matter Content

In general there is a positive relationship between the DM content of silage and its intake by ruminants. In the USA it has been clearly shown that intake is positively related to dry matter content for lucerne and maize silages. Overnight wetting of a silage depresses its intake by sheep, but the addition of water just before offering silage to young cattle did not affect daily intake compared with unwetted silage; it is likely that water outside plant cells is absorbed very quickly from the rumen and does not contribute to the bulk of the food, whereas the volume of intracellular water does, until it is released.

Wilting

It follows that intake can be increased by wilting the herbage before ensilage, although there have been several instances of an accompanying drop in the yield of fat-corrected milk, possibly because of adverse effects on fermentation. Castle (1983) concluded that: ‘.. it is extremely doubtful whether there will be consistent benefits [of wilting] in terms of animal production’. This is in contrast to the conclusion of Osbourn (1967) that: ‘... wilting must continue to be the only method available in practice to reduce this disadvantage of ensilage as a method of conservation’.

It is likely that grass for silage is cut nowadays at an earlier stage of maturity than formerly, and that the effects of wilting are greater with silage of lower digestibility, cut later in the summer. The use of additives now improves the control of fermentation of wet silages (see below), and wilting is recommended more to reduce the volume of effluent than to improve the nutritive value of the silage.

An extreme form of wilting has been investigated by R. Simpson and H. Dove at the University of Melbourne, Australia (personal communication). Pasture is sprayed with half the normal level of glyphosate (a herbicide) 1 or 2 weeks before flowering; this stops growth but does not completely kill the grass, and the soluble carbohydrate content remains elevated for at least 60 days while that of untreated grass declines after flowering. Intake and performance of animals fed this grass are greatly increased compared with those on unwilted material.

Products of Fermentation

The silage-making process ferments soluble carbohydrates to produce organic acids, predominantly lactic, but also significant amounts of acetic acid, and many nitrogenous compounds such as amines. These substances, and those additives that are incorporated to improve the silage, have been under suspicion as the cause of the lower intake of silage, compared with hay or grass, and have been infused into the rumen in a number of experiments.

Silage juice

The importance of fermentation in limiting the intake of silage is thrown into doubt by results of an experiment in which ryegrass was either not fermented, or fermented for 4 or 12 days (Offer, 1997). Juice was extracted from these materials and solutions of dl-lactic acid were prepared to have the same neutralizing values (NV) as the silage juices. When the dried residues were offered to sheep, there was no effect on voluntary intake. When they were offered unmolassed sugarbeet nuts with one of the juices or lactic acid solutions added (1.5 l/kg), there were no differences in intake despite large differences in pH, lactic acid concentration, NV and osmolality.

However, short-term DM intake (during the 3 h following the offering of food) decreased with increasing NV, being significantly lower for the highest NV than for the others but with no difference between lactic acid and silage juice. While this suggests effects on short-term feedback mechanisms or palatability, it will be necessary to conduct studies of any associations that might be learned between the sensory and metabolic properties of different silages.

Offer (2000) conducted a further series of experiments with growing sheep to study what factors might limit silage intake. Silage was made from ryegrass with either 2.5 l/t (LF) or 5.5 l/t (HF) of an ammonium tetraformate additive. Intake of HF was significantly greater than of LF. The two silages then had their

juice extracted and there was no significant difference between intakes of the dried materials. In a third experiment, juices from the two silages were added to unmolassed sugarbeet nuts (SBN) pre-feeding or administered directly into the rumen. The only treatment to significantly depress intake was the one in which juice from LF was infused into the rumen, leading to the conclusion that it was substances in the liquid and volatile phases – rather than in the solid phase – that were responsible for the low intake, but that it was not via an effect on the sensory properties of the silage. In any case, any effects on taste or smell would not be expected to be lasting, unless they were associated with internal discomfort sufficient to generate a conditioned aversion (see Chapter 6).

A comparison has been made of the effects of rapid intra-ruminal infusion of silage juice with a mixture containing the same volatile fatty acids, lactate, soluble carbohydrate, ammonia and nitrate, and was of the same pH and osmolality (Clancy *et al.*, 1977). The depression of hay intake with this mixture was only 40% of the depression with juice, so that other factors such as amines must have contributed to the depressing effects of silage juice.

Lactic acid

Lactic acid is present in silage at concentrations of up to 20% of the organic matter, as well as being a product of ruminal fermentation. The evidence for lactate affecting voluntary intake is somewhat controversial, as 0.16 mol of sodium lactate infused intra-ruminally to goats over 5 h did not affect intake (de Jong, 1981), whereas intra-ruminal infusions of 35 mmol during each of about ten meals/day reduced food intake in goats by almost half, but had a smaller effect in sheep. Compared with VFAs, infusion of lactate had a prolonged after-effect on intake.

When a high physiological concentration of lactic acid was infused into the duodenum of sheep, the intake of concentrates was reduced (Bueno, 1975), probably related to the reduction in stomach motility or to the involvement in propionate metabolic pathways.

Cows can ingest more than 1 kg/day of lactic acid in silage, but this amount added to hay does not depress intake to the same level as that of silage. As stated earlier, it appears that no single constituent of silage is responsible for its low intake, but it is possible that the additive effects of a number of substances might be important.

Nitrogenous components

Grass silage is often found to be eaten in lower quantities by cows than grass hay or maize silage. During the ensiling process, some of the protein is degraded to non-protein nitrogenous compounds while some is rendered indigestible, particularly if overheating has occurred in the silo. It may be, therefore, that some silages are protein-deficient even though their N content may make them appear adequate. There are two ways of overcoming the problem: making

better silage and using supplementary feeding to balance the protein intake. The former implies cutting the forage at a relatively immature stage, while the latter is covered in the section on supplementary feeding below. Chopping and the use of additives have proved very useful, while in northern Europe increasing attention is being paid to ensiling maize.

Infusing the rumen with nitrogenous constituents of maize silage extracts depresses intake of hay. Complex changes occur to nitrogen (N)-containing compounds in forages during ensiling, including the release of N-compounds into the fluid medium where a significant proportion can be lost rapidly from the rumen by onward flow of liquid. The efficiency of utilization of N compounds is generally higher in maize silage than in grass or legume silages. Givens and Rulquin (2004) state that:

New research needs to be aimed at enhancing the utilisation of N in the rumen through a better understanding of N/carbohydrate relationships and the ability of forages to supply degraded carbohydrate. Also more emphasis is needed on understanding of the potentially different role of the different N fractions that exist in silages.

Ammonia

Intake of silage is inversely related to the content of ammonia-N (expressed as a proportion of total N), but infusion of ammonium salts into the rumen has to be at rates that are toxic in order to depress intake significantly. Urea enters the rumen in the saliva in large quantities, and much of this is metabolized to ammonia; urea infusion into the rumen of goats during spontaneous meals depressed intake but was less effective, mole for mole, than ammonium salts (Conrad *et al.*, 1977).

Biogenic amines

The addition of biogenic amines¹ to silage depresses intake, but this effect decreases after a few days (VanOs *et al.*, 1996), suggesting that animals learn that the unpleasant taste and smell are not associated with long-term discomfort. In a detailed experiment, Dawson and Mayne (1995) infused into the rumen or added to the squeezed silage diet several amines (putrescine, cadaverine, gamma amino butyric acid (GABA), putrescine + cadaverine + GABA, 2 g/kg DM) or expressed juice from grass silage, or water into the rumen of cattle for 1 week per treatment. There was no significant effect of any of the treatments on silage intake. They later infused putrescine or gamma amino butyric acid (at 6 g/kg DM) into the rumen of cattle and studied the effects on the intake of grass silage containing three levels of lactic acid (Dawson and Mayne, 1997). The rate of infusion was varied throughout the day in an attempt to match the amount infused with the amount the animal would have consumed if the treatment had been added to the diet. Neither

¹ Naturally occurring amines derived by enzymatic decarboxylation of the natural amino acids, e.g. histamine, serotonin, adrenaline.

putrescine nor GABA significantly affected intake or feeding behaviour. It seems unlikely, then, that these biogenic amines found in silage are responsible for its low intake.

One of the biogenic amines, histamine, is present in some silages in amounts that might depress ruminal motility, but when given at 1 g/day to sheep it does not affect their silage intake. In the presence of formic acid, however, it is thought that sufficient histamine might sometimes be absorbed to cause a reduction in silage intake. Direct infusion of histamine into the abomasum causes a reduction in intake, but the increase in respiration rate indicated that it had a systemic effect, and it can be concluded that it would require a very rapid passage of dietary formate or histamine into the abomasum to obtain the low intake of silage observed in this experiment.

Protein

Although the N content of grass silage implies an adequate protein content, some of the N is as non-protein N compounds while some is in proteins rendered indigestible during ensilage, particularly if overheating has occurred. The provision of a protein source that is largely undegraded in the rumen, but which yields amino acids in the intestines, has been proposed to alleviate this problem. Once again, the results have been variable, Sanderson *et al.* (1992) finding that a fish meal supplement increased silage intake by growing steers, but that the increase was only as great as the increase in live weight. For growing calves, soybean meal did not affect silage intake or performance relative to fish meal, while maize gluten did not affect production in one experiment but did in another (Steen, 1992).

Low N status is not always the reason for low intake, however, as duodenal infusion of casein in sheep offered grass silage *ad libitum* has improved N retention with no effect on intake. Similarly, supplementation of grass silage for young cattle with isonitrogenous amounts of degradable (63 g groundnut meal/kg DM) or undegradable (50 g fish meal/kg DM) protein resulted in no change in silage intake but an improvement in digestibility and in the N retention of the animals.

Sensory factors

Attention has turned to the possibility that the peculiar composition of silage influences its acceptability to ruminants. Buchanan-Smith (1990) fed oesophageal-fistulated sheep on lucerne but then fasted them for 5 h before offering silage with added solutions, with the oesophageal plugs removed to prevent the test foods entering the rumen. Acetate added alone depressed intake, while a mixture of two amines and GABA stimulated intake at low levels but had no effect at higher levels.

The author suggested that the intake of silage with a high acetic content is limited by palatability. However, the animals were sham-fed both during training and experiments so that they had no chance to learn anything about associations

between taste and metabolic properties of the various test foods. It will be necessary to train animals to make such associations before we can draw firm conclusions about the mechanisms responsible for low intakes of silage (see Chapter 6).

Silage Additives

One disadvantage of ensilage is that the product is likely to be variable due to lack of control of the microbial fermentation. Of the approaches to improvement of the situation, two have involved addition of materials to the grass: acids and inoculants.

Acids

Mineral acids were the first to be used, principally hydrochloric and sulphuric. They prevent the growth of harmful bacteria and reduce protein breakdown. Later, formic acid became popular but is difficult to handle as it is volatile. It reduces the production of volatile fatty acids and ammonia by acting as a sterilizing agent. Although it has been associated with decreased voluntary intakes, this can be avoided by supplementation with a high-protein concentrate. Propionic acid can control silage fermentation and increases the intake of maize silage, but it is more expensive than formic and is not likely to replace it.

Acetic acid has been tested, but with little advantage. Formalin is a useful additive for lucerne but not for grass, and it depressed intake when used at greater than 10 l/t.

Because of the relationships between intake and pH, partial neutralization with bicarbonate before feeding has been investigated and it is sometimes, but not always, effective in stimulating intake, especially with calves. In both cattle and sheep it increases water intake.

An alternative way of using acids is as a mixture of salts of carboxylic acids, which is applied at sufficiently high rates to grass before ensilage that fermentation is largely prevented. This results in higher soluble carbohydrate content compared with conventionally made silage, which enhances microbial activity in the rumen when the material is fed and results in higher levels of intake. The use of such carboxylic acid salts gave a milk yield response in cows equivalent to an extra 2.5 kg concentrates/day (Mayne, 1992).

Results, in terms of improved silage intake and milk production, have been variable, as would be expected when the quality of the herbage to which the addition was made is so variable.

Inoculants

Most inoculants use *Lactobacillus plantarum* and, again, quite variable results have been obtained, but they are attractive in use because of their safety of

application. Sometimes their use gives higher intakes than some acid additives, even when the chemical composition of the conserved grass is similar, while in other cases organic acids are better. In a comparison of formic acid, sulphuric acid and a bacterial inoculation as additives in silage making, Mayne (1993) found a significant increase in intake (12%) due to formic acid for first regrowth but a smaller effect of inoculant (4.6%). Sulphuric acid tended to reduce intake of first regrowth, and none of the treatments had significant effects with a second regrowth of grass.

Lack of soluble carbohydrates

With the fermentation of soluble carbohydrates, 10% of grass DM disappears during ensilage. This is equivalent to half of the potential to generate ATP in the rumen and results in a very poor energy supply for microbial growth, even though there is plenty of energy for the animal itself. Microbial growth and activity are therefore restricted, with the consequence that rates of fermentation and particle breakdown of silage are lower than for materials with higher contents of soluble carbohydrates. The problem is, to some extent, overcome by supplying readily fermentable energy to the rumen, i.e. supplementation with concentrates.

Physical Limitation of Silage Intake

Another possible reason for low silage intake is physical limitation, given the slower rate of ruminal breakdown relative to hay. However, it has been noted that ruminal dry and wet matter contents were less in heifers fed on silage than on hay, and it was concluded that silage intake was not restricted by ruminal capacity. The total contractile activity of the rumen and its organic matter content were significantly greater for hay (at equal levels of feeding to cattle) than silage, and more time was spent ruminating on hay when each was fed once per day (Thiago *et al.*, 1992). Whereas hay offered once per day at a restricted level was all eaten in 2 h after having been offered, an equivalent amount of silage took about 10 h. Perhaps, metabolic discomfort accompanies the slow rate of fermentation of silage in the rumen and the animal learns to eat less and/or more slowly to avoid this.

Intake of silage does not always appear to be positively related to digestibility, due to both a small range of digestibilities observed in some comparisons and confounding with other factors, but with a wider range of digestibilities there has been a positive correlation between digestibility and intake. The demonstration that water-filled bags in the rumen (16 l) depressed the intake of a high-quality silage by 16% in dry cows confirms that physical fill of the rumen is important, and the fact that reducing the particle size by chopping or mincing increased voluntary intake by cows and beef cattle supports this.

It has been concluded that silage particles stay in the rumen for longer than those of hay, and there is more pseudo-rumination in silage-fed sheep and

cattle than in those offered hay, suggesting that the slow breakdown of fibres is making it more difficult for the animals to regurgitate. In addition to the possibility that rate of digestion is slow with silages, there is evidence that ruminal motility is depressed; infusion of lucerne silage juice intra-uminally depressed ruminal motility and rate of eating (Smith and Clapperton, 1981). Thus, chemicals in the silage, particularly amines, might act through physical mechanisms.

Degradation rate

From a collation of studies on 136 silages incubated in nylon bags in the rumen of steers, whose intakes had previously been measured, it has been found that, although degradation rate of silages is quite well correlated with digestibility, the relationship with intake is poor (Dawson and Steen, 2000). This puts in doubt the role of degradation characteristics of DM, fibre and N in the rumen on silage intake. Most particle size reduction is achieved by mastication, and degradation in the rumen only accounts for some 20% of particle size reduction.

Silage intake has been found to be related to the time spent chewing. Wilted silage and hay are more brittle and need less chewing during eating, allowing more time for rumination, which may be a critical factor. NDF is a good indicator of the amount of chewing required but, in the study of Dawson and Steen, it was no more closely correlated with intake than several other factors, including soluble N – ammonia N, ADF and lignin.

Chop length

The intake of silage can be increased by chopping the grass at harvest, which improves fermentation in the silo and increases the rate of passage through the digestive tract. In nine comparisons with sheep, mean intake was increased by 56% for silages harvested with a precision-chop machine rather than with a simple flail harvester. This was more effective than chopping just before feeding (McDonald *et al.*, 1991). Young beef cattle ate 66% more silage made from grass cut to 8 mm at harvest compared with that cut to 33 mm, and the finely chopped material was also more digestible.

The intake of silage made from perennial ryegrass and the yield of milk by cows increase as chop length decreases; eating and ruminating times reduce as chop length decreases, but the mean retention time of food particles in the digestive tract is not affected. Occasionally, rumination of finely chopped silage is reduced to the extent that it increases the risk of acidosis because of insufficient saliva production to provide adequate buffering of ruminal fluid. Offering a small amount of unchopped forage, even of poor quality, will usually correct the problem.

Deswysen *et al.* (1978) compared grass silage chopped to either 53 or 18 mm before ensilage or to 18 mm just before feeding. Sheep offered the long

silage had lower intakes and spent less time ruminating. Pseudo-rumination was significantly increased on the long silage, suggesting difficulty in regurgitating the long, slippery strands. There were no differences between silages chopped to 18 mm either at ensilage or just before feeding. Cattle prefer unchopped to chopped silage, and this may be because they get a larger amount of food per mouthful.

The physical effort required by the cow to pull silage directly from the clamp reduces the rate of eating compared with the same silage cut and fed in a trough, and this could be a further physical factor limiting silage intake under some conditions.

Maize Silage

Maize silage has lower levels of acid than grass silage, typically, while having a similar pH. Lactic acid, in particular, is about one-half and acetic perhaps two-thirds of that for grass silage. Maize silage has about 200 g/kg DM of starch, whereas grass silage has very little; as discussed above, a supply of rapidly fermentable carbohydrate is essential for normal microbial function in the rumen.

Because of the low protein content of maize silage, it is better to feed it with grass silage and/or a protein supplement. Mineral and vitamin supplementation must be adequate due to low levels of Ca, P and vitamin E in maize silage. The high starch content can cause acidosis, especially if fed with starchy supplements such as cereals. For these reasons, maize silage should not exceed about 75% of the total DM intake.

Compared with grass silage, cows fed maize silage, or a mixture, ate more DM and produced more milk. Even when high-quality grass silage was available, offering maize silage in addition improved the performance of dairy cows. Offering dairy cows one-third of the forage as maize silage, brewers' grains or fodder beet increased DM intake by about 1 kg/day compared with grass silage alone (Phipps *et al.*, 1993). In a comparison of: (i) maize silage only; (ii) maize silage and lucerne or maize silage; and (iii) lucerne and wheat, intake of digestible organic matter was highest for maize silage alone, even though the digestibility of this was the lowest of the three diets.

The question of whether maize should be cut at an early stage for silage making – in order to acquire high levels of soluble carbohydrates, or later – to achieve a higher yield of DM, was examined by Phipps *et al.* (2000). Silages were made from maize cut at different stages during September and October to give DM contents of 226, 290, 302 and 390 g/kg. These were mixed 3 parts:1 with a high-quality, well-fermented grass silage that was also fed on its own, and the five diets were given to cows during the first 20 weeks of lactation; 8.7 kg of dairy concentrate were given daily. The results (see Fig. 14.1) show that, even compared with good grass silage, inclusion of maize silage will increase forage intake, with an optimum of around 300 g DM/kg.

The results suggest that farmers in marginal areas should consider using maize silage in dairy cow diets and should avoid the production of mature maize silage, since when silage DM content approached 400 g/kg there was a significant

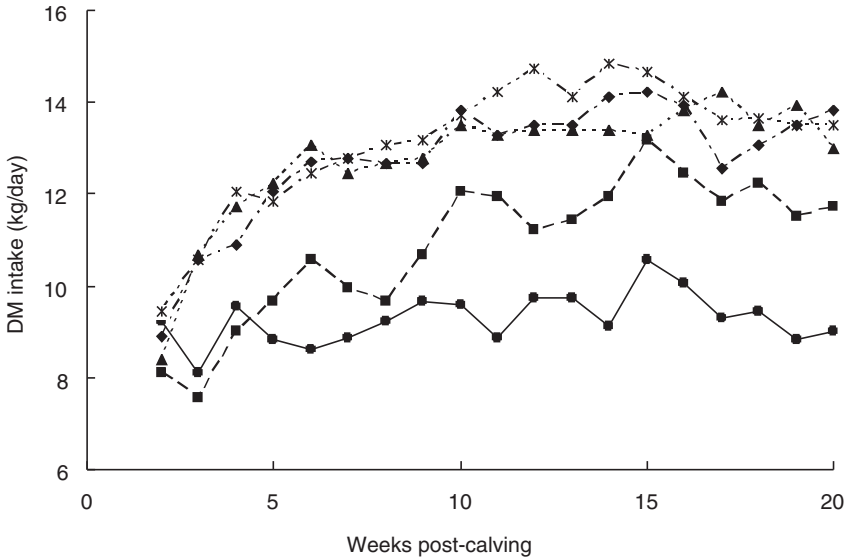


Fig. 14.1. Forage dry matter (DM) intake (kg/day) for cows receiving either grass silage as the sole forage (●) or a forage mixture containing maize and grass silage in a 3:1 DM ratio with maize silage DM contents of 226 (■), 290 (x), 302 (▲) and 390 (◆) g DM/kg (from Phipps *et al.*, 2000).

decline in yield of milk and protein, even though silage intake was not depressed at these high DM contents. Of course, there were many other differences between the four maize silages in addition to DM, as they were harvested at different times of the late summer and early autumn and at different stages of maturity, so care needs to be taken with the interpretation of these results.

Silage is the predominant forage for beef cattle in northern Europe, and the question of grass versus maize arises, as it does for dairy cows. In a comparison of grass silage, maize silage, 1/3 grass:2/3 maize and 1/3 maize:2/3 grass silages for cattle growing from 424–560 kg (Juniper *et al.*, 2005), DM intake was increased linearly as the proportion of maize silage increased, and growth rate increased in parallel. Note that 2 kg of concentrate supplement was given to each animal daily, formulated to give similar CP intakes for each silage treatment, i.e. the low CP of the maize silage was compensated for.

Choice feeding of silages

The optimum ratio of grass silage:maize silage for ruminant animals of different types could be studied by choice feeding. Heifers offered a choice between grass and maize silages eat about 40:60 grass:maize, although this varies widely between animals. Intakes and milk yields have been reported to be significantly higher in heifers offered the choice or just maize silage compared with those on grass silage alone.

Further work with cows (Weller and Phipps, 1985) included the additional treatment of a 1:2 mixture of grass:maize silage, and there was no maize silage-only treatment. For half of the cows, the grass silage was of good quality, for the other half it was of poor quality. Significantly more DM was eaten of the mixture compared with just grass silage. The ratio of grass:maize silage in the free-choice treatments ranged from 30:70–77:23 for poor-quality grass silage and from 48:52–81:19 when the grass silage was of good quality, i.e. better grass silage gave a higher preference. Even with high-quality grass silage, offering maize silage improved performance. Presumably, a beneficial effect of the maize silage (soluble carbohydrates?) was recognized by the cows and they learned that they felt most 'metabolically comfortable' when eating a 4:1 ratio of grass:maize silages.

Dairy cows given free access to hay, maize silage (MS) and grass silage (GS) obtained the most energy from hay during the light phase, followed by MS and GS (Senn *et al.*, 1995). However, during the dark phase, most energy was derived from GS, and hay contributed the least. It is not clear why there is this difference in choice between day and night, although a detailed study of the nutrients supplied by each of the three foods, and the changing requirements of the animals during daytime and night-time, might yield some tentative explanation.

Other Silages

Clover is a good source of protein for ruminants, and there have been several studies of clover silage intake. A mixture of grass and white clover silages had a high intake by dairy cows (15.2 kg DM/cow/day), but there were unusually high substitution rates for supplementation with concentrates, presumably because clover is more rapidly digested than grass, i.e. similar to concentrates. For silages with similar digestibility, red clover silage gives higher food intake and milk yield by cows than ryegrass silage when fed with 7 kg DM/day of a cereal/soybean supplement.

When lucerne was fed to sheep as hay or silage, there was no difference in intake and no difference in response to intra-ruminal introduction of food (Etheridge *et al.*, 1992). Thus, any benefits of clover silage are not very large and it is probably better to ensile a clover/grass mixture than just clover.

Concentrate Supplementation of Silage

Since silage cannot usually be eaten in sufficient amounts to satisfy the nutrient requirements for rapid growth or high milk yield, some supplementary food is normally provided. Supplementation normally depresses forage intake and it is usually observed that the higher the level of supplementation the greater the depressing effect of an additional allocation on forage intake. The reduction in forage DM intake/unit of concentrate DM supplement is called the substitution rate (see Chapter 11), and it is generally concluded that the substitution rate

increases as the level of concentrate allowance rises. For example, increasing the allowance of concentrates from 3 to 6 kg had the greater effect on digestible energy intake and milk production, while the step from 6 to 9 kg/day had the bigger effect on silage intake (Sutton *et al.*, 1992; Fig. 14.2).

In a particularly comprehensive study, Faverdin *et al.* (1991) (see Fig. 11.8) also found substitution rates to increase with increasing levels of supplementation. The average substitution rates with maize silage, grass silage and hay were 0.70, 0.53 and 0.44, respectively.

A substitution rate of 0.51 for barley supplementation of grass silage for Ayrshire cows has been found and, if the supplement was given frequently in small amounts, a more even pattern of fermentation was seen in the rumen, but this did not affect the substitution rate (Gill and Castle, 1983). Supplementation with dried grass cubes has given a substitution rate of 0.36, i.e. a smaller reduction in silage intake per unit of supplement compared with barley; molassed beet pulp, which also has a slower pattern of nutrient release than barley, gives a substitution of 0.4. Although barley supplementation depresses silage intake more than that of dried grass, the resulting level of production is often higher because of the higher digestibility of the barley compared with typical dried grasses.

Bulky supplements depress silage intake to a greater extent than do cereals or dried grass. For example, hay offered to cows depressed silage intake by 0.84 kg/kg, but that still provides a useful increase in total DM intake. Similarly, lactating cows ate significantly more when both hay and silage were offered than when either were offered alone.

It is usually the intention to feed silage *ad libitum*, but in practice this is not always achieved, either because cows wait for fresh silage to be cut down from the face of the silo rather than pulling it off themselves or because they are purposely restricted to avoid wastage. When silage intake is reduced because of restricted access, increasing the level of supplementation does not reduce silage intake.

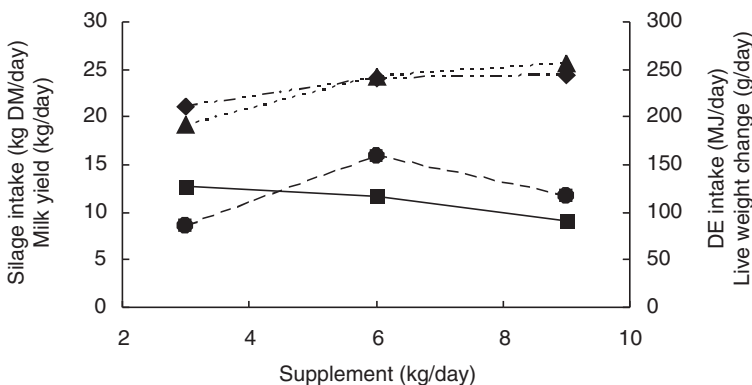


Fig. 14.2. Silage intake (■), milk yield (▲), DE intake (◆) and live weight change (●) of Holstein Friesian cows with three levels of concentrate allowance (from Sutton *et al.*, 1992).

Carbohydrate supplementation

As outlined above, one limiting factor to intake of grass silage is lack of soluble carbohydrates. This suggests that concentrate supplements should be high in readily fermentable carbohydrates; however, these may result in a reduced rate of cellulose digestion and therefore have a greater depressing effect on silage intake than might otherwise be predicted. It has been suggested that giving supplements in small amounts spread over the day would avoid these effects on cellulose digestion. In addition, supplements based on slowly digested materials might allow a higher intake of forage, and this has proved to be the case (Jackson *et al.*, 1991).

Protein supplementation

It has been found that less N is retained by cattle when silage is fed than when hay is fed, and this was originally attributed to the lower voluntary intake of silage. However, recent experiments have revealed that supplements providing greater amounts of protein result in smaller depressions of silage intake. The lower the N content of silage, the greater the beneficial effects of N supplements on intake (McDonald *et al.*, 1991). A supplement of dried lucerne was better in this respect than dried grass, oilseed meals did not affect silage intake at all and soybean meal resulted in an increase in the voluntary intake of silage in some cases. In practice, the provision of 'balancer' cubes high in protein and low in soluble carbohydrate appears to be of considerable benefit.

As well as providing N for the ruminal microorganisms, the diet should also provide sufficient protein that escapes degradation in the rumen (UDP or 'bypass' protein) to ensure that those amino acids that are not produced in sufficient quantities by the microorganisms are available to the host animal. Fish meal is a high-protein material which largely escapes rumen fermentation and has been a valuable, but expensive, ingredient in dairy cow supplements. Its use is not currently permitted in ruminant diets in Europe because of fears concerning feeding products of animal origin to herbivores arising from the BSE crisis.

Proteins of plant origin can also provide an appropriate supply of UDP as well as RDP. Inclusion of soybean meal in the supplement has resulted in an increase in the voluntary intake of silage in some cases. The extent to which the supplement needs to provide soluble carbohydrate and the need for additional protein vary with many factors – especially silage composition – and commercial concentrate supplements for dairy cows are now available tailored to the characteristics of the individual silage.

Supplementary protein can be provided by leguminous trees and shrubs, such as leucaena, particularly useful in arid countries. Supplements of 4 or 8 kg fresh weight of leucaena increased intake of hay by lactating cows from 7.8 to 9.3 and 10.4 kg/day (Muinga *et al.*, 1992); live weight loss was reduced and milk yield increased.

Pattern of supplementation

In a comparison of patterns of allocation of concentrates for silage-fed dairy cows, Taylor and Leaver (1984) observed that feeding at a flat rate of 9 kg/day was accompanied initially by a small increase, followed by a progressive decline in silage intake as lactation progressed; feeding concentrates according to yield gave a similar pattern of silage intake over lactation. On the other hand, giving the same total amount of concentrates but reducing from 11 to 7 kg/day as lactation progressed resulted in a steady increase in silage intake.

Feeding behaviour on supplemented silage

The hypothesis that cows eating a 'non-limiting' food (high concentrate, HC) have longer inter-meal intervals and more variable meal sizes than similar animals given a diet whose intake was likely to be limited by the physical capacity of the digestive tract (high silage, HS) was tested by Tolkamp *et al.* (2002), using the lognormal procedure described in Chapter 2 to determine inter-meal intervals. It was found that the inter-meal criterion was similar for HC (28.0 min) and HS (23.8 min), as was the number of meals (6.4 versus 6.7/24 h), i.e. cows on both treatments showed very similar meal patterns, contrary to the expectations of the hypothesis. Note, however, that because of the much lower DM content of HS, the meals were smaller and had a slower rate of eating of DM than for HC.

These results should not be taken to mean that intake of silage is limited physically, but rather that cows manage their daily intake by means other than inter-meal interval. These authors conclude that detailed studies of feeding behaviour are of little direct help in improving our understanding of what physiological mechanisms underlie the control of voluntary food intake, including that of silage, on a longer timescale.

Acidogenicity of supplements

The effect of supplementary foods of different acidogenicity value (AV) on lactation performance of dairy cows has been evaluated by feeding concentrates formulated with different levels of acidogenicity (but equal contents of ME and MP) and used to supplement grass or maize silage, the later being more acidogenic than the former (Dewhurst *et al.*, 1998a). Voluntary intake of silage and the yields of milk and milk solids were markedly lower with the high AV concentrate, despite the formulated similarity in energy and protein values between concentrates. The voluntary intake of the highly acidogenic maize silage was lower than for the grass silage, though this did not result in significantly lower milk yields. The low voluntary intake of the maize silage was further reduced when feeding the high-AV concentrates. Thus, feeding high-AV concentrates can reduce food intake and milk production, particularly when feeding high-AV forages, such as maize silage.

Total Mixed Rations

The recommendation that concentrate is best given little and often has led to the development of the Total Mixed Ration (TMR) concept, in which concentrates are mixed with chopped silage and perhaps other materials such as sugarbeet pulp in ratios that can vary for groups of animals with different nutrient requirements. This gives advantages in simplified management, but for any group of cows some will be adequately fed by any given mixture of forage and concentrates, others will be overfed and yet others underfed. It is normal practice, therefore, to divide the herd into groups and to feed each a different mix, to satisfy the average needs of the group. Thus, the cost of feeding can be reduced as lactation progresses until forage only is given at the end of lactation.

However, the complication of feeding and milking several groups of cows has been largely responsible for the delay in the widespread adoption of the complete diet system for winter feeding on dairy farms in the UK, although it has become increasingly popular over the last few years as herd sizes have become increasingly large.

In the USA, where herds are often even larger and fed on conserved foods at all times of the year, there is more justification for investing in machinery for handling and mixing the diets. In a comparison of a TMR consisting of 60% forage:40% grain fed throughout lactation, against cows given a 50%:50% diet during the first 21 weeks of lactation, a 65%:35% food for the remainder of lactation and a 85%:15% food during the dry period (Everson *et al.*, 1976), there were no differences between treatments in milk yield or composition. The variable-composition system was closer to the animals' nutrient requirements and resulted in higher milk fat content, more rapid return to calving body weight, lower blood ketone values and earlier post-calving oestrus.

The forage portion of the diet must be chopped, to avoid selection, as small ruminants can take a much higher proportion of leaf than stem material. Forage will normally have been chopped before ensiling.

Ad libitum feeding of a TMR encourages a higher intake than conventional restricted feeding of concentrates with forage ad libitum and therefore gives the potential for better use of forages.

Flavours for silage

Lower than expected levels of silage intake are often ascribed to 'unpalatability', and several attempts have been made to overcome the problem by adding pleasant flavours. A few such attempts have resulted in significant medium-term increases in silage intake: Simax 100 (main ingredients caramel, maple syrup, orange oil, vanilla and citronella) and Palatol (main ingredients ethyl vanillin, isopropyl alcohol, cyclotene and furfuraldehyde 2-methylvaleric acid) increased silage intake by cows in mid-lactation, although milk yield and milk composition were unaffected (Weller and Phipps, 1989); Simax 100 gave similar results in a second experiment.

Further, Palatol, molasses or molasses + Talin (a protein sweetener and flavour enhancer extracted from the fruit of *Thaumatococcus daniellii*) all increased the intake of a poor-quality silage (the molasses probably by supplying soluble carbohydrate), but did not affect intake of a good-quality silage. Milk yield and milk composition were not affected by flavouring agents. Thus, there is evidence that flavours can improve silage intake, but it seems unlikely that flavouring can substitute for nutritional improvement in optimizing forage intake.

Prediction of Silage Intake

Many empirical equations have been derived for the purpose of predicting the voluntary intake of silage by ruminant animals, particularly dairy cows, and some of these have been reviewed by AFRC (1991). Variables used for prediction have included several chemical attributes of silage, such as NDF and non-ammonia N, and several animal characteristics, such as body weight and milk yield. Mean square prediction errors (MSPEs) have typically been at least 15%, but this should be capable of reduction by using more comprehensive data sets, incorporating more variables and using better models. Further discussion of prediction of intake by lactating cows is to be found in Chapter 16.

Additional variables used in more recent studies have included digestibility and rumen degradability, which involve complex and time-consuming animal studies and further laboratory analyses, particularly NIRS. Rather than attempt a comprehensive coverage of the literature, a few examples will be covered in some detail here.

Digestibility and degradability

Ferret *et al.* (1998) fed 11 maize silages to mature ewes and used the ear content, chemical composition, fermentative characteristics, *in vitro* DM digestibility and ruminal degradation characteristics in equations to predict voluntary intake. Good prediction of DM intake ($r = 0.93$; $P < 0.01$; residual SD = 3.9) was achieved using the soluble fraction and the insoluble but fermentable matter derived from the rumen degradation studies. Because of the difficulties of degradability studies the authors suggested that, for a compromise between accuracy and simplicity, reliability and inexpensiveness, the pH and acetic acid concentration of the silages might be used as a predictor of DM intake ($r = 0.80$; $P < 0.05$).

Silage composition

Prediction of potential silage intake by sheep and cows was made by Offer *et al.* (1998) from laboratory silage measurements. A wide range of silage characteristics was included (cutting dates from 19 May to 18 September, wilting periods from 0–48 h and additives of several types) to achieve wide ranges of

compositional variables. A wide range of silage composition was achieved (CVs for DM, CP, DOMD, lactic acid, total VFA and sugar were 0.22, 0.19, 0.07, 0.43, 0.84 and 0.69, respectively). Most of the silages were fed to lambs as the sole food, with hay intake used as a covariate in the statistical analysis, and some were also given to lactating cows along with 7 kg/day of concentrates.

Not surprisingly the best predictions of intake were from equations that included the largest number of conventional compositional variables. However, NIRS analysis (see Chapter 11), both dry and wet, gave even more accurate predictions, with the advantage that such analysis can be carried out quickly and on-farm.

A study of intake prediction for beef cattle, which includes many chemical measures on silage (but not degradability), has been carried out by Rook and colleagues (1990). The data used for analysis came from almost 700 animals on over 60 silages and used live weight, intake and 16 silage characteristics in their predictions. For validation data from another 57 silages were used. In order to produce better estimates than can be obtained from ordinary multiple regression, ridge regression methods were used, and the best equation using parameters which could be relatively easily measured was:

$$I = -5.84 - 0.615\text{CDMI} + 0.098\text{TDM} + 8.65\text{pH} - 0.049\text{NH}_3\text{-N} + 0.429\text{N} + 0.32\text{DOMD} \quad (14.1)$$

where I is intake (g/kg LW^{0.75}/day), CDMI is concentrate DM intake (g/kg^{0.75}/day), TDM is toluene DM (g/kg fresh), NH₃-N is ammonia N (g/kg N), N is total N (g/kg TDM) and DOMD is the digestible OM in the DM (g/kg TDM). The MSPE was 11% of the actual intakes while the multiple regression including all variables gave an MPSE of 14%. It is not, therefore, automatically better to include as many variables as possible in prediction equations; however, this work did not clearly indicate which is the best subset of silage characteristics to measure and so does not lead immediately to reduced analytical costs.

NIRS for silage intake prediction

NIRS has proved to be both accurate and simple and particularly suitable for use within a technical support role for the agricultural industry, as long as appropriate sample preparation and scanning methods are used. An R^2 coefficient of 0.90 has been found in one extensive study between NIRS and intake of grass silage by beef cattle (Steen *et al.*, 1998).

Prediction of substitution rate

Of critical importance to the management of silage-fed cattle is the extent to which silage intake is depressed by the addition of increments of concentrate supplements to the diet (substitution rate, SR, above and Chapter 11). SR increases with increasing level of supplementation and with increasing quality of silage, and McNamee *et al.* (2001) have incorporated these effects in their model for beef cattle.

Means for each combination of silage and concentrate were subject to regression analysis to investigate the relationship between silage intake (y , g/kg $W^{0.75}$) and concentrate intake (x , g/kg $W^{0.75}$). The exponential relationship $y = a + br^x$ was used, where $(a + b)$ represented silage intake when silage was offered as a sole feed, a common value for the parameter r was used for each silage and the line was forced through the same concentrate intake when the intake of each silage was zero, i.e. the concentrate intake when concentrate was the sole feed was independent of silage type. This constraint gave the equation: $y = -b_i(r^k - r^x)$, where k is a constant and is equal to concentrate intake for zero silage intake and i is silage type for each of 11 silages.

Figure 14.3 shows the observed data points for intakes of each silage with different levels of supplementation: the smoothed lines are the predictions developed by their model. A high degree of accuracy is provided when predictions are compared with a wide range of results from experiments at different sites ($R^2 = 0.89$), but note that the voluntary intake of the silage when fed alone must be known, or be capable of being accurately estimated. The predictions for the validation set gave a mean difference between actual and predicted silage DM intake of 8.9% and a mean bias of 1.0%. The success of this model is undoubtedly due to the use of a series of convergent curves, which is biologically more appropriate as it reflects the decreasing significance of the silage quality as silage represents a decreasing proportion of the total diet.

These authors subsequently adapted this approach for lactating dairy cows (McNamee *et al.*, 2005), using predictions of silage DM intake from NIRS analysis, with good results ($R^2 = 0.98$ for the regression of silage intake on level of concentrate supplementation, with a correction for milk yield) providing 93% of predictions within 10% of observed intakes in the validation data.

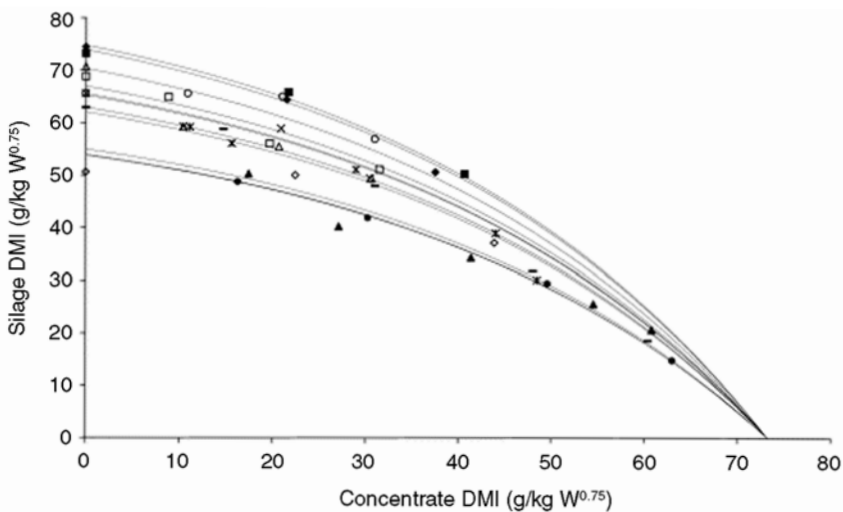


Fig.14.3. The observed (symbols) and predicted (lines) silage DM intakes of 11 silages in supplemented diets with various levels of DM intake when offered as the sole food (from McNamee *et al.*, 2001).

It can be seen, therefore, that the combination of modern analytical methodology – specifically NIRS – and appropriate biological models and statistical analysis is providing ever more accurate predictions of silage intake. There will, however, always be situations in which prediction is poor, especially when one or more variables are outside the range of data used in developing the prediction equations.

Comparison of equations

This section should be read in conjunction with the section on comparison of prediction equations in Chapter 16, which deals with lactating dairy cows fed on foods other than silage.

A very comprehensive data set was assembled by Keady *et al.* (2004), including data from 2425 individual cows from 27 studies at three research centres in the British Isles. The data included wide ranges of intake and milk yield, and the five published prediction models commonly used in the British Isles against which these data were tested were:

1. (from Vadiveloo and Holmes, 1979):

$$\begin{aligned} \text{TDMI} = & 0.076 + 0.404\text{CDMI} + 0.013\text{LW} - \\ & 0.129\text{WL} + 4.12\log\text{WL} + 0.14\text{MY} \end{aligned} \tag{14.2}$$

(see Table 14.1 for definitions of abbreviations and Fig. 14.4 for graphical representation of goodness of fit of predictions to actual intakes).

Table 14.1. Definitions of abbreviations used in intake prediction equations.

C	Concentrate dry matter intake (kg/day)
CDMI	Concentrate dry matter intake (kg/day)
CFV	Concentrate fill volume (UE/kg DM)
CIC	Cow intake capacity (UE)
D	Silage DOMD (g/kg)
DM	Silage dry matter (g/kg)
FE	Forage energy (UFL/kg DM)
FFV	Forage fill value (UE/kg DM)
LW	Live weight (kg)
MUD	Mud adjustment factor for DMI
MY	Milk yield (kg/day)
N	Ammonia N (g/kg total nitrogen)
PQ	Milk fat %
SDMD	Silage dry matter digestibility (kg/kg)
SDMI	Silage dry matter intake (kg/day)
SIP	Silage intake potential (g DM/kg W ^{0.75})
SLW	LW
TDMI	Total dry matter intake (kg/day)
TEMP	Temperature adjustment
WL	Week of lactation

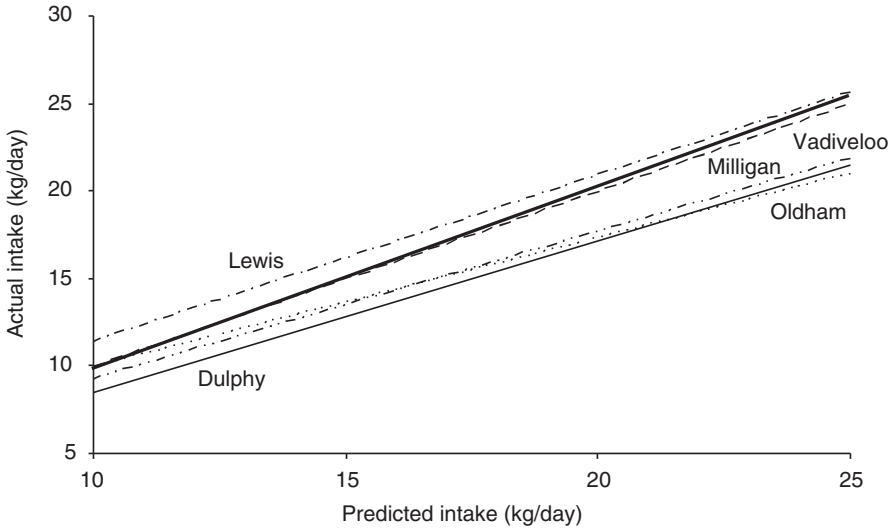


Fig. 14.4. Relationship between actual and predicted dry matter intake for the equations of Vadiveloo and Holmes (1979), Lewis (1981), Milligan *et al.* (1981), Dulphy *et al.* (1989) and Oldham *et al.* (1998) using individual cow observations ($n = 2425$). The thick solid line is that for $x = y$ (from Keady *et al.*, 2004).

This provided the most precise predictions of the five, with an MSPE of 2.9 kg^2/day , even though it did not include variables describing any aspect of silage composition. It should be noted that this equation was derived from data collected from cows fed on hay-based diets. Daily intake was under- or over-predicted by only 0.2 kg DM for actual intakes of 26 and 10 kg DM/cow/day, respectively. However, this equation is useful only in predicting the food intake required to support a given milk yield.

2. (from Lewis, 1981):

$$\text{SIP} = 0.1035\text{DM} + 0.0516\text{D} - 0.05\text{N} + 45 \quad (14.3)$$

$$\text{SDMI} = 1.068\text{SIP} - 0.00247\text{C} \times \text{SIP} - 0.00337\text{CDMI}^2 - 10.9 + 0.00175(\text{MY})^2 \quad (14.4)$$

This model, which included silage compositional variables as well as animal factors and concentrate allowance, under-predicted intake by 5%. The success of this model, and that of Vadiveloo and Holmes (1979), is due to the inclusion of concentrate allowance as a predictive variable – the weight of concentrates is included in the predicted total daily DM intake so it is not surprising that there is a good fit, especially for cows given high levels of supplements!

3. (from Milligan *et al.*, 1981, Cornell Net Carbohydrate and Protein System – CNCPS):

$$\text{TDMI} = (0.0185 \times 0.9 \times \text{LW} + 0.305\text{MY}(0.4 + 0.15\text{PQ})) \times (\text{TEMP}) \times (\text{MUD}) \quad (14.5)$$

This model includes animal and environmental variables, but no information on diet composition. Nevertheless, it provided a lower MSPE than the remaining two models while over-predicting silage DM intake by 12%. When evaluated with data from North American cows and diets, this equation slightly under-predicted intake, however, and the leanness of the cows and the preponderance of maize in US silages is probably responsible for the relative failure of prediction of intakes by cows in the British Isles.

4. (from Oldham *et al.*, 1998):

$$\text{SDMI} = \text{LW} \times (0.01503 + (1/(1 - \text{SDMD}) \times (0.004248 + (-0.0004333/\text{SDMD})))) - 0.4914 \times (\text{C}) \quad (14.6)$$

This model, based on the TPH (see Chapter 11), over-predicted DM intake by 13% and this is due to the lack of variables representing milk yield or stage of lactation. In addition, it includes a constant for substitution rate, whereas this varies with silage quality and level of concentrate feeding (see below).

5. (from Dulphy *et al.*, 1989, French Fill Unit – FFU):

$$\text{CIC} = (22 - 8.25\exp(-0.02\text{MY}) + (\text{LW} - 600) \times 0.01) \times 0.9$$

for primiparous cows and 1.0 for multiparous cows;

$$\text{CFV} = 1.2 \times \text{MY} - 0.69 \times \exp(1.46\text{FE}/\text{FFV}) \times \text{FFV} \quad (14.7)$$

$$\text{SDMI} = (\text{CIC} - \text{CDMI} \times \text{CFV})/\text{FFV} \quad (14.8)$$

$$\text{TDMI} = \text{SDMI} + \text{CDMI} \quad (14.9)$$

This series of equations provided the least accurate predictions of intake, with an MSPE of 17%. However, many of the data on voluntary intake have been derived from mature sheep, and the use of this for lactating cows is not acceptable (Cushnahan *et al.*, 1994).

Keady *et al.* (2004) concluded that, while the equations of Vadiveloo and Holmes (1979) and Lewis (1981) gave relatively small errors of prediction, they both included milk yield, i.e. they were based on the ‘requirements’ of the cows rather on the responses of cows to various levels of input. They state that: ‘Further research is required to establish if a truly predictive model can be derived which will facilitate accurate prediction of food intake based on animal characteristics, excluding milk output, and detailed characteristics of the range of foods offered’. Further description of the comparisons made by Keady *et al.* (2004) is to be found in Chapter 16.

Conclusions

Grass and other types of plant are often conserved during the growing season for use as food at other times of year. Hay, dried grass and silage are common forms of preserved herbage. The intake of silage DM is often seen to be lower than that of hay made from the same sward, although this is not so much a problem now as it was in the past. Low DM content, slow rates of degradation, low pH, high ammonia, nutrient imbalance and unavailability of protein are all

recognized as factors in the depression of silage intake, but the relative importance of these in any given situation is hard to estimate. The greater the degree of fermentation, the more likely is intake of silage to be influenced by the products of fermentation rather than by the nutrients supplied by that silage relative to the animal's requirements (Wilkinson, 2005).

Intake of maize silage is usually higher than that of grass silage, and a useful technique is to mix grass silage with either maize or clover silage to achieve maximum intakes by cows.

Silage is the staple food for dairy cows for a large part of the year in many dairy systems. The risk of producing a poor silage, i.e. one with low intake, can be reduced by the use of additives: bacterial inoculants are now the additives of choice. The potential intake of any forage can be attained only if there is sufficient time for eating, no restriction of water and a favourable social environment. Probably the best way to achieve high forage intakes is to employ well-educated stockmen and to remunerate them adequately for their work.

Supplementation of herbage or silage with concentrates depresses forage intake, although in situations in which there is marginal protein deficiency – such as is often suspected with silages – high-protein concentrates can sometimes lead to increased forage intake.

The problem of predicting forage intake, and therefore being in a position to advise farmers on the correct management of their animals and crops for optimum utilization of forages, has seen some significant developments in recent years, but is by no means solved. Opportunities exist for improving the intake characteristics of forage crops by modern biotechnological methods, but a clearer understanding of the control of voluntary food intake is needed in order to specify the targets for which the plant breeders should be aiming.

15 Growth and Fattening

Animals must grow in order to be able to reproduce. In addition to increased body weight, growth also involves development, i.e. changes in the relative weights of various organs and tissues and changes in their shape. Of particular relevance in this chapter is the change in the ratio of fat:non-fat, which in normal conditions increases, especially after puberty. Despite the overlap between growth and fattening, it is convenient to deal with them separately here.

Changes in voluntary food intake occur during growth and fattening which, to a large extent, meet the changing nutrient requirements for protein and lipid synthesis. If food intake cannot meet these requirements then the rate of growth will decrease and/or body stores will be depleted, hence the reduction in growth of young pigs when the food is diluted, so as to depress digestible energy intake or to slow the rate of fattening of cattle offered only foods of low energy content. It cannot be said in these cases that requirements control intake or that intake controls production: they are interdependent.

Growth

An animal can only attain its potential growth rate when sufficient high-quality food is available. In practice, however, several factors may restrict intake and prevent the young animal achieving its potential rate of growth. For mammals, it is convenient to discuss pre- and post-weaning growth periods separately, as weaning is often abrupt and imposed before the young have begun to eat large quantities of solid food.

The young chick

For the first 2 days after hatching, chicks are not dependent on eating food as they have sufficient reserves from the yolk sac. During this time they peck at

small round objects and quickly learn which are food. They seem to have some innate knowledge, however, as beak-trimmed chicks – which cannot pick up food – show the same initial preference for grains over pebbles as do intact birds. They do not maintain this preference, however, as the pecking is not reinforced by ingestion. Social hierarchy develops within the first 3 weeks, but chicks incubated in the dark – which randomizes the side of the brain responsible for food location and selection (normally the left brain and right eye) – develop a more flexible group structure than those incubated in light. It has been suggested that, by incubating in the dark, there may be a weaker pecking order with fewer low-dominant chicks dying from starvation.

Pre-weaning in mammals

Once the young have recovered from the acute affects of birth, their activities are totally directed to teat-seeking, which is actively encouraged by the dam. Young nose around the underside of the dam and will persist for an hour or two if not rewarded. Calves sometimes do not succeed in obtaining milk from their mothers for over 6 h after birth, but thereafter suck about ten times per day. Most lambs find the teats within 2 h and may then take milk as often as 50 times in the next 24 h. However, by 4 weeks of age, they are suckled only about six times per day.

The mother's milk is the major source of nutrients during early life, with the exception of the calf in the dairy herd, which is usually fed milk substitute after the first 24 h. Within a species both the composition of this milk and the quantity available may be limiting factors. Where the mother does not have enough teats for all the progeny, the weakest of the litter will receive only that left by the others and often die or have to be reared artificially. This often occurs in pigs when the litter is greater than about 14, and in sheep when three or more lambs are born.

Even when individuals receive a fair share, the total amount of milk produced may not supply the full nutrient requirements of the young. There is a negative correlation between litter size and growth rate of the individual in the litter. Supplementation of the diet with a highly palatable food in such a way that the mother cannot steal it (creep feeding) is common practice for young pigs and lambs. The high energy requirements of the rapid relative growth rate of young animals might be expected to predispose them to eat solid food avidly when milk supply was insufficient, but creep foods must be highly palatable and low in fibre to encourage maximum intake.

Pigs

There is little synchrony in the first hour, but after that all piglets within a litter tend to suck at the same time. Piglets soon establish a 'teat order' and thereafter always suck from 'their' teat. Whatever the potential intake, actual intake depends on the milk yield of the dam, which is affected by nutrition, mastitis and metritis. Litter size is obviously an important factor.

The milk produced in the first day or so after farrowing is colostrum, and Devillers *et al.* (2004) developed a method of estimation of colostrum intake based on weight gain in newborn pigs bottle-fed on colostrum. The equation derived from their data was:

$$CI = -217.4 + 0.217 \times t + 1861019 \times BW/t + BWB \times (54.80 - 1861019/t) \times (0.9985 - 3.7 \times 10^{-4} \times tFS + 6.1 \times 10^{-7} \times tFS^2) \quad (15.1)$$

where CI = colostrum intake (g from T0); BW = body weight at CI estimation (kg), t = time since T0 (min), BWB = birth weight (kg), tFS = age at first suck (min) and t = duration of colostrum intake (min), with a root mean-square error of 33 g.

Evaluation with results from a second data set gave good agreement between measured and predicted values ($R^2 = 0.90$). Comparison of colostrum intake estimated with the equation or with the deuterium oxide dilution method in catheterized sow-reared or bottle-fed piglets showed that bottle feeding versus sow rearing had no effect on the relationship between weight gain and colostrum intake. Application of the equation to sow-reared piglets will, however, require a great deal of observation in order to define age at first suck and duration of colostrum intake.

Once lactation is established, the piglet takes enough of its mother's milk to supply about four \times maintenance, depending on genetic potential for protein and fat deposition (which can be very variable): the faster the piglet's growth, the higher its intake. The frequency of suckling is approximately once per hour, declining somewhat after the first few days. About 5% of sucklings do not result in the piglet obtaining milk and it has been speculated that these serve the function of increasing local blood flow in the udder. However, given the costs of unrewarded suckling, it seems unlikely they have an important function. Indeed, the additional massage provided during non-nutritive nursings did not induce higher milk output during subsequent milk ejection.

The frequency of suckling starts to fall after about the 8th day, and this could be considered to be the start of the weaning process. Suckling frequency starts to decline earlier in larger litters (Puppe and Tuscherer, 2000). There is a negative correlation between suckling frequency and creep food intake in the 3rd week of lactation, suggesting that the piglets compensate for the decrease of suckling and consequent assumed reduction of milk intake.

The young pig has some control over food intake; for example, loading the stomach with hypertonic saline or water or giving nutrient loads can depress subsequent voluntary intake. Dilution of a milk substitute containing 4.68 MJ/l to 2.38 MJ/l caused a 36% increase in the intake by piglets, which was not quite sufficient to prevent a reduction of growth rate (Wangsness and Soroka, 1978). While this suggests that young piglets have a mechanism for matching intake with requirements, albeit imperfect, piglets less than 1 week old did not respond to insulin injections (which increase energy uptake and increase intake in adult pigs), indicating an immaturity in the integration of feeding responses at that early age.

When creep food is available, piglets eat little in the first 2 weeks, even if their milk intake is low. A detailed study of creep food intake was made by

Pajor *et al.* (1991) by providing the food in continuously weighed containers and observing which piglets were eating – by means of video recordings. The mean age of first intake was 12 days, and mean intake was only a few grams up to about 20 days, after which intake increased steeply, averaging 63 g during the following week. Although they collected the data, these authors did not describe the characteristics of feeding behaviour, i.e. size and frequency of meals.

With the common adoption of 4-week weaning, it is expected that food intake will be higher at weaning than in 3-week-weaned piglets, because creep food intake increases rapidly in the fourth week (see Fig. 15.1).

Ease of access to creep food is a factor affecting the intake of food by suckling piglets. If there is insufficient space for all the piglets in a litter to eat at once, some will not eat at all. Appleby *et al.* (1992a) gave some litters access to a single, two-space feeder and provided others with four similar feeders from 21 days of age until weaning at 28 days. With the more restricted system, at least four pigs in each litter did not use the feeder at all, while with the more liberal treatment less than one pig per litter on average did not eat creep feed. The ones that did not eat tended to have had higher birth weights and growth rates to 21 days, suggesting that they were satisfied with the milk from the sow and were not highly motivated to eat solid food. Perhaps for this reason they had low growth rates from weaning to day 42, but their growth overall up to 42 days was no different from that of those piglets that ate creep feed. The authors suggest that low food intake before weaning is a predictor, but not a cause, of poor growth after weaning.

Three-week-old piglets have a strong preference for sucrose, glucose, lactose and fructose, but the thresholds of discrimination are higher than in adult pigs.

Calves

Milk is the primary product of the dairy cow, but in modern intensive dairy management it is too expensive to feed to calves. After access to the mother's

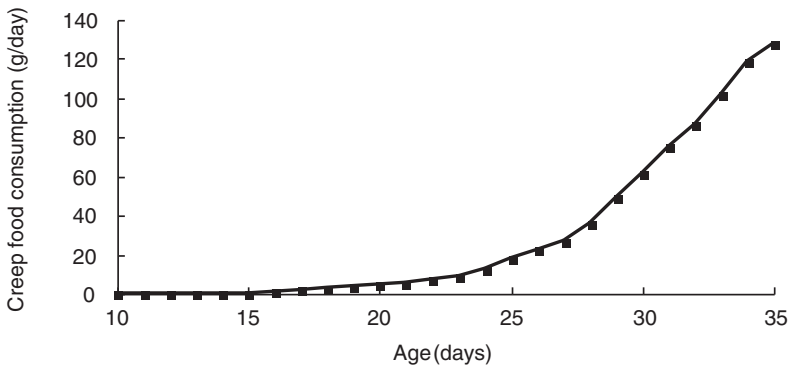


Fig. 15.1. Creep food consumption of an average piglet (from Puppe and Tuscherer, 2000).

colostrum for a day or so, the calf is separated from its mother and fed on reconstituted artificial milk from a bucket or automatic feeder until it is weaned at about 5–6 weeks of age. The quality and quantity of milk offered can both be controlled. Some adjustment of voluntary liquid intake occurs in response to changes in milk concentration in an attempt to maintain a constant dry matter (DM) intake, but this fails if the milk is too dilute. Older calves can compensate better for dilution. Dry matter intake from milk substitute declines when its dry matter concentration is less than about 100 g DM/l and increases, especially in older calves, when the DM content is above about 200 g/l.

Twice-a-day feeding of milk substitute leads to higher voluntary intake than offering one feed per day, although as the calves become accustomed to taking very large amounts of liquid in one meal so intake rises. The temperature of the milk on offer is not a very important determinant of intake, although cold milk (6–15°C) tends to be taken in greater quantities than warm (38°C).

Dry food intake by 4-month-old calves varies inversely with the DM content of the milk, while in lambs at grass solid food intake is also inversely proportional to the allowance of milk. A highly significant relationship between the intake of dried grass (GDMI, g/kg LW) and the amount of milk substitute offered (MS, g DM/kg LW) with 3-week-old calves has been found (Hodgson, 1971b):

$$\text{GDMI} = 7.5 - 0.26\text{MS} \quad (15.2)$$

Calves of different genetic types have been found to show different patterns of milk consumption when suckled by dams of the same type (Mezzadra *et al.*, 1989). Charolais-cross calves consistently took more milk than Angus-cross, while calves sired by Nalore bulls (an Argentinian *Bos indicus* breed) not only took more than Angus-cross calves, but had a completely different shape of curve, starting with very high intakes but declining more rapidly than the Angus. It was suggested that *Bos indicus* calves reduce their dependency on milk at an earlier age than those of *Bos taurus* breeds, perhaps because of the shorter period of the year when good forage is available to support milk production.

Post-weaning

Weaning is followed by much agitation and calling for the mother, which overrides hunger for several hours, especially if the dry food on offer is unfamiliar. The young animal may have difficulty in learning how to locate water and to drink from an unnatural container, and this will further delay the onset of eating.

Although solid food is eaten in small quantities from an early age by the young of many species, they are not usually eating enough to support full growth at weaning, especially when that occurs well before the age at which it would occur naturally. A fall in body weight therefore occurs, which is more severe the younger the animal at weaning. Hunger stimulates a rapid increase in food and water intake (perhaps the latter is critical), and weight gains are resumed within a few days.

Pigs

By weaning, the piglet requires the equivalent of about 475 g of good food per day, but in practice it is several days before it reaches this level of intake: in the first few days it usually manages less than maintenance (Riley, 1989); in one observation the mean intake on days 1–3 after weaning was only 71 g/day, on days 4–7, 120 g and on days 8–35, 518 g. Continuous availability encourages a higher intake than meal feeding, and those fed a meal every 2 h ate more than those given meals every 4 or 6 h.

Water intake is important; it takes about 1 week before water intake levels reach those taken in milk before weaning. For the first time, the animal must separately satisfy its hunger and thirst. Behavioural problems such as navel sucking can occur, presumably due to a desire for the same comfort as provided by sucking the sow's teat. Water intake is very variable in the 2 days following weaning, suggesting that the animals have difficulty finding or using the drinkers immediately after weaning (Barber *et al.*, 1989).

If solid food intake can be encouraged during the milk-feeding period, then the check at weaning will be less severe; highly palatable, sweet concentrate foods encourage high intakes. Sucrose is sweet, provides energy and is commonly included in early-weaning rations. Soluble saccharin also enhances intake of starter foods by early-weaned pigs, but insoluble saccharin is less effective. Moist food is eaten in greater quantities than dry food, but the practicalities of keeping wet food free of contamination such as moulds mean that it has not been widely adopted in practice.

Attempts to familiarize piglets with food and drink before weaning have had variable effects on performance after weaning. Exposure to recordings of sow's chanting, to vanilla odour and flashing lights before offering food to condition eating had no effect on daily intake, even though the anticipatory response was usually elicited. Perhaps putting newly weaned pigs with experienced pigs would speed their learning about food and water, but this would be likely to encourage fighting and the spread of disease. Antibiotics in the food often increase intake after weaning due to suppression of pathogens and by sparing nutrients from microbial degradation; copper sulphate has similar effects. The inclusion of organic acids such as citric in the food sometimes improves intake, perhaps because stomach pH is elevated in stressed piglets, but the results are variable.

Early-weaned piglets are susceptible to cold environments, slippery floors and difficult access to feeders and drinkers. Attempts to improve intake with flavouring agents have usually shown no effect – flavoured foods which were preferred in a choice test were not eaten in any greater amounts when given as the sole food, a not unexpected result (see Chapter 6). However, McLaughlin *et al.* (1983) preference tested 129 flavours and found one with a cheese aroma that did increase intake in a sustained manner when no choice was available. This is unusual and unexplained, as a change in the sensory properties of a food without any change in its nutritional value usually only results in a temporary change in intake.

Many things such as heat-damaged or putrefied proteins depress intake, as do fungal toxins generated by contamination of cereal grains. Rapeseed meal

contains glucosinolates, saponins, sinapines and tannins, all of which depress intake, although it is not clear to what extent they do so simply by their effect on food flavour and to what extent by damage to the gut and toxic effects after absorption. From evidence presented in Chapter 6, it is likely that toxic effects become associated with the sensory properties of the food, so that a learned aversion to toxic foods ensues, whatever their flavour.

Calves

Intake of solid food by calves increases as the daily allowance of milk decreases (Le Du *et al.*, 1976): when given 36 g milk DM/kg^{0.75}, the intake of grass DM was 33 g/kg^{0.75}, whereas when only 6 g milk DM/kg^{0.75} was given the calves consumed 101 g DM/kg^{0.75}.

Between 7 and 13 weeks of age the calf has increasing ability to compensate for the addition of food to the rumen via a fistula, and there is a similar improvement in compensation for removal of digesta. These results support the gradual development of visceral control of voluntary intake in young animals.

The apparent rate of live weight gain may be as fast when calves are weaned early on to solid food as it is when milk feeding is continued, but this is in part due to the increased gut fill. Calves do not voluntarily consume as much solid food DM as they do from milk substitute until their live weight is about 80 kg (Roy, 1980). Voluntary intake rises to about 3.0 kg DM/100 kg live weight at about 120 kg, which is similar to the maximum level of intake seen in lactating cows.

Intake increases as the digestibility of the food increases, implying physical limitation (see Chapter 3). As the calf gets older it can utilize roughage better, and the intake of concentrates may be metabolically controlled, with a negative relationship between intake and digestibility. When various diets with different concentrate:roughage ratios were offered to calves, the all-concentrate food was consumed in greatest quantities up to live weights of 136 kg; at heavier weights the intake of the 80:20 ration was highest.

Lambs

Faichney (1992) observed that sucking Merino lambs given access to solid food from about 3 weeks of age ate little for the first 10 days, but from 4 weeks of age intake increased, with large day-to-day variations, to < 50 g/day/kg^{0.75}. There was little effect of weaning, but the steady increase continued to reach a plateau at 16 weeks, at about 95 g/kg^{0.75}.

The intake of milk substitute by lambs separated from their mothers a few hours after birth increases rapidly to reach about 2.5 l/day at 5 weeks of age, by which time their body weight is 10 kg (Bermudez *et al.*, 1984). When these lambs were abruptly weaned at 5 weeks of age and offered concentrates, forage and water ad libitum, those lambs that were heavier at weaning, through taking more milk, suffered a greater setback when milk was withdrawn, as they had taken less solid food before weaning and took longer to establish an adequate intake of dry food. Within a few days of weaning, the lambs were eating sufficient to resume their pre-weaning growth rate.

Weaning to maturity

Once the stress of weaning is over, the individual grows at a rate characteristic of the species, following a sigmoid curve, unless it is exposed to shortage of food, environmental stress or disease. There have been many attempts to describe the sigmoid growth curve mathematically. Suffice it to say that the daily weight gain accelerates for a period, followed by deceleration to an eventual asymptotic mature size, although fat deposition may lead to further increases in live weight.

As the animal grows, feeding frequency usually decreases while meal size increases. For example, pigs fed *ad libitum* ate ten meals per day soon after weaning, declining to three per day when adulthood was reached.

The voluntary intake of a nutritionally adequate food increases as an animal grows, but is not maintained at the same proportion of live weight. It has been commonly assumed that intake is proportional to metabolic live weight ($\text{weight}^{0.73}$, often rounded to $^{0.75}$), because comparison of mature animals of various species shows this to be an appropriate relationship, both for metabolic rate and for voluntary food intake (Blaxter, 1962). When voluntary intake of individual animals is examined, however, the exponent is much lower than 0.75. Re-analysis of several sets of data show that voluntary intake is related to live weight raised to a power close to 0.6 for an animal as it grows (Forbes, 1971), as distinct to a comparison of mature animals of different weights.

Poultry

As the broiler grows, its daily food intake increases; the increase is not in direct proportion to body weight, however, nor to metabolic body weight (body weight to the power 0.73), but rather to a lower power such as 0.66 (Hurwitz *et al.*, 1978). In a thermoneutral environment, the energy requirement of the bird can be stated as the sum of the requirement for maintenance and that for growth:

$$\text{MER} = 8.0\text{LW}^{0.66} + 8.6\text{WG} \quad (15.3)$$

where MER is the metabolizable energy requirement (kJ/day), LW is the body weight (g) and WG is the weight gain (g/day). This must be an oversimplification, however, as the composition of the weight gain changes as the bird grows, going from predominantly protein in the early stages to greater proportions of fat as the bird approaches maturity. Each successive gram of weight gain will therefore require a greater input of food in view of the greater energy content and lower water content of adipose tissue compared with non-fat tissues, and also the increasing mass of body tissue to be maintained.

Figure 15.2 shows food intake and body weight changes during growth of broiler chickens to maturity (Prescott *et al.*, 1985). Relative to body weight, intake is higher during the rapid early phase of growth, reaching an asymptote of 300 g/bird/day for mature birds weighing about 6 kg.

PREDICTION OF INTAKE Chicken foods, especially those used in the early stages of growth, are well balanced for nutrients, so it has been possible to propose an

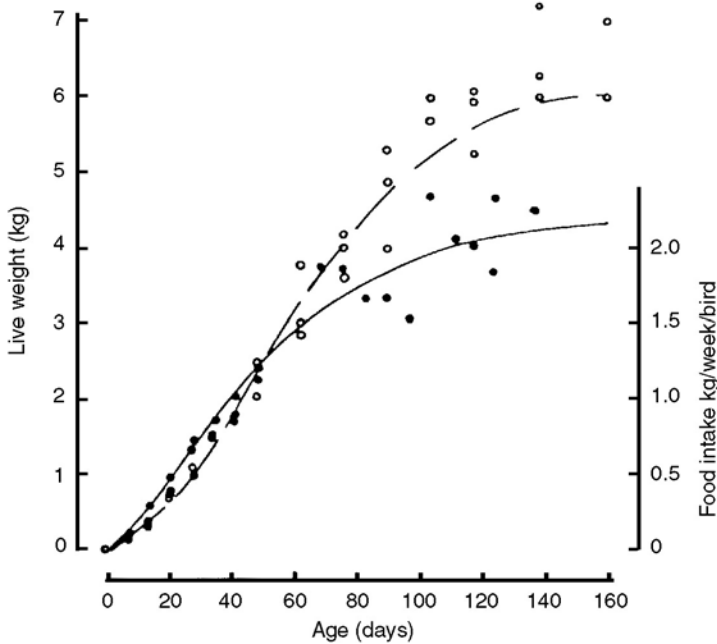


Fig. 15.2. Body weights (open circles) and food intakes (closed circles) of broiler cockerels from hatching to 160 days (from Prescott *et al.*, 1985).

equation for broilers based solely on age. The intake of broiler chicks was measured from hatching to 210 days of age and the following equation was derived:

$$dF/dt = c(1 - e^{-t/t^*}) \quad (15.4)$$

where F is food intake, c is the mature weight, t is the age and $t^*\ln 2$ is the time for an increment of $(c - dF/dt)/2$ (Wilson and Emmans, 1979). This is a curve of diminishing returns, in which the increase in intake is less with every passing day.

NRC (1987) gives tables of intake for various combinations of food, animal and environment, based on the equation of Hurwitz *et al.* (1978):

$$MEI = 7.98BW^{0.66} + 8.57dW \quad (15.5)$$

where MEI is ME intake (kJ/day), BW is body weight (g) and dW is weight gain (g/day).

Pigs

Castrated males eat 7–16% more than entire boars, while gilts eat approximately the same as entire boars (Cole and Chadd, 1989). These differences are related to different propensities to grow and fatten due to the presence or absence of sex steroid hormones.

In order to establish the development of food intake by growing pigs in the absence of environmental and competitive constraints, Tullis (1982) penned

animals individually and offered a balanced food ad libitum. From 5–85 kg body weight intake increased in a manner that was, to all intents, linear, while > 85 kg intake plateaued, albeit with wide fluctuations on a day-to-day basis.

PREDICTION OF INTAKE Whittemore *et al.* (2001a) cover the subject of intake-predicting equations for growing pigs in considerable detail, and the interested reader is referred to their review.

There was little interest in the prediction of voluntary food intake of pigs as long as the domestic pig had a very high propensity to deposit fat above a live weight of about 60 kg and was, therefore, fed at a restricted level to prevent excessive fat deposition. In recent years, however, intensive selection for leanness and the use of uncastrated boars, which deposit little fat, has meant that growing pigs can be fed ad libitum.

NRC (1987) summarized data for intake of creep food by sucking piglets up to 35 days of age from various sources by the equation:

$$\text{DEI} = 46.8\text{DAY} - 634 \quad (15.6)$$

where DEI is digestible energy intake (kJ/days) and DAY is age (days), i.e. intake of creep food is predicted to start at 13 days.

After weaning it can be expected that voluntary intake will be such as to meet the animal's energy requirements and therefore to be proportional to body weight and weight gain. For pigs from 5–117 kg, data fitted the equation (Ewan, 1983):

$$\text{DEI} = 55 (1 - e^{-0.018\text{LW}}) \quad (15.7)$$

where DEI is DE intake (MJ/day) and LW is body weight (kg), while ARC (1981) present the equation:

$$\text{DEI} = 4.7\text{LW}^{0.51} \quad (15.8)$$

The values calculated from these two curves are, in fact, very similar within the normal range of weight, although the ARC example is some 7 MJ/day higher at all stages of growth.

As with poultry, it has not been necessary to include indices of food quality in the equations for growing pigs, as it is assumed that the diets are balanced and that intake of digestible energy is regulated by the pig in order to achieve maximal growth rate. There are, however, several management factors affecting intake, and Kornegay and Notter (1984) have presented equations for predicting the effects of different space allowances for weanling, growing and finishing pigs, in relation to the intakes of animals with ample space.

For optimal food intake, the space allowances were 0.4, 1.06 and 1.09 m²/animal, respectively. There is an effect of group size that is independent of space allowance, which these authors have quantified as a 0.92% decrease in intake per additional pig, in the range three to 15 pigs per pen for weaners, 0.25% for growing pigs and 0.32% for finishers. There is a fuller discussion of effects of space allowance and group size on voluntary food intake by pigs in Chapter 17.

Examples of the use of these prediction equations for pigs are given by NRC (1987, pp. 36–37), with the acknowledgement that the agreement with published results was not always good.

Eissen *et al.* (1999) examined linear, quadratic and cubic equations to fit data on intake in pigs growing from 28–108 kg and concluded that there was no advantage in going beyond the linear for which the equation is:

$$\text{Intake (kg/day)} = 1.23 \text{ kg} + 0.0161 \cdot \text{day (from day 28)} \quad (15.9)$$

This slope is only half that found by Tullis (1982), and highlights the dangers of using equations describing data sets reported in the literature for purposes of pig food intake prediction. The pigs of Tullis were penned and fed individually in experimental facilities, while those of Eissen were group-fed under farm conditions, and Whittemore *et al.* (2001a) have highlighted the differences in intake between these two situations (see below).

If intake potential depends on demand for nutrients and the requirements for maintenance are relatively small, then it should be possible to predict intake (under non-limiting conditions) from rates of deposition of fat and non-fat tissues. Backfat thickness and live weight can be used as proxies for these parameters, and intake has been well predicted for pigs with very different rates of growth and fattening (Whittemore *et al.*, 1995). Lipid (Lt) and protein (Pt) masses (kg) were estimated from:

$$Lt = 1.12 (0.19W + 0.78(P^2) - 9.2) \quad (15.10)$$

$$Pt = 0.44 (0.41W - 0.52(P^2) + 2.4) \quad (15.11)$$

where P^2 is the backfat thickness;

$$\text{energy intake (MJ ME/day)} = 52Pr + 53Lr + 0.44W^{0.75} \quad (15.12)$$

Kyriazakis and Emmans (1999) used the logic that food intake will equal that which is desired to fulfil the metabolic requirements of the day in question:

$$\text{daily food intake} = (1/\text{food energy content}) \cdot (E_M + E_{Pr}/k_{Pr} + E_{Lr}/k_{Lr}) \quad (15.13)$$

where E_M is the energy for maintenance, E_{Pr} and E_{Lr} are the daily rates of energy retention in protein and lipid and k_{Pr} and k_{Lr} are the efficiencies of utilization of energy for protein and fat deposition. An energy cost for cold thermogenesis may also be added ($0.016 \text{ MJ/W}^{0.75}$) for each °C of cold ($T_c - T_e$), where environmental temperature (T_e) is below the lower critical temperature (T_c). Rates of protein and lipid deposition may be adequately described as Gompertz functions in relation to live body weight.

Whittemore *et al.* (2001a) conclude that their ‘analysis suggests that predictions of food intake either from general empirical formulae or from requirement models may be unsafe for the practical estimation of food intake in particular circumstances’. On-farm pigs usually eat less than that predicted from experimental measurements and predictions. Thus there is an important requirement for on-farm measurement to allow more realistic predictions for management purposes: live weight and food intake measurements on at least two pens for at least 2-week periods at the beginning, middle and end of the growth range are recommended (Schinckel and de Lange, 1996).

Whittemore *et al.* (2001a) propose that daily intake (DFI) at any stage can be predicted from the starting and finishing weights, the total amount of food used (the annual food usage/number of pigs fed) and the assumption that food intake follows the form: $DFI = a.Wb$. If on the other hand the total amount of food consumed is not known, then information on daily food intakes of pig groups of varying live weights may be obtained from the farm in question using subsamples of pigs, and the most likely curve describing the relationship between intake and weight (or age) estimated.

INTAKE OF GROWING PIGS IN PRACTICE For practical purposes, the increase in intake up to 85 kg can be treated as a straight line followed by constant intake, i.e. a 'broken stick' relationship between body weight (or age) and food intake, contrary to the theoretical curvilinear response based on Gompertz growth equations (Whittemore *et al.*, 2001a). As the major purpose of research with farm animals is, presumably, to assist with improved economy of growth, can the theoretical relationships be of any real value?

The discrepancy might be due to a number of factors: first the intake of the very young pig might be limited by gut capacity, thereby giving real intakes lower than those predicted from growth curves. Thus they increase their rate of growth when the nutrient density of the diet is increased. Older pigs, on the other hand, 'eat for energy', apparently achieving their theoretical intakes. The lower than predicted intakes at light weights will result in a straightening of the intake curve from 5 to 85 kg body weight. Clearly, it is necessary to make some measurements on a particular farm, and even in a particular building, before reliable estimates of intake in that situation can be made.

Cattle

As with other species, voluntary intake increases with age, eventually reaching an asymptote. However, intakes vary much more at any given age than with poultry or pigs because of the wide range of foods offered, including poor-quality forages.

When the intake of growing cattle is plotted against their metabolic weight (body weight^{0.73}), there is a steady decline with increasing weight. Weight has to be raised to a lower power, close to 0.6, in order to get a constant value as the animal grows, at least for animals on complete, pelleted feeds, as well as for cattle on good-quality pasture. Figure 15.5 (see below) is an example, in which the best fit for intake is 0.29 kg/live weight^{0.54} (Pickard *et al.*, 1969).

In a comparison of 1-year-old cattle of 25 breeds, Taylor *et al.* (1986) found a close relationship between the logarithm of daily food intake and the logarithm of body weight. The regression coefficient of 0.42, indicating that intake was proportional to body weight^{0.42}, is much smaller than intra-breed coefficients, which lay between 0.61 and 0.82, indicating that intake cannot be predicted from body weight alone, without a knowledge of the animal's breed.

However, it was found that foods of different energy concentrations were eaten by growing zebu cattle in proportion to live weight^{0.79}; notwithstanding, within types of food, as the concentration of cell wall constituents fell from 710

to 610 to 540 g/kg DM, the exponent changed from 0.87 to 0.69 to 0.56 (Karue *et al.*, 1973). This suggests that the intake of poor-quality roughages, which is limited primarily by physical constraints, is related directly to body weight, while more concentrated diets are eaten in relation to metabolic requirements. Re-analysis of the data collected from the literature for the chapter on voluntary food intake in the Agricultural Research Council (1980) publication on the nutrient requirements of ruminant livestock gave the equation:

$$\text{DMI} = 172\text{LW}^{0.6} \quad (15.14)$$

Thus there is considerable evidence against expressing the voluntary intake of growing animals in terms of 'metabolic live weight', $\text{W}^{0.75}$, and it is more appropriate to include W^b or $\log \text{W}$ than $\text{W}^{0.75}$ in statistical models relating food intake to body weight.

It is reasonable to assume that intake of complete diets was not limited primarily by physical restraint and that requirements for growth determined intake under the conditions in which these relationships were obtained. An increase in growth rate would therefore be expected to lead to an increase in voluntary intake, and growth stimulants act primarily on growth with a secondary effect on voluntary intake. In one typical set of observations it was found that diethylstilboestrol (DES) improved weight gains by 20%, while intake increased by 6%. Further discussion of growth stimulants will be found later in this chapter.

PREDICTION OF INTAKE Prediction of intake by ruminants is often difficult because of the interactions between animal and diet, and is particularly so under conditions where few reliable data are available on which to base equations, e.g. grazing. Despite these difficulties, there have been numerous attempts at prediction of the voluntary intake of sheep and cattle. Because it is clear that intake is influenced by live weight, energy demand and food quality, it is natural that multiple regression analysis should be applied.

Neal *et al.* (1988) used an equation provided by ARC (1980) for prediction of intake in a computer program to ration beef cattle, as this equation had been found to have lower prediction errors than several others tested:

$$\text{DMI} = 106.5q + 37C + 24.1 \quad (15.15)$$

where DMI is DM intake (g/kg body weight^{0.75}/day), q is the metabolizability of the ration (MJ/kg DM) and C is the proportion of concentrate in the ration (kg/kg). As they observed that this over-predicted by an average of 26% when compared with experimental data, they used this equation but reduced by a factor of 0.26. Predicted silage intakes were still higher than those observed in several experiments, especially for short-chopped silage, and substitution rates were in a narrower range than actually observed. The authors suggested that the model would be much improved by inclusion of indices of silage quality and degradability. Chapter 14 includes examples of prediction of silage intake by cattle.

NRC (1987) published comprehensive compilations of equations on prediction of food intake in beef cattle. The graphs presented there are plots of various equations that have been proposed to predict DMI in beef cattle and, in

some cases, show considerable discrepancy between the predictions of equations from different sources. No validation is presented, in common with most published prediction equations (Pittroff and Kothmann, 2001b) and, as always with this type of approach, predictions of intake should be limited to the range in which the observations on which the equations are based were made.

Having concluded that none of the equations they summarize include all of the important variables, NRC (1987) adopts a factorial approach and presents equations and tables for adjusting predicted intake for diet energy concentration, body fat, initial body weight, breed, genetic variance, anabolic agents, food additives, particle size of diet, environmental temperature, muddiness of ground, forage availability, grazing system, milk production, milk intake, pregnancy and water intake. Space precludes detailed coverage of this work, but the interested reader is strongly recommended to study it.

However, NRC (2000) have more recently provided validation of the equation:

$$\text{DMI} = (\text{SBW}^{0.75} * (0.2435\text{NEma} - 0.0466\text{NEma}^2 - 0.1128)) / \text{NEma} \quad (15.16)$$

for growing yearlings, where DMI is DM intake (kg/day), SBW is starting body weight (kg) and NEma is net energy for maintenance (Mcal/kg DM). In comparison with one set of experimental results from cattle fed high-energy diets, this equation accounted for 76% of the variation with an overall prediction bias of 0.16% and standard error of predicted intake of 0.34 kg. Other data sets were fitted less well but adjustment factors for body fat, breed, food additive, environmental temperature and mud were calculated to adapt the basic equation to different management situations.

The use of such factors as gender and use of anabolic agents as multipliers for the basic prediction equations is not always justified, however. For example, reduction in the DE concentration of a medium-quality diet for an animal with low nutrient requirement results in it eating more as it is not at the 'physical limit', while for an animal with high nutrient requirement a reduction in the DE concentration causes it to eat less as it is already eating to its physical capacity, i.e. there are interactions between the factors affecting intake. Another example is where the intake of a small, fat animal is likely to be reduced more by high environmental temperatures than that of a large, lean animal of the same body weight.

Sheep

What has been said above concerning cattle is largely true for sheep. However, because it is less usual for lambs to be kept intensively, there has been less emphasis on prediction of their intake.

Genetics of intake in growing animals

Intensive selection by breeders over many generations for economically important production traits such as egg or milk production, growth rate and meat production has invariably been accompanied by changes in food intake.

Poultry

The increase in intake in modern broilers may be due to a functional equivalent of hypothalamic lesioning, because it has been found that electrolytic lesions of the hypothalamus caused increased intake (and fattening) in broilers selected for low growth, while having no effect in the high-growth line (Burkhart *et al.*, 1983). However, another interpretation of these results is that the high-growth birds are already eating as much as their gut capacity will allow; it was much more difficult to force-feed broilers of a high-growth line than those selected for low rate of growth (Barbato *et al.*, 1984).

High-growth birds have higher thresholds for the detection of both sweet and bitter substances in the water (Barbato *et al.*, 1982), and it can be concluded that selection for high growth renders birds less sensitive to taste. However, birds selected for high growth take longer than the low-growth strain to adjust their food intake when dextrose is included in the drinking water, suggesting that longer preference tests might be required to determine true preferences.

In addition to a control, random-bred line and a line selected for high live weight gain, other lines have been selected for maximum food consumption and maximum food conversion efficiency (Pym and Nichols, 1979). In the 12th generation of selection, the mean intake from 5–9 weeks of age was 70 g/day for the controls and 72 g/day for the efficiency-selected line, while for the gain- and intake-selected lines it was 100 and 109 g/day, respectively (S. Iskandar and R.A.E. Pym, personal communication).

Whereas the control-, weight- and efficiency-line birds increased their intake when given a diluted diet, those selected for high food intake did not and it was suggested, therefore, that these birds were eating to digestive capacity even with the nutrient-dense diet. This is supported by the fact that they had the most rapid rate of passage of digesta through the tract, the smallest gizzard and proventriculus and the shortest small intestine. The high-intake line also had the highest weight of abdominal fat pad and it is possible that this set a lower physical limit to gut capacity, as proposed for ruminants (see Chapters 3 and 11).

Selection of broilers for high or low fat-pad weight (R.A.E. Pym, personal communication) resulted in a 70% greater fat-pad weight after five generations. However, there was no difference between the intakes of the fat-line (100 g/day from 4–8 weeks of age) and thin-line (97 g/day) birds and neither differed from the random-bred control line, which ate 99 g/day. This shows that the physical size of the fat pad does not directly affect intake. Selection for weight gain alone or for weight gain with a constraint on fatness resulted in higher intakes (108 g/day in both cases).

Broiler chicks may eat no more per unit of body weight than do those of an egg-laying strain, but convert food to live weight more efficiently, grow more quickly and therefore eat more than layer chicks at any given age.

Pigs

For several decades up to the 1980s, selection of pigs for breeding had included selection for low voluntary food intake, on the basis that high food intake was

accompanied by high fat deposition. However, by that time it was realized that selection against high food intake had probably gone too far and that growth and protein deposition were being limited by low intake. De Vries and Kanis (1992) developed a growth model based on a linear-plateau relationship between protein deposition and food intake incorporating a minimum fat to protein deposition ratio and a maximum protein deposition rate. If capacity to eat was too low to realize maximum protein deposition, then increasing the intake capacity had a positive economic value, while if it was too high it had a negative value, whereas previously increased intake was always considered a bad thing! This model was then used to simulate effects of various selection indices and it was concluded that, if intake capacity is too low, selection emphasis should be on this trait.

There is important genetic variation in food intake between and within breeds, e.g. for the Pietrain it is 0.87 of that for the Large White (Webb, 1989), while some breeds (e.g. Chinese pigs) seem to have a bigger capacity for dietary fibre. Within a breed, heritability of intake is about 0.3 and shows genetic correlations with growth rate (positive) and lean content (negative), but not with efficiency of utilization of food. The correlations between test station and commercial farm performance are low (0.25 for growth rate and 0.40 for backfat), so some of the genetic improvement is not being expressed on farms, i.e. there are interactions between genotype and production system. This may be due to test stations using individual feeding and some genes affecting social behaviour not being expressed in the test environment – monitoring intake of individuals in groups is now the norm in pig testing stations, using FIRE systems (see Chapter 2).

After seven generations of selection, with reduction in fatness being the major trait in the selection index, average daily food intake was reduced from 2.71 kg/day in a control, random selection line to 2.51 (Wood, 1989). When selection of pigs was based on an index that included high live weight gain, low backfat thickness and efficient food conversion, voluntary food intake declined for 7 years but then plateaued (Smith *et al.*, 1991). The cumulative responses in intake after 11 years were -0.25 kg/day for boars and -0.19 for gilts.

However, selection for efficiency is difficult as it involves measurement of intakes by individual pigs and, where it has been used, direct selection for efficiency has not always given an improvement. Selection for increased protein deposition and reduced backfat has usually led to improved efficiency anyway, so breeders have not been worried about selecting directly for efficiency. Currently, equipment is available for monitoring individual food intakes and less emphasis is being placed on reduction of backfat. Thus, improvement in efficiency has recently become feasible and attractive. However, efficiency is a ratio of output to input and ratios have poor statistical properties, so that selection responses can be erratic. An alternative is to select against high food intake, but this leads to reduced performance.

Selection for efficiency and leanness on ad libitum feeding caused reduced voluntary intake; from years 2–4 to 6–8 of the Meat and Livestock Commission's Commercial Product Evaluation Scheme (UK), voluntary intake fell by 6%. Paradoxically, when selection was done with restricted feeding, voluntary intake of subsequent generations was found to be increased.

Fat is now at about the right level in pigs, so the only way to continue to improve efficiency is to increase lean tissue growth to reduce the maintenance cost per unit of production. Testing and selection are, therefore, made on ad libitum feeding, penning in groups to allow expression of genes for behaviour under commercial conditions, and recording of individual intakes to measure genetic differences in maintenance which cannot be predicted either from growth rate or backfat. The ability to feed ad libitum due to reduced voluntary intake accompanying selection for low fat deposition has enabled ad libitum feeding systems increasingly to be used commercially, with considerable saving in labour.

Selection on food conversion is inefficient, and further improvement of food efficiency by reduction of fatness is limited. It has been suggested, therefore, that selection should be for high food intake from early in growth when the pig is most efficient, and lean growth is highly associated with food intake to produce a food intake curve corresponding to the curve of lean growth.

GENETIC PARAMETERS FOR DAILY FEED INTAKE PATTERNS From monitoring of daily intake over a 95-day period in Dutch Landrace gilts, it was observed that genetic correlations were low (around 0.3) between intake at start and end of the test, suggesting that intake on different days on test could not be regarded as repeated measurements of a single trait with constant variance and heritability (Huisman and van Arendonk, 2004). It was concluded that it should be possible to manipulate food intake patterns during growth through selection.

Bermejo *et al.* (2003a) have proposed that selection for high relative intake early and low intake later in growth could be based on the parameters of curves fitted to daily intakes over as long a period as possible. Several methods of describing intake curves were applied, including linear-segmented (broken stick) and logistic functions (see Fig. 15.3). Selection can then be on reduced age at which the intake plateau is reached or at which the maximum increment in food intake per day occurs, using the plateau or logistic functions, respectively.

Breeding values of these selection criteria were estimated, which showed that a change in food intake by selection is possible and that an optimization of the food intake curve corresponding to lean growth rate can be achieved. Note that there is not much difference between the two relationships. While the continuous curve gives a good fit for carefully measured intakes (e.g. in a research environment), it is often not possible to differentiate it from the broken-stick model where the data are not so accurately recorded (e.g. in a commercial situation).

This encouraged a larger-scale study in which daily intakes of over 5000 boars were monitored over a period of 9 weeks (Bermejo *et al.*, 2003b). Use of the logistic model showed that the day on test at which the maximum increment in food intake occurred ranged between 71–81 days on test, while the day on which the plateau of intake was achieved varied from 45–48 days on test (90 days of age at start of test). Heritability for parameters characterizing food intake at the beginning of the test period ranged from

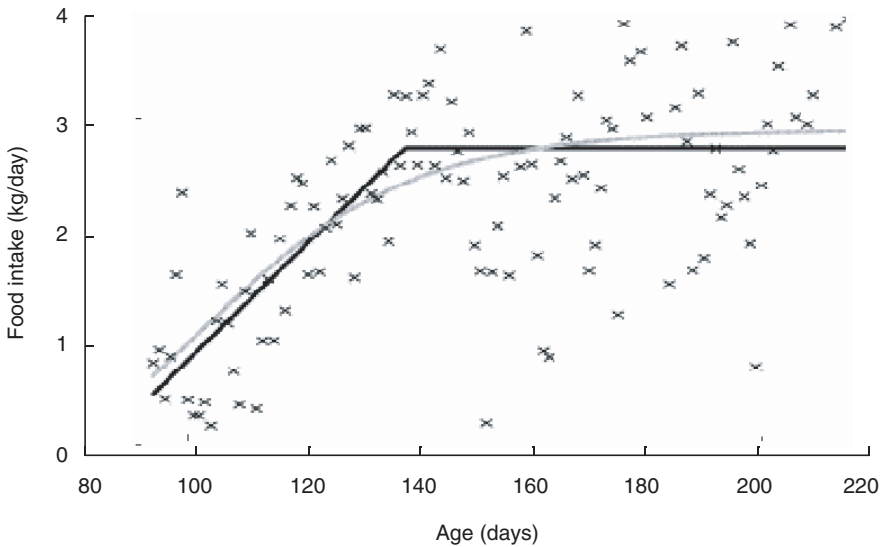


Fig. 15.3. Estimation of daily feed intake using linear-segmented (black line) and logistic (grey line) functions presented for one animal; x, raw data (from Bermejo *et al.*, 2003a).

0.03–0.30 and selection based on the logistic function resulted in a 0.2 kg/day reduction in food intake at the end of the test period, but with only a small effect on intake at the early part of the test. Further analysis, including random regression models, allowed early intake to be increased as well as late intake to be reduced (Bermejo *et al.*, 2003c), and adoption of this method in breeding programmes should lead to improved food efficiency.

Comparison between breeds shows that Pietrain pigs eat less than Landrace or Meishan through most of the growing period (see Fig. 15.4). From 40–70 kg, the Landrace pigs ate less than the Meishan, although the former ate more at 20 kg; the plateau in food intake was reached first by the Meishan, followed by the Landrace, the Pietrain being last.

Expressing intake relative to metabolic live weight ($LW^{0.75}$) shows that food intakes were 0.128, 0.108 and $0.123LW^{0.75}$ for Landrace, Pietrain and Meishan types, respectively. Data collected under commercial conditions show ad libitum food intakes of all three types of pig to be substantially less than the value of $0.12W^{0.75}$ that might be expected from research results.

Neuropeptide Y (NPY) and leptin have been identified as being involved in the control of food intake (see Chapters 4 and 5) and it might be expected that genetic differences in intake would be accompanied by changes in such transmitters as these. This was investigated by Cameron *et al.* (2003), who monitored serum NPY and leptin concentrations after six generations of divergent selection for daily food intake in pigs. At 90 kg live weight, NPY concentration was not affected while serum leptin concentration was increased (3.06 versus 2.45 ng/ml) by selection for high intake compared with selection for low intake. This is consistent with increased leptin resistance in fatter

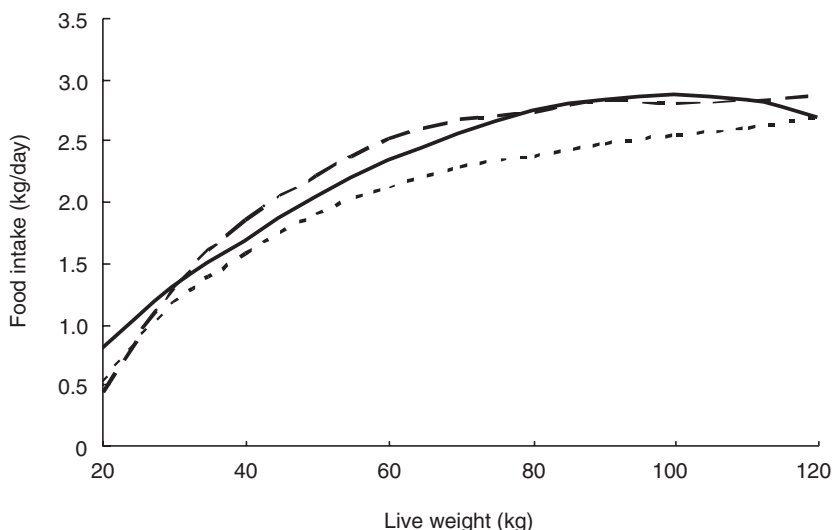


Fig. 15.4. Relationship between daily feed intake and live weight for three pig types: Landrace (solid line), Pietrain (dotted line) and Meishan (dashed line) (from Whitemore *et al.*, 2001a).

animals and humans. The relationship of leptin to either growth or food intake is not sufficiently close for serum leptin to be used as a selection criterion.

It has been found that a line of pigs selected for rapid weight gain (with higher voluntary food intake) had a significantly lower plasma concentration of cholecystokinin (CKK, see Chapter 4) per unit of food consumed compared with the low line, while higher blood glucose, insulin and IGF-1 concentrations and greater basal blood growth hormone concentrations have been found in pigs selected for high weight gain than for control pigs. All of these differences are in the direction expected for animals with higher nutrient demand, which the animal attempts to satisfy by taking a higher intake of food.

Beef cattle

Although intakes of cattle of various beef breeds are similar at the same body weight, those for dairy Holsteins are usually higher, by some 8%, although this difference has disappeared by 450 kg (NRC, 1986). Perhaps, the lower body fat content of growing Holsteins underlies this difference. Another difference is that beef calves are normally with their dams and can obtain milk up to 6 months of age, whereas Holsteins are usually weaned from milk replacer at about 6 weeks and thus have had a longer time to adapt to solid food by the age the comparisons are made. Higher growth potential is likely to be the most important reason.

Between-species comparison of the voluntary food intake of adult animals shows that intake is related to live weight^{0.73} (metabolic live weight). Within a species the level of intake may also be related to metabolic live weight, but the exponent is greater the less digestible the food. This generally accepted

relationship between intake and live weight does not hold good as a group of animals grow or fatten, however, as discussed above. For example:

$$\text{DMI (g/day)} = 172\text{LW}^{0.61} \quad (15.17)$$

calculated from the cattle data used by ARC (1980). NRC (1987) show predictions of intake against net energy content of diet. Intake per unit of metabolic body weight is stable or rising up to about 350 kg body weight, but falls above this weight.

Sheep

Merino sheep selected for high weaning weight had higher food intake than a strain selected for low weight at weaning, which to some extent persisted even when intake was expressed on a per kg basis (Thompson *et al.*, 1985).

Residual food consumption

What is required is not low intake per se but low intake relative to performance, i.e. minimization of the difference between actual food intake and that predicted to be required for maintenance and production, known as Residual Food Consumption (RFC). Selection for low RFC should reduce food intake without affecting performance, thereby improving the profitability of animal production.

For growing animals:

$$\text{Food intake} = b_1(\text{Pr} + \text{Lr}) + b_2W^{0.75} + e \quad (15.18)$$

where b_1 and b_2 are the efficiency coefficients for production and for maintenance, respectively, Pr and Lr are the rates of deposition of protein and lipid, respectively and e is the error term, or RFC (Whittemore *et al.*, 2001a).

Poultry

The concept of Residual Food Consumption (RFC) for laying hens is fully discussed by Luiting (1999). Factors related to RFC are fatness, behaviour pattern and metabolic heat loss. The heritability of RFC is estimated to be 0.37 and it is suggested to use RFC from 25–29 weeks of age in cocks as a selection tool to improve conversion efficiency of laying hens (Katie and Nordli, 1992) as, although it is better to record RFC in hens, it is cheaper to do it for cocks. A breeding programme including RFC was calculated to be 17% more efficient than one without.

Pigs

Although RFC has a lower heritability (0.30–0.38) than food intake (0.45), it is better than that for efficiency of food conversion (0.28) (Mrode and Kennedy, 1993). About half the variation in food intake is residual, the causes of which

include food wastage, physical activity, digestibility and efficiency of utilization for maintenance and/or growth. The use of RFI in selection programmes for pigs warrants further study.

Cattle

Herd and Bishop (2000) found RFC for beef cattle to have a heritability of 0.16 and to be phenotypically independent of size and growth; it was negatively related to lean deposition. RFC was not affected by differences in pre-test rearing treatments, in contrast to live weight at the start or end of test, ADG and FCE. It was concluded that selection for low RFC could reduce food intake without affecting growth rate or mature size, thereby increasing the efficiency of beef production.

Selection for high growth rate or efficiency is likely to increase cow weight, counteracting any benefits in terms of improvements in the performance of the calves during growth. Thus, selecting for low RFC rather than these other parameters has great advantages and is accompanied by better digestibility and reduced heat increment of feeding and activity (Richardson and Herd, 2004). Protein turnover, tissue metabolism and stress contribute at least 37% of the variation in RFC, and it seems as if selection for low residual food intake in beef cattle is accompanied by a reduction in susceptibility to stress. The effects of selection for improved RFC on protein turnover, tissue metabolism, ion transport and stress susceptibility require further research.

Heritability for dry matter intake in lactation has been estimated as being between 0.18 and 0.46, depending on the stage of lactation, but it would appear that the concept of RFI has not been applied to dairy cows.

Compensatory growth

Following a period of reduced growth caused by restriction of food, illness or environmental stress, animals grow at a faster rate than unrestricted animals of the same age. This phenomenon is called compensatory growth and is due to increased voluntary food intake, increased weight of gut contents and improved efficiency of conversion. The latter may be due to reduced maintenance requirements. Whether the increased intake is a result of or a cause of the increased growth is not easy to answer; restriction will have reduced the fat content of the body, which will tend to increase appetite (see below).

Poultry

Compensatory increases in food intake by cockerels following restriction have been demonstrated. However, in our work with broiler chickens, restriction to 85% of ad libitum was not followed by an increase in intake when ad libitum access was restored (Yalda and Forbes, 1990). It must be noted that, during restriction, the protein content of the food was increased to maintain the same protein intake as controls, and protein deposition was not reduced. It may be that

compensation for a period of restriction is due to the low body protein for the animals' age, rather than to reduced body fat, at least in growing broiler chickens.

Pigs

Restriction of pigs from 25–50 kg live weight to half of the ad libitum level of food was followed by increased intakes when free access was given, to the extent of 15% above unrestricted controls. This work was then extended to investigate the ability of growing pigs to compensate for the effects of diet dilution when returned to conventional foods (Owen and Ridgman, 1968). Young pigs up to about 60 kg weight did not recover fully, whereas older pigs did compensate by eating more, although it took some 2 weeks for this to occur. We should note, therefore, that the results of short-term experiments can be very misleading.

Cattle

Ruminants are often subjected to periods of underfeeding, both in the wild and in practical animal husbandry. Therefore, many studies of compensatory growth in ruminants have been undertaken and it is concluded that compensatory growth is largely dependent on compensatory increases in voluntary intake. A significantly higher herbage intake by cattle, which had been fed at a low level during the previous winter, has been seen, compared with those fed at a high level. Figure 15.5 shows the higher intake, for any given body weight, of animals that had suffered a period of restriction before introduction to the experiment (Pickard *et al.*, 1969).

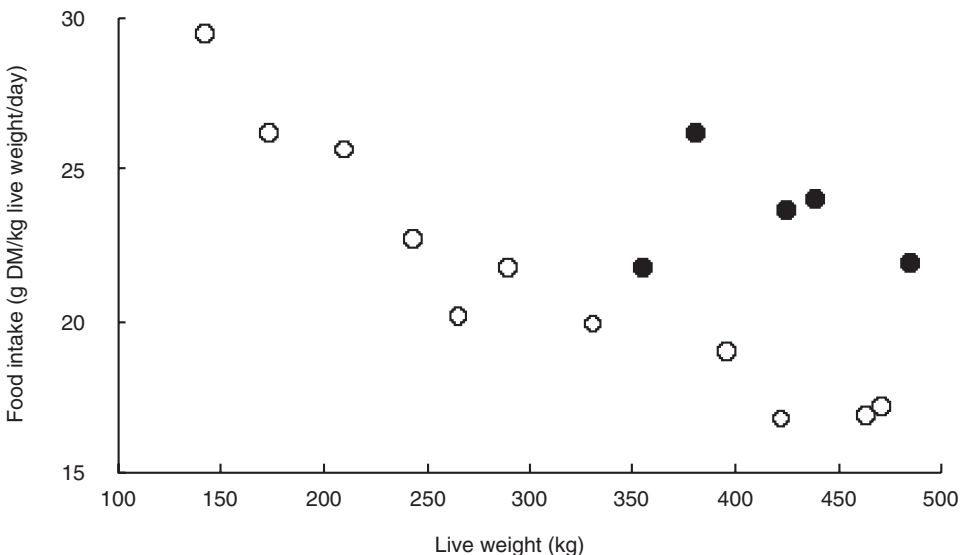


Fig. 15.5. Voluntary intake of a cereal-based food by growing cattle; ○, fed ad libitum throughout; ●, undergoing compensatory growth (from Pickard *et al.*, 1969).

Reduced maintenance requirements may play a part, and the unexpectedly low heat production of adequately fed ruminants after a period of restriction may occur as a result of reduced thyroid hormone secretion.

Sheep

Lambs recover from a period of restricted feeding if subsequently fed *ad libitum*. For example, 4-month-old wether sheep held at a weight of 20 kg for either 4 or 6 months and then offered free access to a good-quality food had a higher food intake and lower heat production than the controls that had been fed *ad libitum* throughout (Graham and Searle, 1975). The increased voluntary intake occurring during compensatory growth is evidenced irrespective of the metabolizable energy content of the diet, although compensation is better on a high-quality food than one of poor quality.

From a review of the literature it can be concluded that, the longer the period of restricted feeding the greater the food intake when *ad libitum* feeding is resumed. Gut fill is very high – as much as 25% of body weight – in compensating lambs, compared with 15% in controls offered free access to food throughout. Although this difference could be due to the greater availability of abdominal capacity in the restricted lambs, which are thinner, it is more likely that the increased rate of utilization of nutrients is the primary stimulus to higher intake which, in turn, resulted in a higher volume of ruminal contents, according to the MTD hypothesis (see Chapter 10). The high intake during compensatory growth is not likely to be caused by low thyroid secretion rate *per se*, however, because treatment of sheep with exogenous thyroxine stimulates voluntary intake even though body reserves may be mobilized to support the higher metabolic rate.

Growth manipulation

Since the middle of the 20th century, several ways of stimulating growth in farm animals have been developed, some of them having been used very widely on a commercial scale. Many countries have now banned most or all, because of fears for human health, and some have never been licensed.

Few, if any, have their primary effect on voluntary food intake but, in several cases, intake is increased, through effects on either digestion or metabolism.

Antibiotics

PIGS When included in pig diets antibiotics often increase efficiency of digestion, but also consistently increase voluntary food intake to a small extent. However, antibiotics are now banned in Europe for routine prophylactic use.

CATTLE Monensin and similar food additives modify ruminal fermentation to increase the production of propionate and reduce methane production. They have been widely used commercially as they improve food conversion

efficiency. In beef cattle there is either no increase in weight gain and reduced voluntary food intake or increased gain with no change in intake. Beef cows produce milk more efficiently, forage intake being depressed from 9.6 to 8.3 and 7.7 kg/day by the inclusion of 50 or 200 mg/day of monensin in the food, with no consistent effect on weight change (Lemenager *et al.*, 1978).

In a second trial by the same authors, weight gains were improved and milk yields were not affected, even though the amount of time spent grazing was decreased by the inclusion of monensin in the concentrate supplement. It has been suggested that the decrease in intake occurring when monensin is included in concentrated foods for cattle is due to an aversion to some sensory cue associated with the malaise resulting from the changes in ruminal fermentation.

Anabolic steroids

POULTRY Oestrogens have been used commercially to stimulate weight gains; their effect, unlike that in ruminant animals, is primarily to stimulate food intake and, in the absence of marked stimulation of true growth, the rate of fat deposition. Even in force-fed broilers, oestrogen treatment significantly increases the weight of food consumed voluntarily. The use of steroidal growth promoters has now been banned in Europe.

PIGS Voluntary intake is decreased during treatment with commercial doses of a mixture of diethylstilboestrol (DES) and methyl testosterone. It is not clear to what extent this reduction is due to direct effects of the oestrogens on intake and to what extent to reduced fat deposition induced by the steroid. Anabolic agents of this type are not used commercially because of the risk of residues in meat and because the growth stimulation is less than in ruminants where intake is not depressed.

The use of uncastrated boars for meat production is more widespread since the rate of lean meat production has increased, and the propensity to fatten is sufficiently low that they can be fed *ad libitum*.

CATTLE Following the discovery in the early 1950s that DES, a synthetic oestrogen, had anabolic properties and was orally active in ruminants, its use was widely adopted in the USA. Voluntary intake is increased in response to increased weight gain due to greater secretion of growth hormone which, by stimulating growth, increases the rate of utilization of metabolites. DES was withdrawn in the early 1970s because of fears concerning its safety for human consumers of meat. In the UK, another synthetic oestrogen, hexoestrol, was used because it is not orally active and is therefore potentially safer, but this has also been banned.

Natural oestrogens, which have very similar biological effects to DES and hexoestrol but a much shorter half-life, were then used on an extensive scale; they stimulate growth in castrated or intact male ruminants and food intake is increased.

Androgens stimulate growth by means other than growth hormone, probably by a direct effect on muscle. Trenbolone acetate was widely used as it

stimulates growth without inducing undesirable male characteristics. It is likely that the effect of androgens on intake is due to the increased demand for nutrients, although a more direct effect was suggested by results showing a large and rapid increase in voluntary intake in ketotic cows treated with 60 or 120 mg of trenbolone acetate. The use of all of these substances as growth stimulants for farm animals is now banned in Europe.

The mechanism by which oestrogens influence DMI is still not very clear, although there is evidence that it regulates the secretion of leptin from adipocytes.

SHEEP Voluntary intake by sheep of a 0.5 hay:0.5 concentrate food was increased by DES from 1.43 to 1.50 kg/day. This increase in intake is the response to increased weight gain rather than its cause, because restricting treated animals to the same weight of food as controls does not completely prevent the increase in weight gain and carcass weight.

Growth hormone (GH)

There was a dose-related decrease in carcass fatness in lambs treated with GH, but live weight gain and food intake from 10–22 weeks of age were not significantly affected, although intake tended to decline as dose was increased from 0.025 to 0.250 mg/kg/day. It can be speculated that the mobilization of lipid reserves and increase in plasma free fatty acid levels caused by GH act as satiating agents.

Corticosteroids

Corticosteroids, whose secretion increases during stress, are catabolic in laboratory animals but have stimulated weight gains and food intake in several experiments with sheep. Doses of 25–75 mg cortisol/day given intramuscularly to sheep for 3 weeks resulted in plasma levels similar to those seen during stress. Intake and weight gains were increased, especially when intake was otherwise low because of seasonal factors. Doses of 100 or 300 mg given three times per week stimulated intake from 934 to 1170 g/day of lucerne and from 1107 to 1306 g/day of a 0.5 lucerne:0.5 barley ration. Cortisol tended to reduce the amount of protein in the carcass, but increased the amount of fat significantly.

Combined cortisone (100 mg of cortisone three times per week) and DES (3 mg implant) treatment, to ascertain whether the higher intake due to the former could be combined with the greater protein deposition induced by the latter (Ellington *et al.*, 1967), increased intake of a pelleted food by sheep from 1.65 to 1.89 kg/day; animals given DES alone had a mean intake of 1.72 kg/day, while those given cortisol had a daily intake of 1.97. Withdrawal of the cortisone treatment 2 weeks before slaughter to reduce fat deposition reduced the mean intake to 1.65 kg/day.

Similar results have been obtained with cattle; subcutaneous injection of 1 g of cortisone acetate three times per week increased voluntary intake significantly from 12.1 to 13.9 kg/day, with an increase in carcass fat.

β -agonists

β -adrenergic agonists were originally investigated for their ability to reduce fat deposition, but were also found to stimulate muscle growth. A commercial dose for steers of 10 mg/day of the β -agonist clenbuterol in the food significantly altered carcass composition without affecting voluntary intake. Overdosing with 500 mg/day to study the toxic effects depressed intake.

Cyproheptadine

Cyproheptadine, a pharmacological antagonist to serotonin, stimulates food intake and growth rate in children and rats. Oral administration of 0.64–1.92 mg/kg live weight/day to growing cockerels caused a dose-dependent increase in daily food intake (Injidi and Forbes, 1987), but there was no improvement in food conversion efficiency and it is unlikely that such treatment would be useful commercially.

Fatness and Food Intake

Relationships between body fat and intake

Most adults of many species maintain a more or less constant body weight despite changes in food quality and climate. This has long been ascribed to a regulation of body fat, and the mechanism has more recently been shown to involve leptin (see Chapter 4). The statement that body fat content is held constant by changes in energy intake (and/or output) cannot now be regarded as sacrosanct. Incorporation of fat in a diet for rats, for example, gives a reduction in intake, but not sufficient to maintain a constant level of digestible energy intake, which remains slightly higher than with the standard food, with the result that the animals gain weight slowly.

Similar phenomena are also observed in chickens and pigs (see Chapter 11). Although this has been ascribed to an improvement in the palatability of the food, it is more likely to be the effect of the higher energy density. A theory of metabolic efficiency, heat production or comfort might account for these observations, as dietary fat is used efficiently for body fat deposition, so diets high in fat do not involve as much metabolic work and/or discomfort as carbohydrate diets.

The influence of fatness on intake of those animals that have been selected genetically for rapid weight gain, e.g. pigs, cattle, sheep and broiler chickens, seems to be less than in other species, e.g. rats, goats and laying hens, which have not been so selected.

Poultry

Force-feeding of mature chickens, at a level which caused great increases in the fat stores, was followed by complete absence of voluntary feeding for up to 10

days and, even 23 days after the cessation of force-feeding, the birds had not recovered their pre-experimental level of intake (Lepkovsky and Furuta, 1971). Plasma triglyceride concentrations were elevated during the period of force-feeding. Force-feeding an amount equivalent to half the previous daily intake depressed voluntary intake to about 63% (i.e. 13% overeating) (Polin and Wolford, 1973). The birds compensated for the loading, but not sufficiently to avoid increased total food intake and fat deposition.

More recently, Yalda and Forbes (1991) have shown that force-feeding of growing broiler chickens the same amount as the voluntary intake of control birds – divided into five meals spread throughout the day – did not completely suppress feeding, which continued at 30% of control to give a total daily intake considerably higher than normal. This resulted in a great increase in fat deposition so it was surprising that, when force-feeding was terminated, voluntary intake increased to 122% of control and declined only slowly to that level over the next few weeks. Apparently, the over-provision of nutrients during force-feeding had stimulated the rate of fat deposition, and this had got the body into such a metabolic state that the high demand for nutrients generated a high voluntary intake.

Mild restriction (130 g/day) of older broilers from 18–47 weeks of age, without increasing the protein concentration of the food, was followed by hyperphagia (180 g/day) for 2 weeks before a steady rate (160 g/day) was achieved (March *et al.*, 1982). Probably, the increased intake was a response to reduced protein deposition during the period of restriction. A problem with these manipulations is that a period of abnormal nutrition is involved, to which control birds are not subjected. This was overcome by reducing body fat content by partial lipectomy involving surgical removal of the abdominal fat pad of chickens (Taylor and Forbes, 1988). Both lipectomized and sham-operated birds recovered their pre-operative food intakes quite rapidly, ate similar amounts of food and gained at similar rates; when slaughtered at 14 weeks of age the lipectomized birds were lighter than the controls by an amount (154 g) similar to the weight of fat removed at surgery (190 g).

The conclusion drawn is that broilers of this age do not compensate for removal of fat by increasing their food intake. However, there might be a difference between: (i) birds that have had all their various fat depots depleted by a period of underfeeding, which can be repleted when ad libitum feeding is reintroduced; and (ii) those in which one fat depot is surgically removed, thus preventing any more deposition at that site – the remaining depots might be depositing fat at the maximum rate throughout and there would be no possibility for them to increase their rate of synthesis after removal of the fat pad.

The abdominal fat pad may not be truly representative of fat in general, as it has a later maturity than other fat depots. It is clear, nevertheless, that the food intake of broiler chickens is not closely controlled by the amount of fat in the body.

Broiler breeder stock become very fat if allowed to eat ad libitum and, in practice, have to be fed at a severely restricted level if reduced reproductive rate is to be avoided (see Chapter 16).

Pigs

Domestic pigs may become grossly overweight, as if the feedbacks from fat are reduced or ignored by the brain. It might thus be suggested that the lipostatic theory does not apply and that intake is limited by the maximum rate of fat synthesis above which precursors will accumulate and prevent higher levels of food intake. Perhaps selection for rapid weight gain (with little regard for composition at a time when fat was more acceptable to the consumer) was a selection against negative feedback from fat to the CNS. Selection against fat deposition in recent years has been accompanied by reduced voluntary intake (see above).

Voluntary intake actually declines in many growing pigs once they have reached around 100 kg live weight (see above). In gilts, this might be due to the onset of oestrus at around this weight, although the intake of castrated males tends to fall more steeply, but from a higher peak.

Cattle

Northern European domesticated breeds of cattle become very fat if offered free access to high-quality feeds, but eventually reach a plateau. Non-pregnant mature Friesian cows fed ad libitum on a pelleted food were still gaining weight at about 1 kg/day when they weighed 700 kg, while smaller-framed Jerseys showed signs of a plateau at about 430 kg (Monteiro, 1972). The Jersey breed has not been selected for rapid growth, while the Friesian is a 'dual-purpose' breed that might have a much greater potential for fattening than the Jersey or other 'pure' dairy breeds.

In a more critical analysis of effects of fatness on intake, Bines *et al.* (1969) fed cows at two levels to bring them into either fat or thin condition. Subsequently, when straw was offered alone, mean intakes were similar for both groups but, when offered hay or concentrates, thin cows ate 31% more or 23% more, respectively, than fat ones, despite the fact that the fat cows were heavier. The weight of ruminal contents was greater in the thin cows than in the fat cows when offered hay, and it was thought that ruminal capacity was limiting hay intake. The higher intake of concentrates by the thin animals was attributed to their greater capacity for lipogenesis.

Sheep

Food intake by sheep is generally inversely related to the proportion of fat in the body. A close inverse correlation between intake of dried grass pellets and condition score was observed in Scottish Blackface ewes (Foot, 1972). In order to examine the relationships between fatness and intake critically, it is better to work with animals whose differences in fatness are imposed by the experimenter rather than by natural differences in fatness. Sheep with an average starting weight of 50 kg were fed differentially until 33 or 7% of their weight was fat (Graham, 1969). Subsequent DM intakes were 65 and 106 g/kg live weight^{0.75}/day, respectively, so that fatness had a clear effect on intake.

Scottish Blackface ewes differentially fed to make them thin (L, mean condition score 2.15) or fat (H, mean condition score 3.15) subsequently ate 2176 and 1727 g DM/day of dried grass pellets, respectively (Sibbald and Rhind, 1997). Mean basal plasma insulin concentration was higher in the H than in the L ewes (43.0 versus 29.0 mU/l). From this and other results it was concluded that the effect of previous body condition on voluntary food intake may be mediated by plasma insulin concentrations providing a long-term feedback signal to the brain. The feeding behaviour of these sheep was studied when they had 6, 12 or 24 h/day access to the pelleted food (Sibbald, 1997). Intakes for the 6, 12 and 24 h food access treatments were 1429, 1686 and 1805 g DM/day, respectively, and there were no interactions between the effects of body condition and food access time. More time was spent feeding by thin ewes (231 versus 197 min/day), but frequency of meals and rate of intake during meals were not markedly affected by body condition, i.e. meal size was greater in the thin animals.

Sheep kept on an *ad libitum* feeding regime of a complete pelleted food, for up to 4 years from the age of 4 months, showed no difference between the level of intake per animal between 12 months of age and 3.5 years of age, during which period they gained in weight from about 30 to 130 kg (Blaxter *et al.*, 1982). It was concluded that: 'Voluntary food intake is established early in life and this determines the ultimate body size sheep attain on a particular diet', because asymptotic body weight was positively related to food intake.

In a similar experiment, Thompson and Parks (1983) offered a pelleted food to Merino and Dorset Horn rams and wethers. Intake increased to approximately 50 weeks of age then declined rather than remaining stable as observed by Blaxter *et al.* (1982), presumably due to the increasing negative feedback effect of accumulating body fat. While the sheep of Blaxter *et al.* (1982) were still growing at 3 years of age, those of Thompson and Parks (1983) had ceased growing by 2 years of age. The latter calculated that, according to their equation for intake predicted as a function of the energy required for both growth and fattening, this difference in age at maturity accounted for the different patterns of long-term food intake in the two experiments.

While the afferent pathway for the lipostatic control of fatness has been supposed to be leptin (see Chapter 4), Tolkamp *et al.* (2007) have used the Ketelaars and Tolkamp theory of intake control (see Chapter 9) to provide a different explanation for the plateau in weight achieved by sheep. They calculated that the efficiency with which fat is deposited declines with body fatness, and derived parameters for their model from two groups of sheep, estimating body fat content from measurements of body condition score. The intake of hay or pelleted food by three other groups was predicted quite well, and extension to include a Gompertz curve for protein deposition allowed good simulation of changes in body weight and condition score. The goodness of fit between observed and predicted results is additional evidence, albeit circumstantial, of the validity of the efficiency theory of Ketelaars and Tolkamp.

Ewes lose their teeth from the age of about 6 years, which can reduce rate of eating, especially of hard foods such as root crops. This is likely to affect only

the intake of foods that are eaten very slowly, however, and Dove and Milne (1991) found almost no difference in intake of long herbage between ewes with full and broken mouths, even though live weight gain and body condition score were lower for those ewes with poorer teeth.

Wild and undomesticated ruminants do not become permanently obese, but show an annual cycle of fluctuating body weight and fatness (see Chapter 17).

Mechanisms for effects of body fat

Some discussion of possible mechanisms for interrelationships between fatness and voluntary intake is also to be found in Chapter 4.

Physical constraints

The underlying reason for the inverse relationship between fatness and voluntary intake in ruminants may be one of competition between abdominal fat and rumen for abdominal space, and there have been several reports of negative correlations between the volume of abdominal fat and that of ruminal contents.

Karkeek (1845) noted that: '... in proportion as an animal (cattle) fattened, so in proportion did the organs which are chiefly concerned with nutrition become diminished in size ... it is rather a remarkable coincidence that the fatter an animal becomes at this period (later stages of fattening), the less food it consumes'. There are negative relationships between the volume of ruminal contents in cows after slaughter and the volume of abdominal fat and ruminal digesta further depressed in advanced pregnancy.

In pregnant ewes slaughtered at various stages of pregnancy, it was noted that the volume of ruminal contents and the voluntary intake of hay was inversely proportional to the volume of 'incompressible abdominal contents' and that abdominal fat was a significant cause of variation in this (Forbes, 1968b). If physical limitation was the sole reason for the reciprocal relationship between fatness and intake, then fat would not depress intake when highly digestible foods were given; however, the work of Orr (1977) showed that intake was lower in fat animals even when a highly digestible diet was fed.

Lean or fat mature sheep (52.2 or 83.2 kg live weight) were offered foods of three qualities (8.4, 10.0 or 12.2 MJ ME/kg DM). In both lean and fat animals, voluntary food intake compensated for differences in ME concentration, although intake was significantly lower in the fat groups. Thus, the fat animals were still controlling their ME intake, but at a lower level than the lean sheep. These experiments show that, in animals with equal propensity to fatten (assuming random allocation of animals to experimental groups), increasing fatness is associated with declining voluntary intake.

The only experiment with ruminants reporting surgical removal of fat is that of Joubert and Uekerman (1971), who removed the tail of fat-tailed sheep, which weighed 1.9 kg in the undocked animals at slaughter. However, the subsequent weight gains were the same as those of non-operated control

animals, and there was no increase in body fat to compensate for the loss of the large tail deposit. As discussed above for poultry, there is a clear difference between reducing body fat by underfeeding and by lipectomy. In the former case the adipocytes are still present, albeit in a depleted state, and will take up precursors for fat synthesis when they become available, thereby exerting an effect on intake. In the latter case the adipocytes are no longer present, and therefore cannot exert such an effect; hence, the lack of a compensatory increase in food intake following the surgical removal of adipose tissue.

Metabolic constraints

The role of hormones and metabolites in the effects of body fatness on food intake has been covered in Chapter 4. However, it has been pointed out that there are weaknesses in the 'leptin hypothesis' (Speakman *et al.*, 2002). These authors developed a theme proposed many decades earlier, that the increase in body weight through overeating leads to an increased maintenance requirement, thereby eventually resulting in stable body weight as long as food intake remains stable.

Speakman *et al.* (2002) provide more physiological and metabolic evidence for this theory, specifically through their observation that, not only does adipose tissue have a maintenance requirement for energy, but weight gain in adult animals is part fat, part lean tissue and the lean tissue deposition has a much higher energy requirement for maintenance than does adipose tissue. Their calculations demonstrate how their theory can predict body weight and intake changes similar to those observed in fattening and fasting animals, without invoking a negative feedback such as that proposed by others as being provided by leptin.

Conclusions

The higher the intake of milk by the sucking animal the lower its intake of dry food, and this can increase the setback at weaning, when the withdrawal of the supply of milk stimulates the intake of solid food, encouraged by creep feeding before weaning. Artificially fed ruminants respond to dilution of the milk replacer by changes in intake in the appropriate direction, but not usually to an extent appropriate to maintain the same intake of energy.

Food intake increases as animals grow, not in direct proportion to live weight but more usually in proportion to live weight raised to the power of 0.6. A period of restricted feeding is followed by higher voluntary intake and a tendency to catch up with the live weight of unrestricted controls.

Although fatness depresses the intake of farm animals, as it does in other species, the effect is less and, as they approach maturity, pigs, broiler chickens, cattle and lowland breeds of sheep become very fat if fed *ad libitum* on good-quality diets. We must accept that the control of food intake is very complex and not expect to be able to make simple statements about its interrelationships with body weight and fatness.

16 Reproduction and Lactation

The changes in nutrient requirements that take place during pregnancy, lactation and egg-laying lead to changes in voluntary food intake, but these are not always well-balanced, and unwanted increases or decreases in body fatness often arise. However, as reproduction is so essential, it has been proposed that changes in food intake at key reproductive events have some selection advantage and are not simply accidental (Weston, 1996). Forbes (1986a) and Ingvarsten and Andersen (2000) have reviewed the physiological changes associated with these changes in intake in ruminants.

Oestrus

A decrease in food intake is often observed at the time of oestrus, when oestrogen levels are high and progesterone is low. Reduction in intake at oestrus allows females to spend more time responding to males. The rut in males, seen so clearly in deer, allows full concentration on mating with a reduced competing drive for food.

There are several changes occurring during female reproduction which are responsible for changes in voluntary intake. Oestrogens, while being associated with small increases in intake when used at low doses as growth promoters, depress intake when secreted in larger quantities (50 $\mu\text{g/day}$ in the ewe) by the ovaries at oestrus or by the placenta in the last few weeks of pregnancy.

Although it is known that there are oestrogen receptors in the brain and it had been assumed that the primary effects of oestrogens on behaviour were through these receptors, gonadal steroids also have important effects on peripheral tissues, and changes in the metabolic activity of these tissues also cause secondary changes in feeding behaviour.

Pigs

During the week that included oestrus in sows, the total food intake was found to be 4 kg lower than in each of the other 2 weeks of the cycle. The most likely reason for this is that blood oestrogen levels are high at oestrus.

Cattle

In the cow, total food intake sometimes declines at oestrus, less time is spent eating and there also seems to be a change in the choice of food. J.H.M. Metz (personal communication) noticed that the intake of concentrates declined while that of hay increased at oestrus (cows usually eat about 0.2 of their intake as hay if it is available free choice with concentrates).

Sheep and goats

Concentrate intake is often decreased for a day or two around oestrus, and daily intake was depressed in a dose-dependent manner when oestradiol was infused intravenously into lactating goats, at the rate of 8 g food/ μg oestradiol, although there was no effect on the intake of hay, offered simultaneously (Forbes, 1986a). The concentrate intake of goats was further depressed at oestrus by an amount equivalent to that caused by 50 μg of oestradiol/day – approximately the rate of secretion of oestrogens by the ovary during oestrus.

The differential effect of oestrogens on the intakes of concentrates and forage is also illustrated by the results of an experiment in which oestradiol was infused into castrated male sheep. When hay was offered, intravenous infusions of oestradiol at up to 400 $\mu\text{g}/\text{day}$ had no consistent effect, but when a complete pelleted diet was offered a 90 $\mu\text{g}/\text{day}$ infusion caused a lower food intake, followed by a significant increase in intake after treatment was stopped. Note also that when given hay *ad libitum* and a restricted amount of concentrates, goats nevertheless reduced their intake of the latter only when infused with oestradiol or during oestrus.

The effects of oestradiol infusion on intake of an optimal food were greater in fat wethers than in thin (Weston, 1996; Fig. 16.1). Given that adipose tissue absorbs steroids, it would be expected that blood levels of oestradiol would have been lower in the fat animals, so the effects in this experiment were not likely to have been on the CNS, but on adipose tissue itself. Oestrogens affect adipose tissue metabolism, and adipose tissue can influence food intake (see Chapter 15), so the effects of oestrogens on food intake are likely to be through both peripheral and central effects.

Pregnancy

In simple-stomached mammals, there is increased food intake during pregnancy to match the high nutrient requirements of large litters of fetuses. On

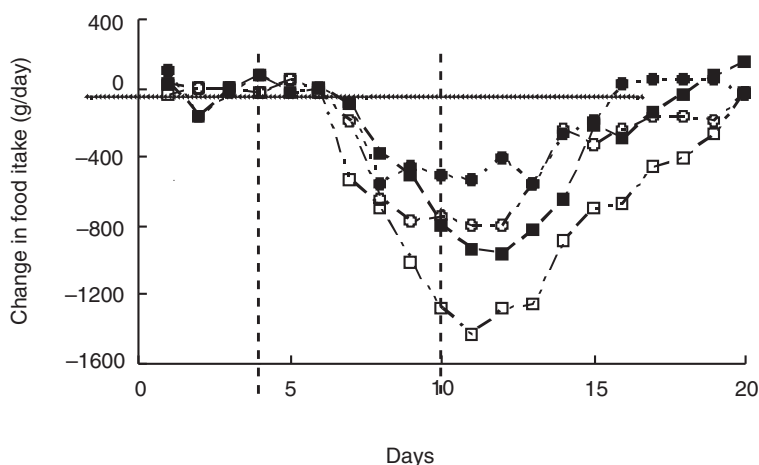


Fig. 16.1. Effect of continuous intravenous infusion of 73 (solid symbols) or 160 (open symbols) μg β -oestradiol on the food intake of fat (squares) or thin (circles) adult wether sheep. The horizontal line at zero change of intake corresponds to intakes of 1600–1800 g DM/day; the vertical lines indicate the start and end of infusion (from Weston, 1996).

the day of parturition, intake is very low as the mother prepares her nest and enters the first stages of labour.

Pigs

The pregnant sow tends to overeat and is usually fed at a restricted level to prevent over-fatness. The severity of the restriction, and the difficulty of ensuring that individuals in a group get their fair share, has engendered significant criticism and a great deal of research.

The possibility of using a food with high fibre content to restrict pregnant sows' intake has been investigated. In one experiment, six foods were formulated to have equal digestible energy content, by including 650 g/kg sugarbeet pulp (SBP), 360 g/kg straw, 370 g/kg oat husk, 460 g/kg malt culms, 610 g/kg rice bran or 670 g/kg wheat bran (Brouns *et al.*, 1995). Five of these were eaten at 6–8 kg/day, with the sows gaining weight excessively, but the food that included SBP was eaten only at 2.3 kg/day, which gave a small weight loss. In a second experiment, voluntary food intake decreased from 5.0 to 3.0 kg/day when the inclusion level of SBP increased from 400 to 650 g/kg. The intake of SBP tended to remain constant at 2.0 kg/day for all diets, suggesting that intake was limited by gut capacity (see Chapter 11).

This prompted studies with a food containing 600 g/kg of unmolassed SBP, and it was confirmed that this allowed sows to be fed *ad libitum* throughout pregnancy without becoming obese. Low-ranking sows are at a disadvantage when fed conventional food at a restricted level in a group, but not when fed *ad libitum* on the beet pulp-based food. The rate of eating of this food is much

slower than that of a conventional diet. It was subsequently confirmed that the 600 g/kg SBP can be fed ad libitum to gilts in their first pregnancy without excessive weight gain. Such a feeding system reduces fighting amongst sows, as well as preventing excessive weight gain, and is therefore thought to be good for the animals' welfare.

Food intake of sows given ad libitum access to food containing 45% SBP increased up to the sixth week of gestation and then decreased to parturition (van der Peet-Schwering *et al.*, 2004), but there was no difference in intake of a standard food during lactation compared with sows given conventional food at a restricted level during gestation, nor were there differences in productive parameters such as litter size and piglet growth. SBP is readily available in many northern European countries, but not in many other parts of the world. In reviewing the whole subject of high-fibre diets for sows, Ru and Bao (2004) highlight the need for research into alternative sources of fibre for use in other parts of the world.

In the last few days before parturition it might be expected that sows would be more motivated to make a nest than to seek food. Hutson (1992) trained sows to lift a lever to obtain straw, twigs, a portion of food or nothing. Just before farrowing, they lifted for food most frequently by a factor of 20–433 times, demonstrating that motivation for food completely overshadows that for nesting materials. However, in two of the food-reinforced sows, the onset of nest building resulted in complete cessation of responding for food. As in most aspects of this subject, there are considerable between-animal differences.

Cattle

Although pregnant ruminants may increase their voluntary intake in mid-pregnancy, this increase is proportionately smaller than that which occurs in the pig, and often so small that it is not noticed.

There is often a noticeable decrease of intake in late pregnancy; Ingvarsten *et al.* (1992) presented a comprehensive table of 20 groups of cows from nine publications showing changes of voluntary intake in late pregnancy ranging from an increase of 0.2%/week to a decline of 9.4%/week. In their own observations, heifers in the last 14 weeks of pregnancy reduced intake of a complete food by 1.53% (0.17 kg)/week, with an even higher rate of decline in the last 2 weeks, sometimes as much as a 30% reduction during the last 5–7 days prepartum. In the last month of pregnancy, cows spend less time eating than those in early pregnancy or non-pregnant cows.

There is a significant correlation between the decline in the last 6 weeks before parturition and the birth weight of the calf, suggesting that limitation of ruminal capacity might be responsible for the decline, given the large volume of abdominal capacity occupied by the fetus.

DM intake declines from about the 26th week of pregnancy in dairy heifers by 1.53% (or approximately 0.17 kg)/week until 3 weeks before calving (see Fig. 16.2). In a more recent study, in which the energy density of the diet remained constant during the last 168 days of pregnancy (Ingvarsten and

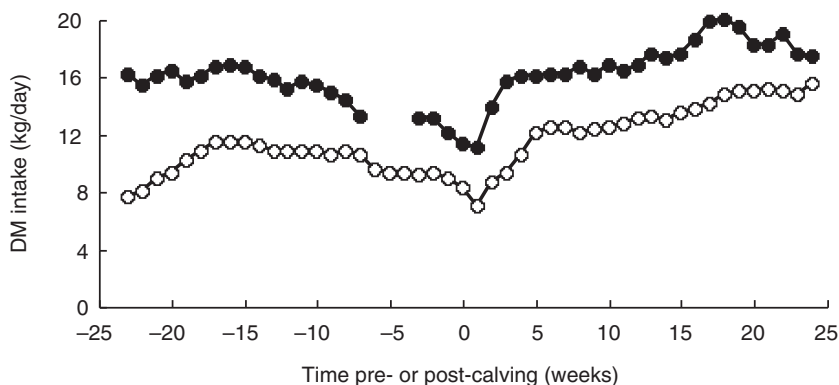


Fig. 16.2. Voluntary intake of food by heifers (○) and cows (●) from mid-pregnancy to mid-lactation (from Ingvarlsen and Andersen, 2000).

Andersen, 2000), a similar decline was observed in the last 12 weeks of pregnancy both in heifers and lactating cows when diet energy was high (11.6 MJ ME/kg of DM), while the decline was much smaller with lower-energy foods (10.2 or 8.3 MJ ME/kg of DM). This is contrary to the hypothesis that the reduction of intake in late pregnancy is caused by physical compression of the rumen by the uterus, and more in line with observations in non-pregnant ruminants that intakes of concentrates are more severely affected by oestrogens than those of forages (see above). It appears as if the role of physical constraints has been overemphasized in ruminants, and that metabolic and endocrine changes in late pregnancy also have a role in this dip in intake.

Many other authors have noted declines in intake, both of forage and concentrates, but there is no need to list these as they are covered by Ingvarlsen and Andersen (2000) and in the first edition of this book (Forbes, 1995).

Sheep

Small increases in intake in mid-pregnancy have been noted with grazing ewes and with ewes fed on hay. In some cases there is increased intake in mid-pregnancy in single-bearing ewes but not in those carrying twins. For example, Fig. 16.3 shows the intake of hay by ewes of the Speckle-faced Welsh breed. This figure also shows the decline in intake in ewes in the last few weeks before parturition (Forbes, 1968a).

Intakes of silage in the last 6 weeks of pregnancy by ewes with twins and multiples were 86 and 81% of those with singles, respectively (Orr and Treacher, 1989), similar to the figures for good hay. With poor-quality hay or straw, however, the differences were much greater (63 and 71%, respectively), suggesting that the quality of the forage food has an influence on the severity of the decline. However, some observations show that the fall in intake in the last

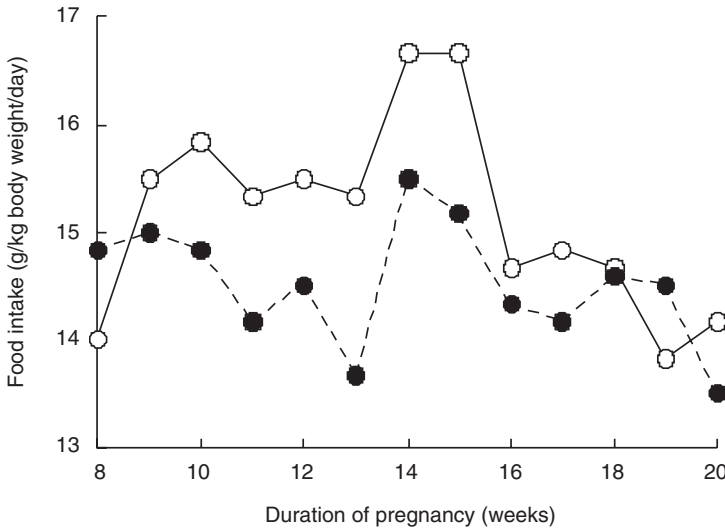


Fig. 16.3. Intake of hay by ewes carrying single (○) or twin (●) lambs between weeks 8 and 20 of pregnancy (from Forbes, 1968a).

few weeks of pregnancy in ewes occurs both with medium and good forage to the same extent, suggesting that there is a reduction in capacity to utilize energy. Voluntary herbage intake has also been noted to decline in late pregnancy, especially with twin-bearing ewes.

The fact that forage intake usually falls in late pregnant ewes has prompted the practical use of concentrate supplements, given at increasing levels in the last 6 weeks before parturition. This has often been practised in experiments as well, leading to uncertainty about the cause of the decline in forage intake. For example, increasing the rate of supplementation of silage from 400 to 600 to 800 g/day over the last 6 weeks of pregnancy showed that silage DM intake declined from 758 to 552 g/day in those ewes fed the concentrates once per day, from 853 to 782 g/day in those given the supplement twice or thrice per day and from 996 to 876 g/day in those animals for which the supplement was mixed with the silage (Wylie and Chestnutt, 1992). It is not possible to apportion the cause of the decline in silage intake between pregnancy and substitution for concentrates.

Fat ewes are particularly susceptible to declining voluntary intake in late pregnancy, and there is a greater reduction in intake of a standard food in late pregnancy in ewes that have been fed at a high level – or on good-quality silage – in mid-pregnancy compared with that of ewes on poor silage.

Prediction of intake

A model was developed to predict hay intake of pregnant ewes, linearized to enable the use of linear programming techniques:

$$\text{HOMI} = \text{COMI}(1.90 - 0.076\text{WEEK} - 1.87\text{HOMD}) + 2069\text{HOMD} - 88\text{LS} + 17.4\text{LW} - 1325 \tag{16.1}$$

where HOMI is hay OM intake (g/day), COMI is concentrates intake (g/day), HOMD is hay OM digestibility (g DOM/g OM), LS is litter size and LW is body weight (kg) (Neal *et al.*, 1985). Rations were formulated to include the maximum proportion of hay while remaining within the intake limits provided by the equation; requirements were calculated from ARC (1980). The model was validated by comparison with other experimental results and found to perform reasonably well but in general to predict lower voluntary intakes of hay than often observed, which the authors ascribe to the high level of wastage in many large-scale experiments.

Similarly, Orr and Treacher (1989) compiled results from several of their experiments with pregnant ewes fed silage and produced the equation:

$$\begin{aligned} \text{SOMI} = & 1063\text{COMI} + 2882\text{SOMD} - 3.20\text{SOMD} \times \text{COMI} + \\ & 462\text{WEEK} - 14.71\text{WEEK} \times \text{WEEK} + 0.034\text{WEEK} \times \text{COMI} + \\ & 1.92\text{SDM} - 71.7\text{LS} + 9.08\text{W} - 5516 \end{aligned} \quad (16.2)$$

where SOMI is silage OM intake (g/day), COMI is intake of concentrates (g/day), SOMD is OM digestibility of silage (g/g), WEEK is week of pregnancy, SDM is silage DM (g/g), LS is litter size, and W is body weight of the ewe 8 weeks before lambing.

Causes of declining intake in late pregnancy in ruminants

Physical factors

It has been suggested that the commonly observed decrease in intake is due to the compression of the rumen by the growing uterus, exacerbated by abdominal fat. The displacement of the rumen by the growing conceptus is graphically illustrated by Forbes (1968b), who killed sheep at several stages of pregnancy, froze the whole body, cut cross-sections of the abdomen and presented photographs of mid-abdominal sections. There was a negative relationship between the volume of ruminal contents at slaughter (RV, l) and the volume of 'incompressible abdominal contents' (uterus plus abdominal fat, IAC, l) in ewes that had been fed on hay (Forbes, 1969a):

$$\text{RV} = 10.3 - 0.37\text{IAC} \quad (P < 0.001, r = 0.51) \quad (16.3)$$

Intake during the last 2 weeks before slaughter (FI, kg/day) was positively related to volume of ruminal contents at slaughter:

$$\text{FI} = 0.48 + 0.033\text{RV} \quad (P < 0.01, r = 0.28) \quad (16.4)$$

The decline in intake was proportionately less than that of ruminal volume, probably as a result of the increase in rate of passage. These relationships provide no more than circumstantial evidence for a physical cause of the decline in intake in late pregnancy.

Endocrine factors

Even if physical competition has some effect on prepartum voluntary intake, it does not provide a complete explanation for the decline in intake because there have been some observations of a decline when concentrates were the sole or main food (Ingvarsen and Andersen, 2000); it is unlikely that physical factors would have been dominant in the control of intake in these circumstances. The decline in intake by cows in the last 3 weeks of pregnancy was steeper for high-concentrate than for high-forage foods, which does not support a purely physical theory for depression of intake.

In view of the effects of oestrogens on food intake described above, and the fact that oestrogen secretion by the placenta increases in the last few weeks of pregnancy to rates similar to or greater than that at oestrus, it has been suggested that the late pregnancy decline in intake may be due entirely or partly to oestrogens. Plasma oestrogen concentrations increase to around 300 pg/ml during the first half of pregnancy in cows, and then remain steady until about 1 month before calving, from which point there is a steady increase to around 2000 pg/ml a week or so before parturition. In the last few days, levels reach 4000–6000 pg/ml. Thus, during the last week of pregnancy oestrogen dominates and is likely to be a major factor in the decrease in food intake observed in late pregnancy. A highly significant negative correlation has been reported between food intake and serum oestradiol-17 β concentrations in ewes in late pregnancy.

Progesterone blocks many of the actions of oestrogens, so Bargetloh *et al.* (1975) investigated the effect of progesterone on the decline of voluntary food intake in late pregnancy in cows. Progesterone at the level of 0.25 mg/kg/day was given subcutaneously for 15 days before the expected date of calving, and treated cows ate 17.1 kg DM/day in the last 6 days of pregnancy compared with 11.7 kg DM/day for untreated controls. Pregnancy was prolonged in two out of the five treated cows, and such treatment cannot be contemplated in commercial practice.

Metabolic factors

An imbalance between the nutrients required by the ewe and fetus(es) might be expected to reduce food intake. To see whether a shortage of amino acids and/or glucose were limiting intake in grass-fed pregnant ewes, Barry and Manley (1986) infused glucose and casein into the abomasum. Voluntary intake 4 weeks before lambing was increased by the infusion from 0.6 to 0.85 MJ/kg^{0.75}. Intake of the infused animals then declined in the last 4 weeks whereas that of non-infused control groups increased towards parturition, and the authors suggested that the higher level of intake in the infused animals rendered them more prone to the intake-depressing effects of pregnancy, while intake of the non-infused controls was limited by the imbalanced diet rather than the effects of late pregnancy.

Other possible reasons for the decreased intake in late pregnancy – especially the very low levels in the last few days – include discomfort, preoccupation with

seeking a suitable place for parturition or other endocrine changes associated with parturition (e.g. corticosteroids, prostaglandins, oxytocin, relaxin). Whatever the cause, it seems that mixed feeding with forages supplemented by concentrates avoids too serious a decline in voluntary intake at a time when fetuses are very susceptible to undernutrition.

Lactation

Females of many species can eat enough during lactation to support milk synthesis without having to call on, to any great extent, their body reserves, as long as good-quality food is available ad libitum. The onset of lactation at the time of parturition is almost always accompanied by a sharp increase in food intake, but this lags behind the increase in nutrient requirements for lactation.

Pigs

Voluntary food intake during lactation in sows is frequently insufficient to provide the nutrients required for the synthesis of milk constituents, with the consequence that body reserves are called on, the resulting lean condition affecting subsequent reproductive success (Eissen *et al.*, 2000). The emphasis on leanness in breeding programmes seems to have reduced intake, and this is especially evident in primiparous sows, in those overfed during gestation and in sows kept in a hot environment.

Food intake is low immediately after parturition but increases rapidly, peaking in the second or third week of lactation. The level of intake after this peak is related to the number of piglets being suckled; Fig. 16.4 demonstrates this relationship (Koketsu *et al.*, 1997), and it can be seen that maximal intake is reached at a litter size of about 11–13. O’Grady *et al.* (1985) estimated food

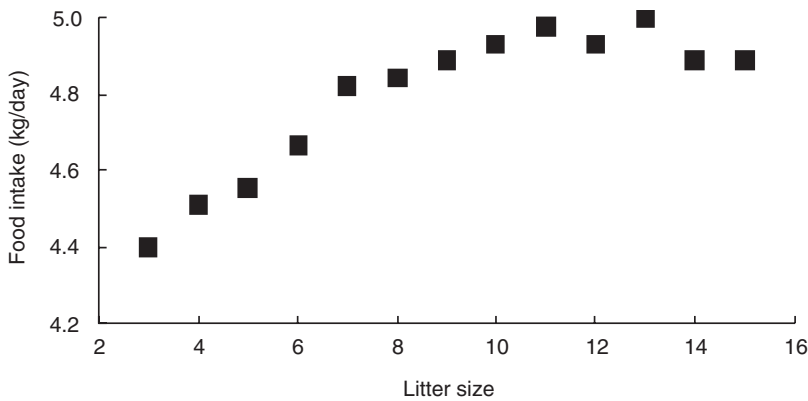


Fig. 16.4. Relationship between litter size and sow lactation food intake (from Koketsu *et al.*, 1997).

intake to be related to litter size with a linear (0.22 kg/pig/day) and a quadratic response ($-0.01 \text{ kg /pig}^2\text{/day}$), giving a maximum food intake at a litter size of 14 piglets.

The voluntary intake of lactating sows depends partly on the intake during pregnancy and on fatness at parturition. The fatter the sow at farrowing the less she eats during lactation, so there is a higher intake during lactation in sows that have been restricted to about half of ad libitum during pregnancy than in those given as much as they could eat. The lower food intake during lactation following higher levels of feeding in pregnancy is accompanied by reduced meal size rather than changes in meal number. Data from the literature have been compiled and are displayed in Fig. 16.5, from which this negative relationship can be clearly seen. There are significant negative relationships between fatness and food intake, but with widely varying regression coefficients in different studies, ranging from 19–129 g/day/mm of backfat thickness (Eissen *et al.*, 2000). Likely causes of the intake-depressing effects of body fat are given in Chapter 15.

Although concentrations in blood of NEFA during late gestation were not significantly affected by the feeding levels of rearing or gestation, those of glycerol were significantly higher in fat sows. Levels of NEFA and glycerol were always higher in fat than in lean sows in early lactation, but whether these cause, or are caused by, the lower food intake of fat sows is unclear.

It has been suggested that high levels of food intake in pregnancy, and the resultant increase in body fatness, render the sow less sensitive to insulin (Eissen *et al.*, 2000). Higher blood glucose concentrations will therefore arise

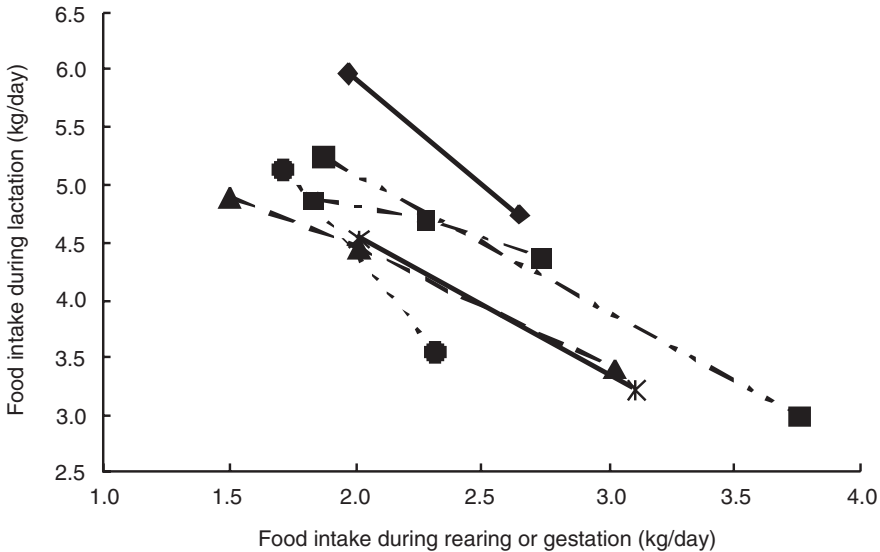


Fig. 16.5. Relationship between daily food intake during rearing (◆) or gestation (other symbols) and voluntary feed intake during lactation of sows (compiled by Eissen *et al.*, 2000).

after a meal, which may be more satiating. Additionally fat mobilization is likely to be increased, providing more NEFA for oxidation, again a satiating factor. It has indeed been found that fatter sows are more glucose intolerant than thin sows during late gestation, with higher glucose and lower insulin concentrations and a greater intolerance to glucose compared with lean sows. Immediately after parturition, the rate at which glucose is cleared from the blood is much slower for the fat sows, a symptom of insulin resistance.

Even the level of feeding during rearing can affect glucose tolerance during lactation, fatter sows being more resistant to insulin and less tolerant of glucose in mid-lactation than similar sows fed less during rearing, and therefore leaner. It seems, therefore, that impaired glucose clearance is more likely caused by body composition at farrowing per se than by a high feeding level during the preceding gestation. The lower voluntary food intake of fat sows during lactation, compared with thin sows, could be concluded to be due to differences in glucose tolerance and insulin resistance.

Fatness at parturition can also affect the number of mammary secretory cells, so that fatter sows have a lower potential to secrete milk and thus a lower requirement for nutrients, leading to lower food intake than in leaner sows. However, this effect on litter growth rate has not been noted in all studies, suggesting that the number of secretory cells is not limiting milk yield in all cases.

Body protein reserves might also limit milk production and thus voluntary intake. Gilts given a low-protein food (90 g/kg) in pregnancy ate almost 50% more in lactation if they were given a 180 g CP/kg food compared with those given a food containing 120 g CP/kg (Mahan and Mangan, 1975), while others given a high-protein food (170 g CP/kg) in pregnancy ate only 5% more when given the higher-protein food in lactation, i.e. those protein-restricted during pregnancy were trying to regain the lost body protein.

Providing a high-protein food during gestation has been shown to increase food intake during lactation, while a high-protein lactation diet can also increase voluntary food intake. It seems, therefore, that low body protein reserves may limit voluntary food intake through a constraint on milk production of sows during lactation. This is likely to be a limiting factor only for food intake, however, when the protein supply of the lactation diet is not optimal in relation to the body composition of the sow.

The pattern of intake during lactation follows that of milk yield, rising for the first 4 weeks and then declining, even though milk yield remains high. The decline might be caused by the increasing fatness that often occurs, but this does not happen with modern genotypes that have a greatly reduced propensity to fatten compared with those of a decade or more ago (see Chapter 15). It is acceptable to feed *ad libitum* from farrowing onwards.

In a summary of results from many sources, there was an average food intake for sows during lactation of 5.17 kg/day, with gilts consuming 15% less (NRC, 1987). However, there is considerable variation about this mean, 10–12% of gilts and 3–4% of sows eating < 3 kg/day. There are often fluctuations in intake during lactation, and a consistent reduction between days 10 and 15 after parturition has been observed in one study.

Environmental temperature

Given the large amount of heat produced by the very high rate of metabolism of lactating sows, it is not surprising that they are particularly susceptible to high environmental temperatures. Typically, a 1°C increase in temperature depresses intake by 0.1 kg/day. In one particular situation, an increase in environmental temperature from 18 to 28°C decreased voluntary food intake by 40%, while going from 20 to 30°C depressed intake by 43% (Messias de Bragança *et al.*, 1998). In these cases, sows kept at 20°C and fed a similar amount of food to sows fed *ad libitum* but kept at 30°C had a higher litter pre-weaning weight gain, explained by the reduction in milk yield at high temperatures, and probably due to diversion of blood to the skin for the purpose of increased cooling.

Parity

Food intake by sows increases up to parity 6 or 7 (NRC, 1987). Sows in their first lactation eat significantly less than in subsequent lactations but this can be increased by providing a high-protein diet, whereas this is not the case for multiparous sows, probably a reflection of higher maternal protein requirements of primiparous sows; however, lower protein body reserves of primiparous sows may also play a role (Eissen *et al.*, 2000). Bear in mind that litter size also increases with parity number, so there is confounding. In addition, body weight also increases with age, resulting in increased maintenance requirements driving a higher food intake.

Prediction of intake

For lactating sows, intake increases up to day 17 but then declines (NRC, 1987), approximately in line with the pattern of milk yield:

$$\text{DEI} = 56012 + 2491\text{DAY} - 7.19\text{DAY}^2 \quad (16.5)$$

This prediction should be adjusted for environmental temperature:

$$\text{Percentage change in DEI} = 0.0165(T_o - \text{EAT}) \quad (16.6)$$

where T_o is the optimal temperature and EAT is effective ambient temperature:

$$\text{EAT} = 0.065\text{DBT} + 0.35\text{WBT} \quad (16.7)$$

where DBT is dry bulb temperature and WBT is wet bulb temperature (°C).

Although nutritional and management practices have been suggested to alleviate the problem of low intake in lactation, an additional way would be by means of appropriate breeding programmes. A heritability of 0.19 has been estimated for voluntary food intake of lactating sows, so intake can be changed by selection. Sows selected for low daily food intake eat less than those selected for high intake, despite a leaner body composition and the fact that within a genotype intake is negatively related to fatness.

Cattle

Cows normally eat their fetal membranes, sometimes before they are fully separated.

Intake is invariably higher in lactating cows than during pregnancy, or in comparison with non-lactating cattle. The nutrient requirements for lactation are up to five times the maintenance requirement. This high demand for nutrients may, by removing metabolites rapidly from the blood, reduce the level of stimulation of chemoreceptors, so that physical limitation assumes greater importance than it does in similar, but non-lactating, animals. Voluntary intake usually increases rapidly after calving, but often this increase is slower for cows with abnormalities of various sorts, especially when fed silage rather than hay; this delay is not so severe with maize silage as with grass silage. Once the trauma of calving is over, voluntary intake increases, but usually at a slower rate than necessary to support the rapidly increasing demands of the mammary gland. Examples of patterns of intake from 2 to 20 weeks of lactation of cows fed on silage are shown in Figs 14.1 and 16.6.

That intake increases after calving is not surprising. The fetus and fetal fluids occupy some 70 l in the parturient Holstein Friesian cow, and the sudden disappearance of this bulk allows for a large increase in the capacity of the digestive tract, particularly the rumen. Therefore, if intake is limited primarily by physical mechanisms, a large and rapid increase would be expected immediately after calving. However, the increase that invariably takes place is much slower than could be explained by this simple physical mechanism. While milk yield usually peaks at around 7 weeks after calving, voluntary intake reaches its highest level up to 22 weeks post-calving.

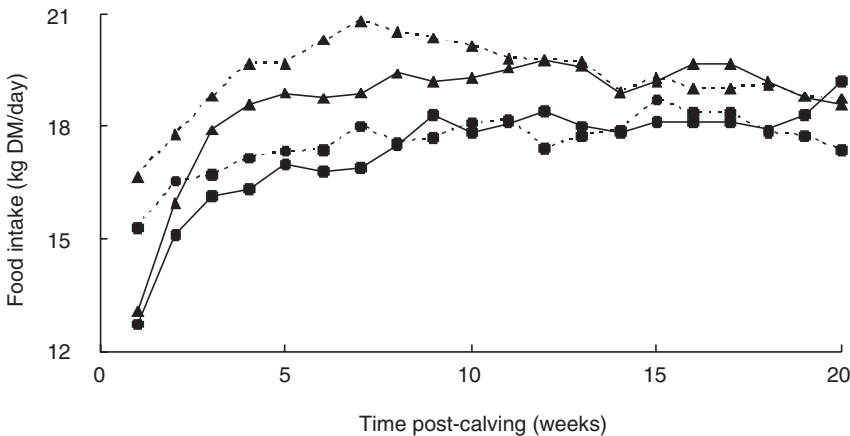


Fig. 16.6. Intake of hay by lactating cows that were either fat (F, condition score (CS) 3.5) or thin (T, CS 2.0) at calving and supplemented with concentrates that were either high (H, 74 g/kg DM) or low (L, 45 g/kg DM) in undegradable protein; ●—●, FH; ●---●, FL; ▲—▲, TH; ▲---▲, TL (from Garnsworthy and Jones, 1987).

The limitation on intake assumes greatest importance with high-yielding dairy cows. The rapid increase in requirements during the first few weeks of lactation is not usually matched by such a rapid rise in voluntary intake, and this lag is longer with forages and with heifers than with cows. Heifers are particularly susceptible to low intake of poor foods.

Body condition

Fat cows eat less silage and lose more weight than thinner ones in early lactation, and cows fed at maintenance level during the dry period eat about 10% more during the first 4 months of lactation than those fed at 1.8 of maintenance during the dry period. There is, however, no difference in milk yield and the need to 'steam up' (give extra supplementary feeding) before calving is questioned. However, cows that have become very thin during lactation should be fed in order to build up some reserves during the dry period.

Cows that were thin at calving (condition score (CS) 2.15 or 2.00) had their intake of hay reduced by a high level of UDP in the concentrate, while intake by fat cows (CS 3.15 or 3.50) was increased by such a supplement compared with that by a concentrate low in UDP (Garnsworthy and Jones, 1987; Fig. 16.6). It is possible that the fat cows could utilize the additional protein by mobilizing fat to provide energy to balance the increased protein supply.

Moreover, thin cows given a high-energy food (13.0 MJ/kg DM) ate more than fat cows and produced the same amount of milk (Jones and Garnsworthy, 1989). When a poor-quality food (9.8 MJ/kg DM) of the same crude protein content (180 g CP/kg DM) was given, intake was not affected by body condition, with the result that thin cows produced significantly less milk; this was suggested to be due to physical limitation of intake, but it is difficult to agree with this in view of the evidence that thin animals have a higher ruminal capacity (see Chapter 15).

The level of feeding before calving did not affect intake in the work of Cowan *et al.* (1981), but a lactation diet containing 147 g CP/kg DM gave higher intakes than one containing 111 g. The increased intake with the higher-protein food was greater when it contained 40% forage than for a 60% forage food.

Heritability of food intake in cattle

There are large individual variations in intake of cows of similar milk yields that are consistent throughout lactation, suggesting that efficiencies differ greatly between cows. Heritabilities have been estimated as: milk yield, 0.20; fat and protein yield, 0.15; live weight, 0.34; dry matter intake, 0.52; efficiency, 0.13. This shows that responses in efficiency following selection for fat and protein yield will be only 47–74% as great as those selected directly for efficiency, i.e. if the selection objective is to improve efficiency then achieve record intake!

Prediction of food intake by dairy cows

There has been major interest in predicting intake for the lactating dairy cow: Conrad (1987) has summarized the prediction of food intake by dairy cows under North American conditions, while the review of Forbes (1988b) describes the UK situation. Prediction of intake of silage, including some examples from dairy cows, is covered in Chapter 14. The chapter on predicting feed intake in the book by Chamberlain and Wilkinson (1996) is especially useful as a practical guide.

Although the curves of milk yield and voluntary food intake of cows during early lactation are approximately parallel there is usually a lag in voluntary intake, and simple regression is not adequate to describe the relationship. The goodness of fit has often been found to be improved by inclusion of a term for the stage of lactation. Cows are usually given supplementary feeding during lactation, and this invariably depresses forage intake; concentrate allowance is therefore a useful additional term to include in prediction equations. Intake is often more closely related to live weight than it is to milk yield, so live weight is often included as a predictive variable.

An approximate prediction of intake by dairy cows, taking live weight and milk yield into consideration, is provided by:

$$\text{DMI} = 0.025\text{LW} + 0.1\text{MY} \quad (16.8)$$

or, for high-yielding cows

$$\text{DMI} = 0.022\text{LW} + 0.2\text{MY} \quad (16.9)$$

(Ministry of Agriculture, Fisheries and Food (MAFF), 1975), where DMI is total DM intake (kg/day), LW is live weight (kg) and MY is milk yield (kg/day).

A large set of data was assembled from 385 cows in 26 experiments at five sites (Vadiveloo and Holmes, 1979). Of the many regression models fitted, the one that explained most variation was their equation 2:

$$\text{FDMI} = 0.015\text{LW} + 0.21\text{MY} - 0.57\text{C} - 0.095\text{WL} + 4.04\log\text{WL} - 4.14 \quad (16.10)$$

where FDMI is forage DM intake (kg/day), C is the amount of concentrate supplement (kg/day) and WL is the week of lactation. The constant for milk yield is similar for equations MAFF (1975) and to the ME requirement for milk secretion, and suggests that cows can adjust intake quite well to compensate for increased energy requirements when fed supplements according to recommendations.

In a comprehensive study by Rook *et al.* (1991), data from 251 lactations of cows fed 14 different silages were used for prediction. Concentrates were given at flat rates not closely related to milk yield. Data from 192 lactations on 15 silages were used for validation. Five food variables were available and, with this small number of variables, no problems of co-linearity amongst them were found. The negative relationship between level of concentrate supplementation and silage intake was linear over the range of conditions studied, with a coefficient (i.e. substitution rate) of -0.39 kg/kg.

Live weight was best handled by using post-calving weight as an index of frame size, and deviations from this as an index of body condition change. Better

prediction was obtained using yield of milk fat plus protein than simply milk yield, milk fat or milk energy. There were no important effects of silage composition variables. The best model (equation 6 of Rook *et al.*, 1991), overall, was:

$$I = -3.74 - 0.39\text{CDMI} + 1.49(\text{MF} + \text{MP}) + 0.007\text{LW} \quad (16.11)$$

where I is silage intake (g DM/day), CDMI is concentrate allowance (kg DM/day), MF is milk fat (g/kg), MP is milk protein (g/kg) and LW is live weight (kg). This equation gave an MSPE for weeks 3–9 of 1.88 (kg/day)^2 and, for weeks 10–20, 1.52 (kg/day)^2 . At 17 and 15% of mean intake, these MSPEs were better than those of Vadiveloo and Holmes (1979) (19 and 16% for early and mid-lactation, respectively).

There was greater variation in intakes in early lactation than later on, and improvement was obtained by considering weeks 3–9 separately and fitting time effects explicitly. The comprehensive equation for weeks 3–9 (equation 7 of Rook *et al.*, 1991) was:

$$\begin{aligned} I = & -4.28 - 0.46\text{CDMI} + 1.44(\text{MF} + \text{MP}) + 0.006\text{PCLW} + \\ & 0.01\text{LWD} - 0.0002\text{LWD}^2 - 0.005\text{NH}_3\text{-N} + 0.012\text{DOMD} + \\ & 0.77\text{WL} - 0.04\text{WL}^2 \end{aligned} \quad (16.12)$$

(MSPE 2.12 (kg/day)^2)

where PCLW is post-calving live weight (kg), LWD is live weight deviation from post-calving weight (kg), $\text{NH}_3\text{-N}$ is ammonia nitrogen (g/kg N), DOMD is digestible organic matter in the dry matter (g/kg DM) and WL is week of lactation; while for weeks 10–20 (equation 8 of Rook *et al.*, 1991) it was:

$$\begin{aligned} I = & -57.7 - 0.48\text{C} + 3.09(\text{MF} + \text{MP}) + 0.006\text{PCLW} + 0.011\text{LWD} - \\ & 0.00003\text{LWD}^2 + 0.184\text{DOMD} - 0.0001\text{DOMD}^2 \end{aligned} \quad (16.13)$$

(MSPE 1.74 (kg/day)^2)

However, there was discontinuity between these models of the two stages of lactation and discrepancy in prediction of intake at the intersection (9–10 weeks of lactation). The remaining error was due mainly to random variation rather than consistent bias, and suggests that emphasis should be given to obtaining more and better data rather than developing more sophisticated models. It was speculated that great improvements in prediction should not be expected, as for groups of animals it was probably much better than for individuals. Investigation of the lag between change in milk yield and change in intake, and possibility of autocorrelation between successive weeks, did not yield any improvements in the models. The authors suggest that specific models for different situations be developed rather than a global equation.

Roseler *et al.* (1997a) developed new equations using predictive variables that can easily be measured under commercial conditions: parity, milk yield, milk protein, body weight (BW), BW change, days pregnant, ambient temperature, relative humidity and night cooling. Their predictions were compared with independent data sets. A simplified prediction equation of DMI for farm application based on milk protein yield and BW at calving, with adjustments for ambient temperature for early lactation, gave an MSPE of $2.75 \text{ kg}^2/\text{day}$ with an R^2 of 0.84 for multiparous cows:

$$\text{DMI} = 8.4 + 0.006 \text{ calving BW} + 12.2 \text{ Milk protein kg/day} \quad (16.14)$$

The authors emphasize that the equations they developed must be used in situations close to those in which they were developed, in this case one in which Holstein cows are fed highly digestible diets because dietary fill effects are not considered.

In early lactation it is common for cows to mobilize body reserves that substitute for ingested food, and later in lactation to replenish these reserves by eating more than required for maintenance and lactation.

The importance of live weight change as one of the predictors of intake was realized by Bines *et al.* (1977), whose equation for heifers was:

$$\text{DMI} = 0.16\text{MY} + 2.45\text{LWC} + 0.011\text{LW} + 4.25 \quad (16.15)$$

where LWC is live weight change (kg/day).

However, live weight change is difficult to measure over short periods in ruminants, and its interpretation is uncertain due to short-term effects of gut fill. Also, there is considerable uncertainty in most situations as to whether mobilization is the cause or the effect of a change in food intake.

Curran *et al.* (1970) found that, for cows in the first 4 weeks of lactation, live weight did not contribute usefully and the best equation was:

$$\text{DOMI} = 0.22\text{LWC} + 0.64\text{CDM} + 4.6\text{D} - 0.17\text{MY} + 0.003\text{MY}^2 - 6.8 \quad (16.16)$$

where DOMI is digestible organic matter intake (kg/day), LWC is live weight change (kg/day), D is digestibility (g/kg) and MY is milk yield (kg/day), with a limit of prediction for a single cow of 13%.

The list of independent variables to be included to obtain the best correlation varied at different stages of the investigation, demonstrating the inadequacy of this approach to the general prediction of intake. The predominance of digestibility as a predictor in these equations demands that this parameter be known (or predicted with accuracy), and this is not feasible in practice; in the work of Curran *et al.* (1970), digestibility was estimated from regressions equations based on data of dry cows and wether sheep. These authors concluded that: '... attempts to predict the intake of single cows are unlikely to be worthwhile in practice ... but the mean intakes of groups of 30 similar cows could be predicted with an acceptable level of accuracy for practical applications'. Note that the constant for LWC is more than ten times greater in the equation of Bines *et al.* (1977) than that of Curran! This gives some idea of the scale of the problem of incompatibility between different publications using the empirical approach.

Prediction will be much better if previous records are available from individuals or groups of animals. While typically this would be milk production and live weights in previous lactations, intake and efficiency recorded for a few weeks in early or mid-lactation are well correlated with these measures over the whole of the same lactation. Regression of food intake over the first 38 weeks of lactation on intake measured over shorter periods within that time showed intake in weeks 5–10 of lactation to be highly correlated ($R^2 = 0.76$) with intake over the whole 38 weeks (Simm *et al.*, 1991). Thus, it is possible to monitor intakes for a short period (e.g. using the LUCIFIR system, see Chapter 2) and to use these in the index for selecting heifers for a breeding programme.

Comparison of prediction equations

A comprehensive comparison of prediction equations for dairy cows is that of Neal *et al.* (1984). These authors have used data collected over a period of 9 years from British Friesian cows fed silage ad libitum plus various supplements, to compare with the predictions of seven equations.

1. Equations 16.8 and 16.9 (MAFF, 1975).

2. Equation 16.10 (Vadiveloo and Holmes, 1979, equation 2).

3. Equation 16.15 (Bines *et al.*, 1977).

4. $TDMI = [0.135LW^{0.75} + 0.2(MY - Y5000[n])] M$ (16.17)

where Y5000 is the average milk yield for week n with a total lactation yield of 5000 kg and M is the adjustment for the month of lactation (ARC, 1980).

5. Equation 14.2 (Vadiveloo and Holmes, 1979, equation 1).

6,7. Equations 14.3 and 14.4 (Lewis, 1981).

Actual and predicted weekly intakes were compared by calculating the mean square prediction error (MSPE):

$$MSPE = 1/t \sigma(A - P)^2 \quad (16.18)$$

where A is the actual intake and P the predicted intake. When the observed weekly live weights were used, both equations 1 and 2 of Vadiveloo and Holmes (1979) and that of Lewis (1981) gave the least MSPEs. Table 16.1 includes the MSPEs for nine widely quoted equations, from the work of Neal *et al.* (1984), Rook *et al.* (1991), Roseler *et al.* (1997a) and Keady *et al.* (2004), each of which used different data for validation.

Many farms have no facilities for weighing cows; when the estimated weight after calving was used, together with notional live weight changes, equation 1 of Vadiveloo and Holmes (1979) was the best. All the equations that gave the best predictions were those derived from cows kept in similar conditions to those used for this comparison; they all also included some aspect of food quality, though only that of Lewis (1981) specifically incorporated indices of silage quality, and Rook *et al.* (1991) found little advantage in including silage characteristics in prediction equations for dairy cows.

Those equations that have no term for stage of lactation have high MSPEs in early lactation when intake is lower than expected. Least MSPE in the comparisons of Neal *et al.* (1984) was 1.8 kg DM²/day for heifers and 2.2 kg DM²/day for cows when weekly live weights were used; this lack of accuracy is a cause for concern but, in view of the complex factors affecting and controlling intake, it is doubtful whether further empirical investigations will be of benefit.

In a test of accuracy and robustness of seven prediction equations for US conditions, it was found that most MSPEs for mean DM intake of groups of animals were > 10% of the mean, while for individual cows all MSPEs were > 20% of the observed mean (FuentesPila *et al.*, 1996). Similarly, six equations were assessed and all found to predict intake poorly, at least at some stages of lactation (Roseler *et al.*, 1997b). The equation with the best accuracy (MSPEs of 15.6, 12.9, 7.9, 5.3

Table 16.1. Mean square prediction errors (MSPEs) for equations predicting the voluntary intake of cows, compared with independent data (from Neal *et al.*, 1984; Rook *et al.*, 1991; Roseler *et al.*, 1997b; Keady *et al.*, 2004).

Source	Equation	MSPE (kg DM/day) ²				
		From Neal <i>et al.</i> (1984)				From Keady <i>et al.</i> (2004)
		All cows	Heifers	Adult cows	Weeks 10–26	
Vadiveloo and Holmes (1979) (equation 1)	14.2	2.1	2.1	2.2	1.74	2.9
Lewis (1981)	14.3, 14.4	2.5	2.0	2.8	2.11	5.5
MAFF (1975) (average yield)	16.9	3.3	2.7	3.7	3.05	
Agricultural Research Council (ARC, 1980)	16.18	3.5	3.5	4.3	5.75	
Rook <i>et al.</i> (1991) (equation 8, weeks 3–9)	16.13				1.74	
Milligan <i>et al.</i> (1981)	14.5					8.9
Dulphy <i>et al.</i> (1989)	14.7, 14.8, 14.9					11.4
Oldham <i>et al.</i> (1998)	14.6					10.8
Roseler <i>et al.</i> (1997a)	16.15				2.75	

and 6.3 kg²/day for multiparous cows for weeks 1–9, 10–24, 25–36, 37–48 and 49–60, respectively) was the modified equation of the NRC (1989):

$$\text{DMI (kg/day)} = -0.293 + 0.372 \times \text{FCM (kg/day)} + 0.0968 \times \text{BW}^{0.75} \text{ (kg)} \quad (16.19)$$

However, the overall mean bias (predicted minus observed) of the prediction of weekly DMI of a single cow was high for all equations. The mean bias for the NRC equation was +6, +3.4, –1.3, –2.1 and –2.8 kg/day for weeks 2, 4, 8, 10 and 20 of lactation, respectively.

Bovine somatotropin (BST)

With the development of genetic engineering it has become possible to produce large quantities of a bovine growth hormone analogue, called bovine somatotropin (BST), which stimulates milk yield when administered to cows. The results of short-term trials indicated that this is not accompanied by increased food intake; indeed, initially there is a tendency for food intake to decrease. It has been demonstrated that the energy for the extra milk comes initially from fat mobilization, but that food intake starts to rise after about 2 weeks of treatment and does not decline as rapidly as in untreated cows in mid-lactation.

Long-term experiments have often been confounded by the practice of changing the composition of the food depending on the milk yield of the cows, making it difficult to know what the effect of BST is on voluntary intake. For example, Bauman *et al.* (1984) treated cows with bGH or BST for 188 days, starting 84 days after calving. Intake of a complete food remained higher than for control cows from about the fourth week of treatment. However, the quality

of the food was adjusted according to the quantity of milk production so that the BST-treated cows, by producing more milk, were fed more digestible, higher-energy food than controls, which would be likely to result in increased intake (see Chapter 11).

In another experiment, in which control and bGH-treated identical twin cows were offered the same freshly cut grass, after 8 weeks of treatment control cows ate 15.5 kg DM/day while twins given 50 mg bGH/day ate 16.7 kg DM/day; in the 22nd week of treatment the intakes were, respectively, 15.4 and 17.5 kg DM/day (Peel *et al.*, 1985).

Sheep

After lambing there is a slow rise to a peak, trailing behind milk yield, so that weight loss is common, particularly with poor-quality foods. This lag is longer with forage diets than with concentrates. Peak intake is normally seen at weeks 4–6 of lactation. For a range of foods, lactating ewes ate more than wethers, even with diets low in digestible energy concentration where there was a positive relationship between digestibility and intake, implying physical limitation to intake. This makes sense only if we propose that increased nutrient demand allows the animal to accommodate a greater degree of gut fill, as envisaged by the MTD hypothesis (see Chapter 10).

Forbes (1969b) recorded the voluntary intake of hay and the milk yield during the first 7 weeks of lactation in Speckle-faced Welsh ewes, 11 with single lambs and four with twins. Mean hay intake over the period of observation (I , kg DM/day) was positively related to milk yield (MY , kg/day) and live weight change (LWC , kg/42 days):

$$I = 0.76 + 0.5MY + 0.03LWC \quad (16.20)$$

The weight gain of the lambs from 2–7 weeks of age (WG , kg/day) was positively related to the hay intake of the ewe (kg/day):

$$WG = 0.17I + 0.05 \quad (16.21)$$

Although lamb weight gain was probably dependent on milk yield, it is not certain whether milk yield determines intake or vice versa; almost certainly the two are interdependent.

During lactation, thin ewes eat more than fat ones, in proportion to the difference in rate of disappearance and extent of digestion of the food (Cowan *et al.*, 1980):

$$I = (54 - 1.2BF)/(MRT(1 - DMD)) \quad (16.22)$$

where I is the intake (kg DM/day), MRT is the mean retention time of particles (h), BF is body fat (kg) and DMD is the DM digestibility. This might be taken as evidence to support the idea that low intake in early lactation is due to physical limitation, but the fat effect could equally be a metabolic phenomenon (see Chapter 15).

Other reasons for the lag in intake might be slow metabolic adaptation to increased nutrient requirements and hypertrophy of the digestive tract and

liver; there is no sound information on likely maximum rates of hypertrophy of these tissues, although it has been suggested that the potential for hypertrophy greatly exceeds the observed rate of increase in intake (Forbes, 1986a).

Another possible reason for the slow increase of intake in early lactation is slow recovery from the effects of endocrine changes in late pregnancy. Although short exposure to small doses of oestrogens has a reversible effect on voluntary intake (see above), more severe treatment can have long-lasting effects. When moderately fat dry ewes were injected with a high dose of 17β -oestradiol (10 mg) on 2 consecutive days there was a 60% decrease in intake of a pelleted diet, which took at least 2 weeks to recover to pre-treatment levels (J.M. Forbes, unpublished observations). Extremely high rates of oestrogen production that might have this sort of effect occur in the last few days of pregnancy. The hypothalamus of cattle seems to be very sensitive to oestradiol in the first few weeks of lactation.

Clearly, further work is required to elucidate the usual lag between increasing nutrient demands and the increase in voluntary intake in early lactation; it is unlikely that the answer to this question will be a simple one.

From a series of eight experiments, each with 48 ewes, Bocquier *et al.* (1987) derived the equation:

$$\begin{aligned} \text{HDMI} = & 346 \pm 58A \pm 45B + 672W - 28.9\text{WEEK} \times \text{WEEK} - \\ & 1.53\text{EC} + 12.8\text{EBW} + 39.9\text{EBWC} + 1.72\text{LGR} - 1.28\text{NDF} - \\ & 0.55W \times \text{NDF} + 0.002\text{EC} \times \text{NDF} - 0.07W \times \text{EC} \end{aligned} \quad (16.23)$$

where HDMI is hay DM intake (g/day), A = + for mature, - for old ewes, B = + for Romanov cross ewes, - for Limousines, EC = concentrate allowance (g/day), EBW = ewe body weight at lambing (kg), EBWC = ewe body weight change during lactation (kg/6 weeks), LGR = litter daily gain from 7–28 days (g/day) and NDF = neutral detergent fibre content of hay (g/kg DM). Despite the complexity of this equation, it accounted for only 53% of the variation in hay intake.

The Laying Hen

The nutrient requirements for egg-laying place a great demand on the hen's metabolism and, not surprisingly, laying hens eat much more food than those not in lay. It is normal for eggs to be laid on consecutive days, with a single non-laying day separating the 'clutches'. Modern breeds have long clutches and produce more than 300 eggs/year. Mean egg production is correlated with food intake between groups of birds with different rates of production (see Fig. 16.7), and high-producing birds gain less weight (Ivy and Gleaves, 1976). Between individuals there is a positive correlation between food intake and shell thickness and between the weight of the egg and food intake on the same day, but it is not clear which is cause and which is effect.

Laying birds eat more on egg-forming days than on non-egg-forming days, presumably in response to the increased requirements for nutrients when egg constituents are being deposited. For 2–3 h before oviposition the following

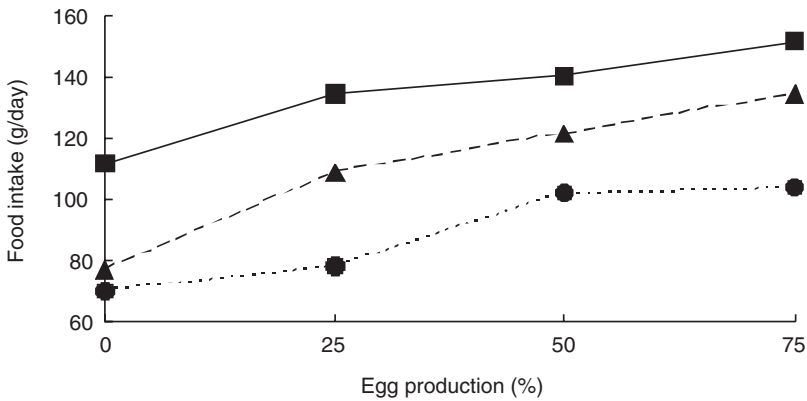


Fig. 16.7. Food intakes of hens at four levels of egg production offered foods of three energy concentrations: ■, 8.4; ▲, 10.5; ●, 12.5 MJ ME/kg (from Ivy and Gleaves, 1976).

morning feeding activity is depressed, as the hen is occupied with pacing or setting. In broiler hens kept in continuous light, food intake is also lower during the hour or two before oviposition, and intake increases markedly for a short period afterwards. Perhaps compression of the gastrointestinal tract by the egg inhibits feeding just before oviposition.

There is also a depression about 32 h before oviposition, which is approximately the time of release of luteinizing hormone, and an increase around ovulation and for several hours after entry of the egg into the uterus; this latter change may be related to the demands for calcium for deposition of the shell (see Chapter 12). The increase in food intake that occurs after ovulation is accompanied by increased intake of oyster shell (a source of calcium), and so is the peak 20–22 h later (Mongin and Sauveur, 1979).

At normal environmental temperatures around 21°C, hens ate 116.6 g on egg-forming days and 102.2 g on non-egg-forming days (Morris and Taylor, 1967; Fig. 16.8). At 30°C, intakes were 100.9 g and 78.6 g, respectively. When intakes from 09.30 to 14.30 were examined, it was seen that on egg-forming days it was 23.2 g while on non-egg-forming days it was 19.7 g. Intakes from 14.30 to 09.30 the next morning were 101.8 g and 75.3 g, respectively, a true reflection of the effect of egg formation. These authors speculated that it is probably the increase in protein requirements to support the albumen deposition that is responsible for this effect of egg-laying on voluntary intake by the hen.

Prediction of food intake

For laying hens in controlled environments, where the temperature range is not large, the following equation was found to be satisfactory for individually caged layers:

$$\text{MEI} = (3.14 - 0.031T)\text{LW}^{0.75} + 33\text{WC} + 9.6\text{EM} \quad (16.24)$$

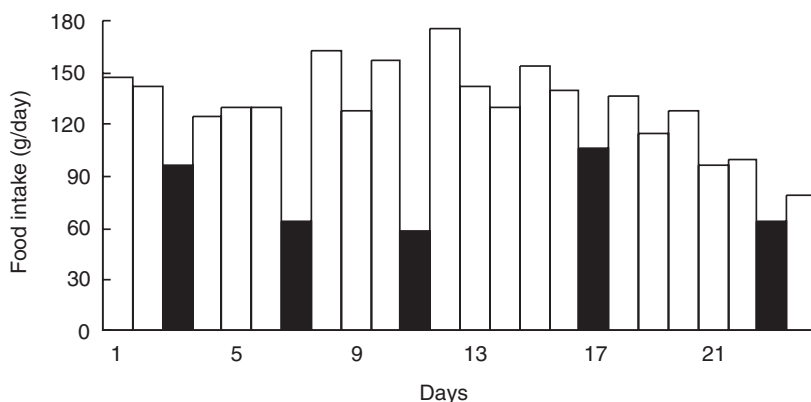


Fig. 16.8. Daily food intake of a laying hen in relation to egg formation. White bars, egg-forming days; black bars, non-egg-forming days (from Morris and Taylor, 1967).

where MEI is the ME intake (kJ ME/bird/day), T is the ambient temperature ($^{\circ}\text{C}$), WC is the weight gain (g/bird/day), EM is the egg mass (g/bird/day) and LW is the live weight (g) (Byerly, 1979).

A survey of the literature for experiments relating intake by hens to diet digestibility provided data from which was derived the equation:

$$\text{EI} = \text{Y11.3} + (0.000547)\text{Y11.3} - 0.147(\text{DIETE} - 11.3) \quad (16.25)$$

in which EI is energy intake (kJ/bird/day), Y11.3 is the intake of a food with 11.3 MJ ME/kg and DIETE is the ME content of the food in question (MJ/kg) (Morris, 1968b).

Under US conditions:

$$\text{MEI} = \text{W}^{0.75}(173 - 1.95\text{T}) + 5.50\text{WC} + 2.07\text{EE} \quad (16.26)$$

where MEI is ME intake (kJ/day), T is ambient temperature ($^{\circ}\text{C}$), WC is change in weight (g/day) and EE is egg production (g/day) (NRC, 1984b). This assumes a nutritionally balanced food with an ME concentration typical of normal commercial practice.

Conclusions

Reproductive status can have a marked effect on food intake in the female. At oestrus, intake is often temporarily depressed by the oestrogens secreted by the ovaries, but it is not clear the extent to which this is a direct effect on the brain or to a change in metabolism in liver, muscle and adipose tissue. In sows, intake increases in pregnancy which would – unless prevented by restriction of food allowance – result in gross deposition of fat.

In the last few weeks of pregnancy there is often a decline in intake in ruminants, probably caused by competition for space in the abdomen and by

the increasing oestrogen secretion by the placenta. On the day of parturition very little is eaten, but then intake increases at the start of lactation. In cows and ewes this increase is not usually fast enough to keep pace with the increase in milk yield, as a result of which body reserves are mobilized. After the peak of lactation, the level of voluntary intake stays high and reserves are replenished.

There is a rhythm of food intake in the laying hen related to the requirements for deposition of the components of the egg. It is not clear whether this is dependent on the changing requirements for different nutrients at different times of day, or to the changing hormone levels that accompany these fluctuating requirements. Hens eat less on days in which an egg is not being formed and, over a longer period, intake is proportional to the number of eggs laid.

17

Environmental Factors Affecting Intake

This chapter considers intake responses to changes in temperature, photoperiod, the social environment, housing and feeding conditions, and disease. These are all external factors that are not directly associated with the characteristics of the food(s) on offer or with the genetic make-up of the animal. In many cases, however, there are interactions between food and intrinsic and environmental factors, so all of the features of the control of intake, and factors affecting it, covered in previous chapters must be borne in mind.

Environmental Temperature

Unless otherwise stated, the term environmental temperature will refer to the effective ambient temperature, which is the actual temperature modified by the effects of humidity, wind and rainfall. Above the thermoneutral zone, body temperature rises and so food intake decreases in order to reduce the heat production associated with feeding, digestion, absorption and metabolism, in an attempt to prevent an excessive increase in body temperature. Below the thermoneutral zone, heat production must increase in order to maintain body temperature, and intake rises to provide substrates for this increased heat production.

Poultry

Feeding behaviour is erratic at very low temperatures and few data are available on the quantitative responses. Below an optimum temperature, which depends on the size and feathering of the birds, food intake increases and the efficiency of conversion into body weight gain declines; above this temperature, food intake and growth are depressed. For broilers in the later stages of growth, this

optimum temperature for efficiency is 21°C. A similar temperature is optimum for growing pullets and for laying hens. Every 1 degree of increase between 25 and 34°C results in a 1.0–1.5 g/day decline in food intake by laying hens; above 35°C the decline is greater.

In a detailed experiment (Cooper and Washburn, 1998), individual broiler chickens were monitored from 28–49 days in environmental temperatures of 32 and 21°C. After 7 days, body temperature was significantly higher at 32°C, with the difference between environments ranging from 0.5–1.0°C. While the correlations between body temperature and food intake were mostly low and not significant in the cooler environment, in the hot environment body temperature was significantly correlated with food consumption.

More generally useful results can be obtained from an experiment involving several temperatures, rather than just two as in the previous example. May *et al.* (1998) applied five treatments from 23 to 31°C to broilers from 21–49 days old. Figure 17.1 shows food intake plotted against environmental temperature at seven body weight points. While intake is hardly affected by temperature when the birds weighed 600 g, by the time they were approaching slaughter weight (2–5 kg) there was a large depression in intake, from a level of around 215 g/day at 23°C to about 180 g/day at 31°C.

These results emphasize the difficulty of maintaining maximum growth rate right up to the time of slaughter, as house temperature usually increases with body weight given the fixed stocking density normally adopted in commercial broiler production.

In broiler chicks, the depression of food intake and growth at high environmental temperatures can be partially reversed by supplementing the diet with ascorbic acid (vitamin C). Plasma corticosterone is reduced during such treatment, water intake increases and body temperature falls. Birds can be trained to know the difference between supplemented and unsupplemented foods, and are then able to select their desired intake of ascorbic acid (see Chapter 13).

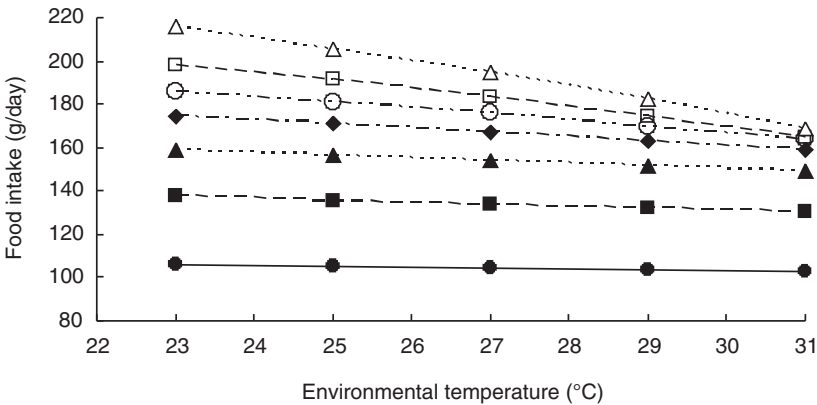


Fig. 17.1. The effect of environmental temperature on food intake of broiler chickens for a range of different body weights at the start of exposure. Body weight: ●, 600 g; ■, 900 g; ▲, 1200 g; ◆, 1500 g; ○, 1800 g; □, 2100 g; △, 2400 g (from May *et al.*, 1998).

For laying hens, food intake is negatively related to environmental temperature between 5 and 30°C. Below the optimum temperature of 21°C, egg numbers decline but the increased food intake is driven by the increase in heat production necessary to maintain a constant body temperature. Above 21°C food intake is depressed to prevent an increase in body temperature, and egg production suffers.

Pigs

Growing pigs

The temperature above which voluntary intake is depressed varies with the size of the animal. Younger or thinner pigs have a greater surface:weight ratio and can more easily get rid of excess heat than older or fatter animals. Thus, at any given temperature above the thermoneutral zone, intake by heavy pigs is depressed relatively more than that of lighter pigs.

When the effective environmental temperature is below that required for metabolic comfort, energy demand for cold thermogenesis increases and this leads to higher voluntary food intake. At temperatures < 20°C, the decline in intake is steeper (21 g/°C) than between 20 and 25°C (7 g/°C). Close (1989) re-analysed data from four experiments that yielded the equation:

$$MEI = 9.6 + 0.075ET + 0.52BW - 0.012ET*BW \tag{17.1}$$

where MEI is ME intake (MJ/day), ET is environmental temperature (°C) and BW is body weight (kg). Thus, ME intake increased by 0.16 MJ/day for each °C decrease in ET for pigs of 20 kg and by 1.12 MJ/day for pigs of 100 kg (see Fig. 17.2).

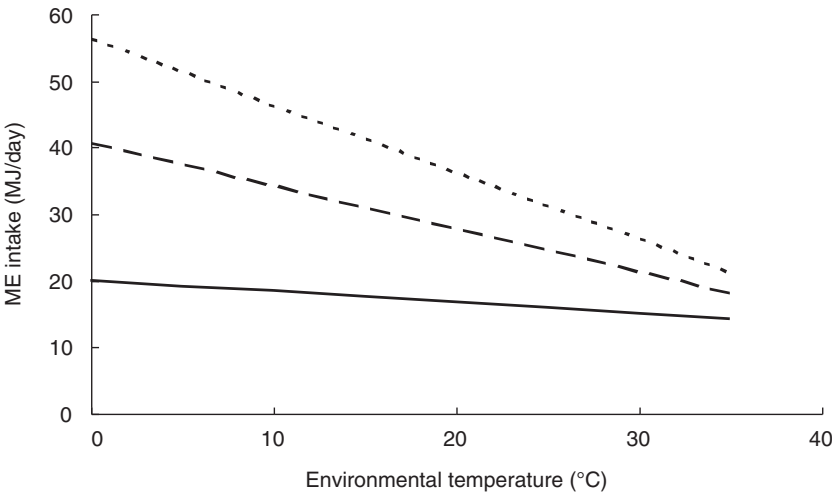


Fig. 17.2. Effect of environmental temperature on ME intake of growing pigs at three body weights: —, 20 kg; - -, 60 kg; · · ·, 90 kg (from Close, 1989).

For growing/finishing pigs, intake decreases as environmental temperature rises; over the range 5–30°C the relationship is:

$$PCI15 = 126.3 - 1.65ET \quad (17.2)$$

where PCI15 is the percentage change from the level of intake at 15°C and ET is environmental temperature (°C) (NRC, 1987).

The increase in intake under cold conditions does not usually prevent retardation of growth, and so the proportion of food energy retained in the carcass is reduced. However, the increase in voluntary consumption is sometimes greater than that necessary to maintain weight gain, and occasionally cold-stressed growing pigs have been found not only to eat more than controls but also to gain more weight. An explanation for this might be that the diet was marginally protein-deficient, so that increasing the rate of energy utilization rectified an excessively high energy:protein ratio.

Food intake of pigs kept chronically at 10°C stayed high for at least 24 h after moving to 25°C, and there was a closer relationship with metabolic rate than with body temperature. Plasma levels of thyroid hormones changed within a few hours after changes in environmental temperature, but food intake took at least 4 days (Macari *et al.*, 1986). Transferring thyroidectomized pigs from hot to cool was accompanied by increased intake, but not vice versa, and these authors concluded that thyroid hormones, while not controlling intake directly, are responsible for the metabolic adaptations affecting intake.

In theory, food intake is expected to be stable throughout the zone of thermal neutrality, to increase below the lower critical temperature¹ (LCT) and to decrease above the upper critical temperature, eventually reaching zero when environmental temperature exceeds body temperature. In practice, however, the relationship between environmental temperature and voluntary food intake is close to being linear, over the range 6–30°C (NRC, 1987). In very cold environments the potential intake may not be realized due to physical limitations, but this will depend on the age and relative gut capacity of the animal, and on the physical characteristics of the food (see Chapter 11).

It is not practicable to monitor all the factors affecting heat loss in many situations, and it is proposed that body temperature is a suitable proxy for predicting and modelling the pig's response to different environmental temperatures (Fialho *et al.*, 2004).

Cool temperatures do not increase colostrum intake in newborn piglets, as they become less vigorous and spend less time sucking. This means that it is difficult to arrange for optimum temperatures for both sow and piglets in the same house. Once they get to about 1 week of age, piglets do respond to cooler temperatures by taking more milk. Reduced temperatures at night, when growing pigs have a lower body temperature, increased intake and growth by about 10%, but with no improvement in efficiency.

¹ The environmental temperature below which the animal must increase its heat production in order to maintain a stable body temperature.

Sows

Voluntary intake by lactating sows fell by 12% when environmental temperature increased from 21 to 27°C and by 25% when it was increased from 16 to 27°C. This led to greater weight loss at the higher temperature (Lynch, 1989).

Temperature has a particularly great effect on lactating sows: weight loss of lactating sows increased as environmental temperature increased, although the use of wet food and higher energy food have increased the daily intake of the sow. As well as sows losing more weight, piglets grow more slowly at higher temperatures.

Renaudeau *et al.* (2004) have summarized the effects of ambient temperature on food intake by pigs, using the results of several experiments. Figure 17.3 gives the results, expressed as multiples of maintenance requirements in order to show pigs of all sizes, from weaners to mature sows, on the same scale. The range of temperatures, 18–29°C, encompasses temperatures normally encountered in housed pigs in northern Europe. It can be seen clearly that the sow, with her large body size relative to surface area and great heat production due to lactation, is the most severely affected. The marginal reduction in intake at 18°C, compared with that at 19°C, is surely not realistic, as at low environmental temperatures intake is increased to try to meet the increased heat losses below the LCT.

Diet can be manipulated to reduce the effects of high temperature, and fat inclusion improves performance under hot conditions as it has a lower heat increment than carbohydrates. Sows ate more of a food containing 200 g CP/kg than one containing 140 g/kg at 16°C but less at 28°C, presumably due to the high heat increment of protein metabolism.

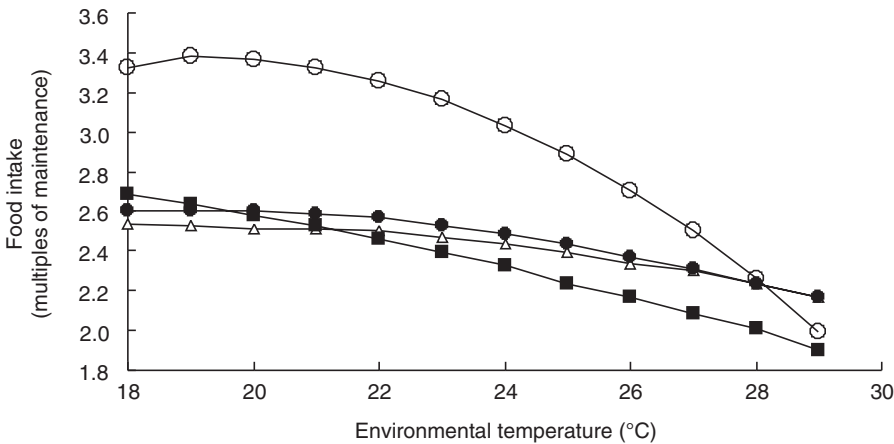


Fig. 17.3. Summary of effects of environmental temperature on voluntary food intake (multiples of maintenance requirements) by: newly weaned piglets (2 kg, Δ); growing pigs (45 kg, ●); finishing pigs (90 kg, ■); and lactating sows (270 kg, ○). Maintenance requirements are taken as 0.44 MJ ME/kg^{0.75}/day for sows and 1.0 MJ ME/kg^{0.60} for the others (from Renaudeau *et al.*, 2004).

Amongst the ways available to reduce the effects of heat stress on pig performance is to select for heat tolerance. Renaudeau *et al.* (2004) discuss the best selection criteria, but acknowledge that little is known about genetic diversity for heat tolerance within or between pig breeds. They suggest that indicators of heat sensitivity (heat shock protein), heat production (residual consumption, uncoupling protein) or heat dissipation (respiratory rate, cutaneous heat conductivity) could be used as selection criteria.

Ventilation

Ventilation rate can also affect growth and food intake in pigs, with significant depression in intake at very low ventilation rates. Too high a rate of ventilation – which induces high air speeds – can also affect intake, as an increase from 10 to 56 cm/s in air speed is equivalent to a 4°C fall in air temperature, in terms of its effects on pigs. However, huddling together at low effective temperatures will reduce the cooling effect, and the results from individually penned pigs are not directly applicable to groups of pigs (Mount, 1968).

At high temperatures, evaporation is very important as a means of losing heat. At thermoneutral temperatures, increasing the relative humidity from 50 to 95% had no effect on voluntary food intake or growth, but at 28 and 33°C, each 10% increase in humidity depressed intake by 36 g/day. Localized cooling of the head or even just the snout increases intake by sows, especially at high temperatures. When snout cooling was provided, sows kept in a hot environment (29°C) increased their intake from 3.99 to 4.86 kg/day and reduced weight loss from 19.8 to 14.3 kg/28 days (McGlone *et al.*, 1988). A water drip increased intake to 5.29 kg/day and weight loss was 10.8 kg/28 days, while with both snout cooling and a water drip intake was 5.84 kg/day and weight loss was 2.0 kg/28 days.

Cattle

Disruption of feeding behaviour occurs in cattle at very low temperatures (< -10°C), especially in beef cattle, which are more susceptible to increased heat losses because their heat production is less than that of dairy cows. DM intake by grazing beef cattle increases when daily temperature increases or decreases from the mean of previous days, but the magnitude of the response is very small. Fluctuations in temperature in the range of -16 to +8°C have a minimal effect on intake or grazing behaviour, and it can be concluded that fluctuations within that range within a familiar environment are minimally stressful.

In sub-zero conditions, with a range of minimum daily temperatures from 0 to -35°C, grazing time of beef cows (GT, h/day spent eating) decreased in proportion with minimum daily temperature (MDT, °C), more so for younger cows than for older (fatter?) cows:

$$GT = 9.32 + 0.16MDT \text{ for 3-year-old cows} \quad (15.3)$$

$$GT = 9.02 + 0.009MDT \text{ for 6-year-old cows} \quad (15.4)$$

with little effect of snow cover (Adams *et al.*, 1986). Increase in gut motility under cold exposure leads to increases in rate of passage, which could be responsible for increases in food intake if physical constraints are limiting intake.

Under hot conditions, provision of shade increases intake, as evidenced by body weight increase and lowered plasma free fatty acid levels. As with sows, head cooling can be beneficial, as it increased the food intake of cattle working on treadmills under hot conditions.

Animals usually acclimatize to changes in environmental conditions so that the acute effects of heat exposure may be more severe than the chronic effects on food intake; heifers exposed to temperatures that increased from 18 to 29°C caused growth to be depressed during the 20-day period after the change, but not subsequently, even though the high temperature was maintained. Short-term observations can, therefore, give misleading results. One way in which cattle adapt to hot conditions is by eating more at night when it is cooler, which allows them to eat more than would be predicted from the results of experiments with continuous exposure to hot environments in a heat chamber.

Although heat stress has a greater effect on the intake of *Bos taurus* than on *B. indicus* cattle, the level of intake is generally higher in *B. taurus* (Colditz and Kellaway, 1972); first-cross animals had similar levels of intake to Friesians at the lower temperature but, under heat stress, they ate more than either pure breed, an example of hybrid vigour or heterosis.

As the proportion of concentrates in the diet is increased, so the heat increment of feeding decreases; this can be used to alleviate heat stress to a limited extent. For any given type of food, ruminal VFA concentrations reach a peak faster after a large meal in steers at 35°C compared with those at $\leq 29^\circ\text{C}$, suggesting that this accounts for the lower food intake and that foods resulting in lower ruminal acetate production might be useful in hot areas.

In addition to the direct effects on the animal, high environmental temperatures affect the growth of food plants. Typically there is an increase in the proportion of cell wall constituents (CWC), especially in tropical grasses, because of faster maturation. The increased stem:leaf ratio, as well as depressing nutritive value, will also reduce the acceptability of the herbage.

In a comprehensive review of effects of high environmental temperatures on lactating cows, Kadzerea *et al.* (2002) found that food intake in high-yielding lactating cows begins to decline at ambient temperatures of 25–26°C. Above 30°C it drops more rapidly and, by the time it has reached 40°C, the decline can be as much as 40%. The reduction is particularly large if the food is high in forage, as fermentation produces large amounts of heat and VFAs are utilized relatively inefficiently, thereby generating heat during their metabolism in the body.

Prolonged heat stress allows adaptation to occur, especially by feeding patterns being changed and a greater proportion of the daily intake being taken during the cooler periods, i.e. at night. The reduction in food intake is the primary cause of reduced milk yield under hot conditions, as maintaining intake by introducing food into the rumen of heat-stressed cows greatly reduced the depression in yield.

Sheep

Cold environments

Below the LCT the animal has, by definition, to increase its rate of heat production in order to maintain its deep body temperature within the narrow range compatible with normal function. This increase in energy requirements would be expected to result in increased food intake, and this is indeed so. At a fixed level of feeding, sheep eat faster in a colder environment and there is an increase in ruminal motility, a reduction in the volume of ruminal contents and in the extent of digestion of cell wall constituents.

Thyroxine secretion is increased by reducing the environmental temperature, and this might be responsible for increased voluntary food intake. Treatment of sheep with 1 mg thyroxine/day increases food intake, but weight gains are reduced; the increase in intake is due, presumably, to the greater energy required to support the increase in metabolic rate. Implants of 60 mg given subcutaneously at 3-month intervals also stimulate intake. While body weight is lost in the first month, food intake is even higher in the second and third months after implantation, as weight is regained. Again, it is apparent that intake is responding to changes in energy expenditure.

Shearing

Shearing increases heat production in sheep, and this is matched by increased food intake (about 25% at 13°C). This increase in voluntary intake occurs about 1 week after shearing, although heart rate increases at once and there can be marked shivering during the week between shearing and the start of hyperphagia; the rise in intake peaks at some 50% above the pre-shearing level. The increase in intake after shearing is not usually accompanied by any difference in live weight gains, compared with controls, suggesting that the increase in intake is a response to the increased heat losses. During the few weeks after shearing intake is inversely related to environmental temperature but, by about 2 months after shearing, the difference in voluntary intake between shorn and unshorn sheep has disappeared; sufficient wool has grown to afford adequate protection by this time.

There was little effect on the intake, already high, of a highly digestible lucerne-based food but a marked increase with low-intake, poorly digestible forages (Minson and Ternouth, 1971). It would appear that the high level of intake on the more concentrated food was providing sufficient heat for shearing not to push the animal below its LCT. The increase in intake following shearing tends to be greater in lighter ewes, as they have less subcutaneous fat to compensate for the loss of the fleece.

These results from sheep show that, although the response takes at least 1 week, increased heat loss is compensated for by increased voluntary food intake to provide the necessary metabolizable energy. If heat production is already high, then shearing does not bring the animal to below its LCT and intake is unaffected.

Hot environments

Sheep are also affected by high temperatures. Shorn lambs, whose LCT was approximately 13°C, were exposed to environments ranging from -5 to +35°C with the following relationship (Brink, 1975):

$$\text{DMI} = 111.3 - 0.52T \quad (17.5)$$

where DMI was the dry matter intake (g/kg live weight^{0.75}) and T was the temperature (°C). The depression of intake at high temperatures is probably smaller with high-concentrate rations than with forages, because the latter have a higher heat increment.

As with cattle, acclimatization can ameliorate the acute effects of high temperatures, and the true effect of a hot climate on food intake by sheep can only be assessed in well-acclimatized sheep.

Photoperiod

The most obvious difference between day and night as far as feeding is concerned is the ease with which animals can see their food. However, the regular sequence of dark and light in a 24 h cycle acts as a synchronizer to entrain diurnal rhythms in many biological functions that are not directly dependent on the presence of light or dark. In many cases it is not known whether rhythms of approximately 24 h are entrained, in which case they should correctly be called circadian rather than diurnal rhythms. It is important to consider time-of-day when studying the control of food intake (Forbes, 1982).

Poultry

Poultry do not normally eat during darkness. If daylength is short (< 8 h), however, hunger overcomes the reluctance to eat at night, and feeding occurs to a limited extent during darkness. In continuous darkness intake is as high as in long daylengths, indicating that lack of visual contact with food is not the only reason for the aphagia normally seen at night. If chickens are subjected to constant illumination, following experience of light-dark cycles there is a residual rhythm of feeding, although this does not remain at exactly 24 h. Chickens that have been in continuous light from hatching do not show such a rhythm unless some event such as servicing occurs sufficiently regularly for it to be used as a *zeitgeber* or synchronizing agent.

Within the light phase, the rate of taking meals is not usually constant. There is often a peak at the beginning and/or at the end of the light phase (Savory, 1979). Laying hens tend to show this peak in the evening, presumably to fill up the crop for the night, while non-layers usually eat more in the morning. Whilst the evening peak might be related to the laying cycle in the hen, when it occurs in non-layers it implies anticipation of darkness; this is obviously possible when

the light dims slowly at the end of the day but not when the lights go out abruptly. Birds that show a feeding peak before dusk eat more than other, similar, birds that have peak feeding activity shortly after dawn.

Broiler chickens seldom show the pre-dusk peak unless the lights dim slowly, and maximum intake is achieved by the use of 23 h lighting, by intermittent illumination or by simulated dusk. When the daylength is extended by adding 3 h, the evening feeding peak moves to 3 h later over a period of about 3 days. If the extra 3 h are added at the beginning rather than at the end of the day the evening peak does not move, showing that the hen can predict the time at which the lights will go out rather than the length of the light phase; perhaps servicing at a fixed time of day acts as an indicator.

To determine whether domestic fowl can anticipate a period of food deprivation, individually housed pullets were maintained in a circadian-free environment and, for 30 days, half were shown a coloured card during the final 1 h of food availability, prior to food deprivation of 8 or 12 h (Petherick and Waddington, 1991). There was no indication subsequently of increased intake to fill the crop when the coloured card was shown. In addition, it has been found that broilers are able to anticipate withdrawal of food if this coincides with the onset of darkness, but not in continuous light. Continuously lit birds consume more at the onset of a 12-h period of food availability whereas those with a dark period eat more towards the end of the light period. Thus, the ability to predict food unavailability depends specifically on a daily period of darkness and not just on a period of fasting.

When chickens are exposed to ahemeral cycles,² their feeding pattern shows signs of keeping to a cycle of approximately 24 h. Thus, laying hens kept under 21 h cycles (12 light (L):9 dark (D) or 11L:10D) show an 'evening' peak of feeding activity which continues into the early part of the night (Bhatti and Morris, 1978). Conversely, hens in 30 h cycles (12L:18D or 20L:10D) eat considerably less in the last few hours of the light phase than would be expected.

When the light phase is divided by a dark phase in the middle (skeleton photoperiod, for example 2L:8D:2L:12D), some food is eaten during the 8D period, which the bird treats as 'day', rather than as 'night'. Feeding, therefore, is not 'switched' on by light and off by darkness, but rather is related to a metabolic rhythm that is entrained by the pattern of lighting.

Mechanisms

It has been established that the pineal gland is an important mediator of the effects of photoperiod on reproduction and growth, both in birds and mammals. The pineal receives information from the eyes via the superior cervical ganglion and influences other parts of the brain by the secretion of hormones, particularly melatonin. Melatonin given during the daytime might be expected to cause the cessation of feeding. Not only did this prove to be the case, but cockerels actually went to sleep for up to 3 h after intraperitoneal

² Lighting cycles other than 24 h.

injection of 10 mg melatonin (Bermudez *et al.*, 1983). This dose is clearly unphysiological but, as much of the melatonin will be extracted by the liver and the remainder will be separated from the brain by the blood–brain barrier, the amounts entering the sensitive parts of the brain may be within the physiological range. At lower rates of injection there is dose-related hypophagia with drowsiness, but not sleep.

If melatonin is responsible for the nocturnal aphagia in chickens, removal of the pineal gland – which is the major source of melatonin – would allow feeding to take place at night. This did occur, although the quantity eaten during the 12 h of darkness (4.4 g) was much less than that eaten during the daytime (Injidi and Forbes, 1983). Total daily intake was significantly higher than in sham-operated birds, and growth was significantly faster. Thus the pineal plays a role in the circadian patterns of feeding, but is not the only factor.

As voluntary food intake is related to energy requirements, the effect of melatonin may be to lower the metabolic rate of the sleeping or drowsy bird. Measurement of oxygen consumption showed that it was significantly depressed within the first 1 h after injection of melatonin. Simultaneous injection of triiodothyronine (T_3 , 200 μ g, intramuscularly) blocked the effects of melatonin on sleep and feeding immediately, but the stimulating effect on metabolism was not shown until 3 h later (Bermudez *et al.*, 1983); the effects of these hormones are, therefore, direct and not via effects on metabolic rate. As T_3 concentration in plasma is lower at night and melatonin injection depresses T_3 concentration, thyroid hormone metabolism may be involved in the diurnal cycle of food intake and metabolism.

Pigs

Pigs that had free access to food and were observed for 24 h periods ate for at least twice as long per hour during the day compared with at night. There is typically a peak of feeding activity in the late afternoon, with 10 min/h spent eating in that period of the day (see Fig. 2.11). There are few reports in the literature of effects of photoperiod on the voluntary food intake or productivity of pigs, although in one study intake was increased if 16 h or more light per day was provided to lactating sows, compared with short daylengths.

Cattle

The overall feeding pattern is related to photoperiod, with larger, more frequent meals during the day, but this can be modified if the middle of the day is very hot, when cattle eat more at night – especially if the moon is bright (Dulphy *et al.*, 1980).

In winter, more time is spent eating during the hours of darkness, since the days are too short to allow cattle to meet their requirements during the day. Beef cattle in open feedlots spend up to 75% of their feeding time between 06.00 and 18.00 h. Reversal of lighting or lengthening the hours of light is

accompanied by changes in feeding behaviour, so that feeding takes place predominantly during the light period. When fresh food was provided after each meal so that any circadian changes in food intake could not be caused by changes in the availability or palatability of the food (Chase *et al.*, 1976), meals occurred more frequently during the period from 08.00–20.00 h, with a peak around 08.00 (inter-meal interval of about 80 min); during the early part of the night the inter-meal interval averaged 180 min, while from 24.00–06.00 h it was about 300 min.

While some studies under naturally fluctuating conditions have shown small increases in voluntary intake with increasing daylength, artificial extension of natural winter days has shown bigger effects. Peters *et al.* (1980) showed a significant increase in the voluntary intake of heifers given a complete food and provided with 16 h of light/day compared with those under natural winter daylengths in Michigan, USA (5.20 versus 4.80 kg/head/day), or those under continuous light (4.86 kg/day). The effect on live weight gain preceded that on food intake, supporting the hypothesis that the effects of long photoperiod on food intake are due to the stimulation of growth and the increased energy requirements.

In dairy cows exposed to 16 h of fluorescent lighting/day compared with those kept under natural lighting conditions, from October to March (9–12 h/day), food intake was increased by 6%, which approximately matched the requirements for the recorded increase in milk yield of 1.4 kg/day (Peters *et al.*, 1981). Adjusted for parity and milk yield, the food intakes were 17.4 and 16.4 kg DM/day, respectively.

Deer

Deer are farmed in many countries and can therefore be classed as 'farm animals'. The justification for including them here is that, being more seasonal in their behaviour and food intake than species with a longer history of domestication, they show in an exaggerated form the effects of photoperiod on feeding behaviour. In males, the depression in food intake induced by short days is even more marked than in the female and, at the time of the 'rut' – the breeding season – males eat very little for several weeks.

Figure 17.4 shows food intake by stags, Suffolk rams and Soay rams subjected to an artificial 6-month pattern of lighting (Kay, 1979). The Suffolk breed of sheep is representative of highly domesticated breeds and the amplitude of the intake cycle is less than that of deer, while that of the Soay – a relatively undomesticated breed – is proportionately at least as great as for deer. The fact that intake follows daylength – even though this is in a 6-month cycle – shows that it is photoperiod, rather than temperature or nutrition, that is controlling the circennial rhythm in animals under natural conditions.

Meal size is markedly different at different times of year, although it is little different between day and night (Rhind *et al.*, 1998; Fig. 17.5). In contrast, number of meals changes little over the year but is always considerably greater during the day than in the night.

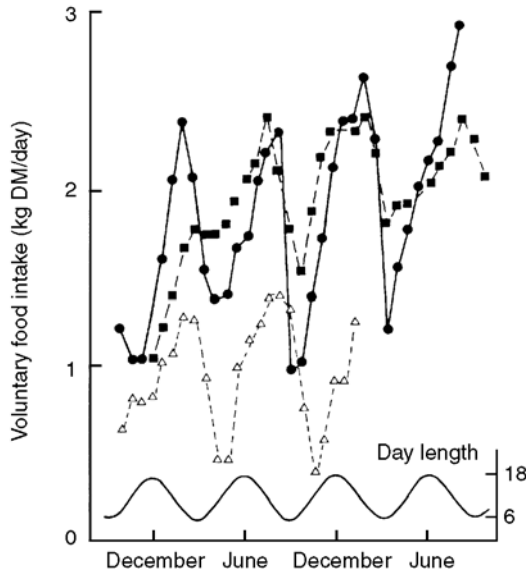


Fig. 17.4. Intake of balanced foods by stags (●), Suffolk rams (■) and Soay rams (△) subjected to an artificial 6-month pattern of lighting (from Kay, 1979).

Deer given foods with ME concentrations in the range 8.5–11.0 MJ ME/kg DM (all with 156 g protein/kg) decreased their DM intake with increasing dietary ME concentration to give an approximately constant intake of ME per unit of metabolic LW (Webster *et al.*, 2000; Fig. 17.6). However, the relationships between ME concentration and DM intake were significantly different between spring and winter. In winter there was a small but significant positive relationship, and in spring a small but significant negative relationship between ME intake and ME concentration. This example featuring deer is included because it neatly includes both dietary and environmental factors.

Sheep

Lambs kept during long days eat more than those in short days due to the stimulation of growth. Although growth is increased by long daylength, even at restricted levels of feeding, the maximum response is obtained when the animal is allowed to fulfil its increased growth potential by ad libitum feeding. Exposure of growing lambs to fixed daylengths of either 8 or 16 h/day resulted in higher intake of a complete pelleted food in the longer photoperiod (Forbes *et al.*, 1979). However, neither the speed of onset nor the statistical significance of this increase were as great as the effects on growth rate and gut fill, so the additional nutrient requirements of stimulated growth probably caused a secondary increase in food intake. This conclusion is supported, since the effect of photoperiod on growth can still be seen in pair-fed lambs (Forbes *et al.*, 1981).

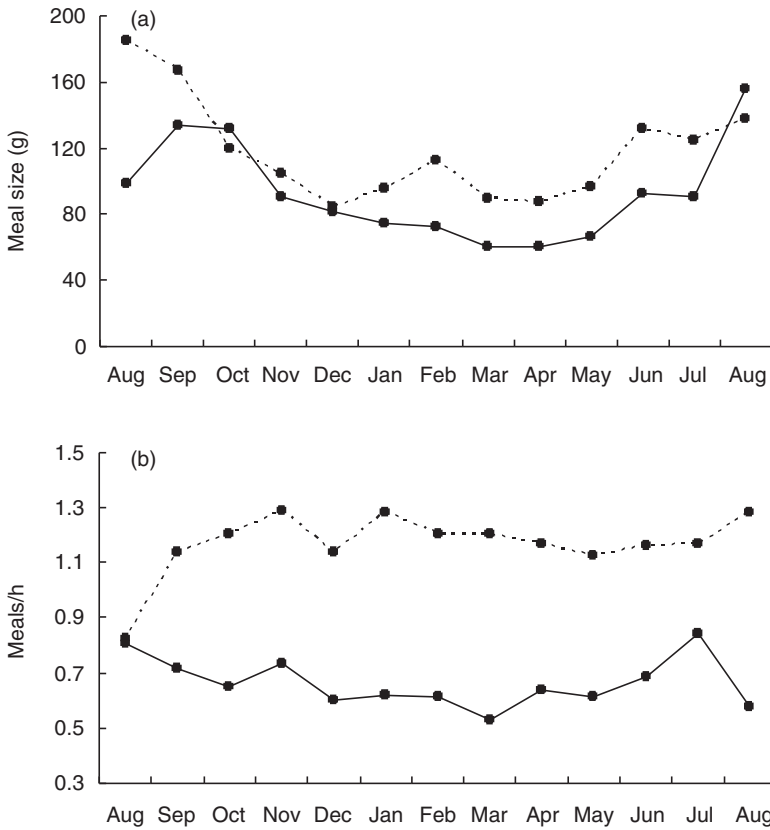


Fig. 17.5. (a) Meal sizes and (b) number of meals/h at monthly intervals in deer fed ad libitum and kept in the natural annual rhythm of daylength, i.e. shortest day is in December. - - -, the daylight period between dawn and refilling of the feed bins; —, the period between dusk and dawn (from Rhind *et al.*, 1998).

A 1 h ‘flash’ of light in the middle of long nights is as effective as long days (Schanbacher and Crouse, 1981). Figure 17.7 shows the number of meals taken during hourly intervals in 8 and 16 h daylengths and with a 1 h ‘flash’ in the middle of the night. In all treatments there was a lower feeding frequency during darkness, although there was more feeding in the middle of the long nights and a sharp peak during the ‘flash’. The daily intake of a complete food was increased from 1.62 kg/day under 8L:16D to 1.83 kg under 16L:8D and 1.79 kg under the 7L:9D:1L:7D ‘flash’ treatment. Meals are smaller and occur less frequently at night than during the day in housed growing lambs.

Since significant amounts of food are eaten at night, there is no question of a block such as that caused by melatonin in chickens; 200 or 400 µg melatonin injected into the lateral ventricles of sheep had no effect on feeding (Driver *et al.*, 1979). The metabolic rate of ruminants is lower at night, although not sufficiently so to account for the large difference between daytime and night-time intake.

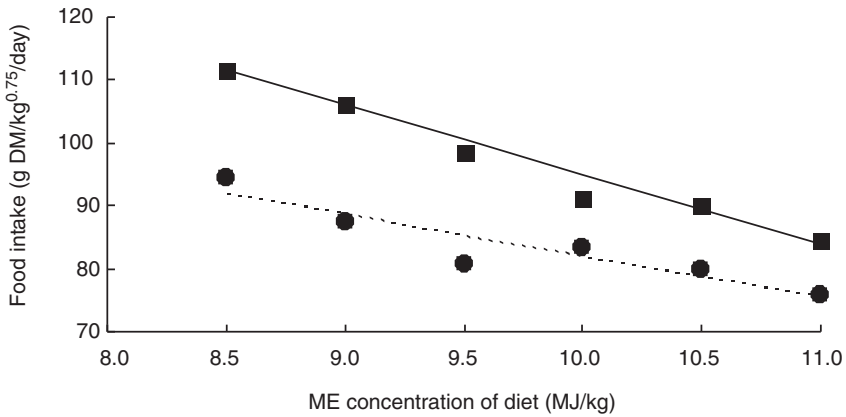


Fig. 17.6. Effect of ME concentration of diet on voluntary intake of DM by growing male red deer calves. ■, spring; ●, winter, with lines of best fit (from Webster *et al.*, 2000).

Sheep fed ad libitum on hay showed higher intake during the day, especially after fresh food has been offered. Ruminal volatile fatty acid concentrations increase during the day and decrease at night, so the animals are not eating in order to achieve constant conditions in the rumen, nor to achieve a constant metabolic rate. Although they do not sleep deeply, ruminants become less aware of their surroundings at night and may also be less aware of internal signals. Sheep trained to self-stimulate in the postero-lateral hypothalamus showed reduced self-stimulation during the 12 h dark phase with a compensatory increase during the day, so that the total activity was the same as for sheep kept in continuous lighting, under which there was no diurnal rhythm (Baldwin and Parrott, 1982).

Under conditions of natural lighting in latitudes where there is a marked annual rhythm in photoperiod, sheep show an annual cycle of daily food intake, with a peak a few weeks after the longest day and a nadir after the shortest day. Artificial manipulation of photoperiod showed that long days stimulate wool growth and that three-quarters of the variation in wool growth was associated with variation in food intake. Kay (1979) and his colleagues have shown that the intake cycle is caused by changes in photoperiod rather than in temperature or food quality, by compressing the annual lighting cycle into 6 months (see Fig. 17.4). It would appear that the intake, growth and fattening cycles have greater changes in unimproved breeds of sheep, such as the Soay, compared with improved breeds like the Suffolk.

Superior cervical ganglionectomy, which prevents fluctuations in pineal function, reduces but does not totally inhibit the cycle of appetite in Soay rams kept under 6-month compressed annual cycles of lighting (Kay and Suttie, 1980). This annual cycle of food intake is associated with a parallel cycle of fasting metabolic rate in sheep (204–264 kJ/kg^{0.75}/day) and, in Soay rams, the estimated maintenance requirements for metabolizable energy were 400 (midwinter) and 530 kJ/kg^{0.75}/day (summer).

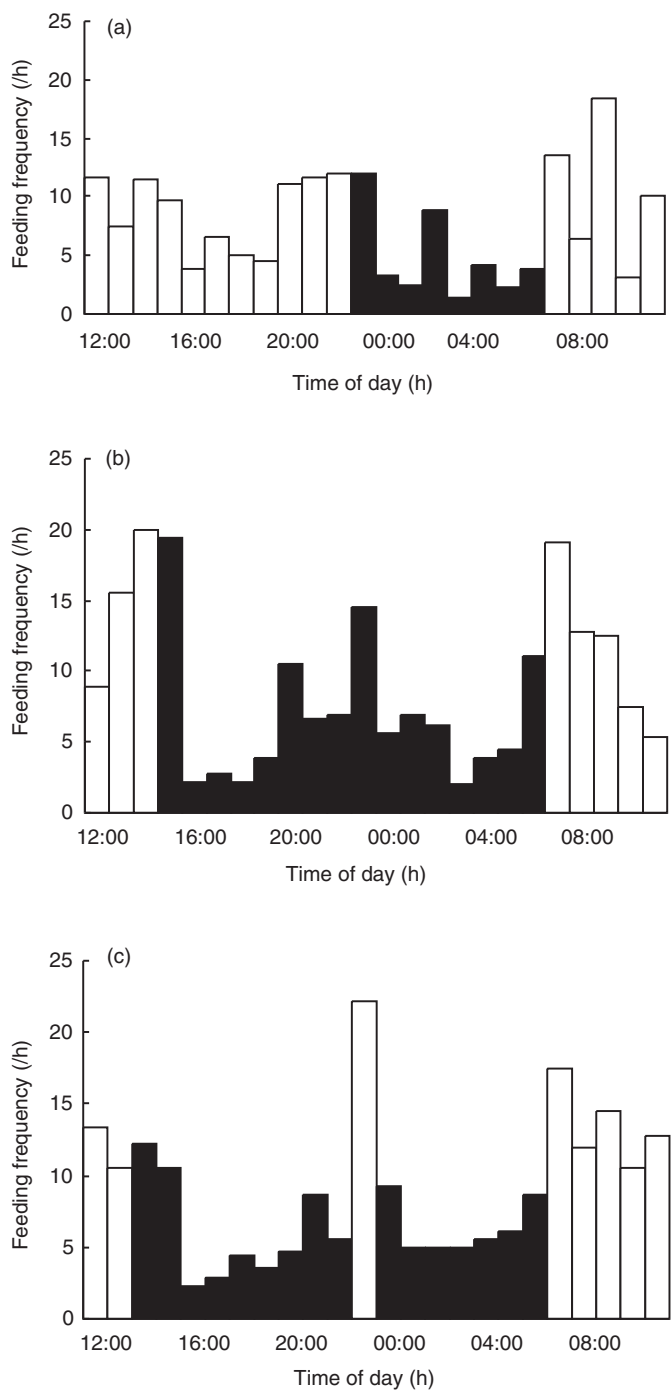


Fig. 17.7. Feeding patterns of ram lambs in (a) 16 h days, (b) 8 h days and (c) 8 h days with 'flash' in middle of the night. Solid bars, hours of darkness; open bars, hours of daylight/'flash' (from Schanbacher and Crouse, 1981).

Plasma leptin concentrations are lower in lean sheep under short days compared with those in fatter sheep in long days, and the seasonal pattern of circulating leptin concentrations reflects that of adiposity and matches the pattern of food intake (Adam and Mercer, 2004). Given the conventional belief that leptin inhibits food intake these observations seem paradoxical, but in fact it appears that leptin receptors are down-regulated in long daylengths.

Lactating ewes in long days ate 16% more food (lucerne *ad libitum* with a constant proportion of a concentrate food) and produced 25% more milk than similar animals kept in short days at the same time of year (Bocquier *et al.*, 1997). At 150 days post-lambing, all animals were put under 12L:12D conditions and intakes became almost equal after a further 30 days. The timing of the changes in yield and intake strongly supported the idea that the effect of daylength was primarily on milk production and that this, in turn, influenced food intake.

Occasionally, environmental factors other than daylight can entrain a feeding rhythm. For example, sheep on North Ronaldsay, Western Isles, Scotland, that eat mostly seaweed as they are restricted to the outer part of the island, exhibit a grazing pattern that is controlled by the tide.

Rhind *et al.* (2002) provide a comprehensive review of the effects of photoperiod on intake by ruminants and discuss likely mechanisms at the hormonal and neural levels, but conclude that: 'the sequence of neuroendocrine signals through which a change in photoperiod can alter food intake is poorly understood'.

Exercise

Enforced exercise reduces food intake and growth rate of pigs with no effect on back fat thickness; it is not clear whether the reduced time spent eating is due to fatigue or stress.

Although most studies with cattle have shown no significant effect of exercise on voluntary food intake in the short term, intake by cattle of rice straw supplemented with 18 and 27 g concentrates/kg live weight was reduced by 11 and 14%, respectively, when oxen worked to increase their energy daily expenditure by 1.3–1.6-fold (Pearson *et al.*, 1999). However, there was no depression due to exercise with a diet of hay which had higher ME but lower nitrogen content than the straw. On both diets there was a return to pre-work levels of intake in the week after exercise. If work takes up a significant proportion of the time available for feeding, then intake is likely to be reduced with forages with slow rates of intake.

When intakes have been monitored over long periods, however, there are seen to be increases – of the order of 15% over a period of 2 years, for example – in cows that worked about 100 days/year.

Walking cows for 2–3 km/day does not affect food intake compared with similar cows not exercised. Hereford × Friesian cows exercised 5 days/week for 3 weeks over 10.6 km/day, with 480 m/day climbing with 4 kg/day of supplement and barley straw *ad libitum*, showed no effect on straw intake but

body weight was lost when exercising and gained when not (Matthewman *et al.*, 1993). This confirms previous results that animals performing moderate work and given poor forage do not in the short term increase intake, and that intake may even decrease when animals work.

In sheep exercised on a treadmill over 9 km/day at 3 km/h up a 10° gradient for 6 days, intake of chopped hay was decreased from a pre-exercise level of 1347 to 1125 g OM/day, with little effect on rumen retention times (Henning, 1987). The time taken to complete the work (3 h) is unlikely to be sufficient to explain the observed reduction in hay intake, as limiting animals to 21 h/day access to food does not affect daily intake.

In the short term, therefore, exercise tends to reduce intake rather than increase it in parallel with the increase in energy expenditure. Long-term exercise must result in a compensatory increase in intake, otherwise hard-working animals would die of underfeeding.

Group Size and Stocking Density

The presence of competition for feeding space exerts a major influence on feeding behaviour, rate of eating being increased when there are more animals per feeder. In some studies, but not others, social dominance has been found to be correlated with food intake, growth, milk production or egg production; this is especially true where there are not enough feeding spaces for all animals to eat at once.

Even with a well-balanced food available *ad libitum*, intake might be insufficient. Many farm species show social synchrony of feeding and it is possible that some individuals cannot get to the trough during these feeding periods, sometimes being excluded by dominant members of the group. In many cases the deprived animals compensate by increasing their feeding rate and/or by eating at less favoured times of day.

In many of the studies reported there has been confounding between group size, stocking density and trough length per pig, so that it is often difficult to reach conclusions about their relative importance.

Poultry

Food intake of broiler chicks from 1–42 days, stocked at 10, 15, 20 or 25 birds/m², was significantly lower at the two higher densities (3842, 3838, 3738 and 3518 g/42 days, respectively) (Valdivie and Dieppa, 2002). Although this was accompanied by reduced live weight gain, the yield of meat/m² was increased by the higher stocking densities, with no difference in conversion efficiency.

Pigs

Group size and floor area per pig are important factors affecting stress. Pigs generally grow more slowly as stocking density increases, due largely to an

effect on food intake (Whittemore *et al.*, 2001a). An optimum space allowance of $0.04 \text{ m}^2/\text{W}^{0.67}$ has been proposed, with a linear depression of intake by 20% at a space allowance of $0.02 \text{ m}^2/\text{W}^{0.67}$. NRC (1998) propose that, at stocking rates $< 1.1 \text{ m}^2/\text{pig}$, ME intake be adjusted by $(0.773 + (0.429\text{SP}) - (0.203\text{SP}^2) - 1)$ for pigs $< 50 \text{ kg}$, or by $(0.617 + (0.701\text{SP}) - (0.320\text{SP}^2) - 1)$ for heavier pigs, where SP is the space allowed (m^2/pig).

Increasing the area per animal, with groups of eight bacon pigs, from 0.56 to 1.19 m^2 , resulted in an increase in food intake from 2.46 to $2.73 \text{ kg/animal/day}$. There was a reduction in food intake when space was reduced from 0.25 to $0.17 \text{ m}^2/\text{pig}$ (Lindvall, 1981), and a further 10% reduction if space was reduced to 0.13 m^2 , although other work has failed to show such an effect.

As group size increased from three to six to 12, even though the floor area per pig was maintained, food intake declined from 2.57 to 2.33 to 2.27 kg/day with Duroc pigs weighing $35\text{--}50 \text{ kg}$ (Heitman *et al.*, 1961). For group size, each additional pig in a pen of weaners reduces intake by 0.9%, while for growing and fattening pigs the reduction is 0.25 and 0.32%, respectively. These effects are likely to be due to reduced heat losses in the larger groups.

In a comprehensive study of group size, 640 pigs, growing from 23 to 95 kg over 12 weeks, were kept in groups of 10, 20, 40 and 80, with feeder access and floor space kept equal per pig (Schmolke *et al.*, 2003). Food intake was not affected by group size and there did not seem to be any effect on the welfare of the pigs.

In an analysis of the results of 20 published studies using almost 22,000 animals, Turner *et al.* (2003) found reduced growth rates in larger groups, although food intake was affected only in the early stages after weaning, as social dominance orders were re-established after mixing of pigs. However, several other studies have not found significant or lasting effects of group size on food intake, when feeder access and floor space were equal between groups.

The results of several experiments show that pigs eat less when in larger groups (Morgan *et al.*, 1999). Grouped pigs eat fewer and larger meals than those single-housed, but this is due to a limitation of trough space because, if more feeders are provided, the number of meals increases and they become smaller, similar to the situation in individual pigs.

Pigs in groups take fewer meals, eat faster and, in some studies, eat less per day than pigs penned individually. The effect on meal number was most obvious with groups of 20 pigs compared with 5, 10 or 15, presumably as a result of greater competition and less time for individuals, especially those low in the dominance order, to eat.

Sheep

As the space allowance for lambs was increased from 0.37 to 0.62 to $0.99 \text{ m}^2/\text{head}$, intake increased from 1.36 to 1.32 to 1.49 kg/day , with no effect on cortisol, adrenaline or noradrenaline (Horton *et al.*, 1990).

Feeder Design and Feeding Space Allowance

Poultry

Battery cages with wide fronts allow a feeding pattern more closely related to the hens' requirements (more first thing in the morning and just before dusk) than a deeper cage with same floor-space per bird, which has less feeding space per bird. When the front of the battery cage is vertical bars, hens feed most frequently singly, while with horizontal bars they feed usually in threes, i.e. closer to the birds' inclination to synchronize their feeding.

Pigs

Feeding is stimulated by the sight of other pigs eating, so there should be enough feeder space for all pigs in a pen to eat at once; by the time they reach 90 kg they require about 350 mm of trough length per animal. Barriers separating the heads of pigs at feeding reduce the incidence of fighting. Where the feeding space provided does not allow several pigs to eat simultaneously, dominant pigs will hinder the lower-ranking pigs' access to the feeder, and aggressive behaviour can be caused by inadequate feeder space. Competition for access to the feeder can occur with as few as four growing/finishing pigs per feeding place. Increasing from one to two the number of feeding spaces available for 20 pigs, daily food intake of the pigs increased but with no significant effects on growth rate or food conversion efficiency (Morrow and Walker, 1992).

Piglets offered creep food in a single or three times the normal number of feeders had the highest intake in this latter situation by 2.1 times at 3 weeks of age and 1.4 times at 4 weeks, as a result of less competition for feeder access.

The feeding behaviour of pigs housed in groups of ten, given access to a four-space trough, was significantly different to that demonstrated by pigs with access to a single-space feeder. Those animals with access to the four-space feeder visited the feeder more frequently and for shorter durations, eating only a little per visit, compared with pigs kept in the groups with access to only a single-space feeder (Neilsen *et al.*, 1996; Table 17.1). These authors commented that previously, the differences in the feeding patterns between animals housed either individually or in groups had been attributed to the differences in the social environment in terms of less competition and fewer social interactions. However, in this experiment the social groupings were the same, although the pig:trough ratio did differ, therefore access to the feeder is an important factor affecting feeding behaviour in its own right.

Pigs working for food by having to roll a 'food ball' (the Edinburgh foodball, Young and Lawrence, 1993) to obtain small rewards of food at irregular intervals, seem to limit their intake by the amount of time spent foraging rather than the weight eaten, analogous to the apparent unwillingness of sheep to spend more than about 12 h/day grazing.

Given the variation in results from different experiments on group size, stocking density and feeder space, care must be taken before including such factors in predictions of food intake for pigs.

Table 17.1. Feeding behaviour and performance variables for group-housed growing pigs given access to either a single-space or a four-space feeder (means of 2 days and 7 days, respectively) (from Neilsen *et al.*, 1996).

	4-space	1-space	SED	P
<i>Means per pig:</i>				
No. of visits (09:00–20:00 h)	53.5	9.2	3.36	<0.001
Food intake (g/visit)	24	149	13.6	<0.001
Meal duration (min/visit)	0.67	4.67	0.360	<0.001
Daily food intake (g/day)	1760	1766		ns
Daily live weight gain (g/day)	810	813	48.6	ns
Food conversion ratio (g/g)	2.25	2.23	0.111	ns

Cattle

A moderate amount of competition for feeding space affects the feeding behaviour of cows low in the dominance order, but they compensate by eating at less favoured times of day. Stronger competition results in some animals having insufficient time to eat as much as they would under less time-limiting conditions. The number of cows per feeding position above which daily intake is depressed is variously reported as two and five, but this will depend on the rate of eating of the forage. Using a LUCIFIR system, Elizalde and Mayne (1993) did not find that silage intake by cows was significantly depressed until the number of animals per food station exceeded five. Less than 0.2 m/cow of trough space is likely to reduce intake.

Grant and Albright (1995) provide a comprehensive review of the effects of feeder space on the behaviour and intake of cattle.

Sheep and goats

Goats have a greater reach than sheep of the same body weight, so can eat food spread more widely behind any given type of barrier.

Social Stress

Pigs

When weaner pigs from several litters are mixed there is a short period of stress until a dominance order has been established, but this does not appear to affect voluntary intake. Intake of pigs in mixed-sex groups (gilts and castrated males) was lower by 1.8% compared with the mean for single-sex groups; although this is a small effect, it was obtained from experiments with a total of 3200 animals (Ollivier, 1978), and so may have biological and economic significance.

Competition for food is also affected by the amount of food obtained during each press of a panel. With feeders set to dispense either 1.4, 2.7 or 5.3

g/response, food intakes by growing pigs (ten to one single-space feeder) were 1.97, 2.14 and 2.21 kg/day, respectively, resulting in growth rates of 727, 797 and 845 g/day, respectively, and improved conversion efficiency (Morrow and Walker, 1992). Feeding times were 110, 78 and 87 min/day with 52, 46 and 42 entries/day, respectively.

Pigs worked for longer at the low setting, which generated more queuing at the entrance to the feeder. There were fewer aggressive contacts when two feeders were provided, but no difference in food efficiency or growth rate compared with that for a single feeder. Morrow and Walker (1994) recorded queuing for feeder access but this was not related, in this experiment, to position in the social rank. It would be interesting to note the order with which pigs obtain access to the feeder and whether those animals with long waits or forced to take 'out-of-hours' visits were subordinate.

In groups of sows, however, the social dominance order is the same as the feeding order to obtain a restricted amount of food from an automatic feeder. Feeding by some of the lower-rank animals is disrupted by return visits by more dominant sows, and experience is a major factor in determining the social hierarchy. In a competitive feeding situation sows lower in social ranking have lower daily gains, which appears to be related to their lack of competitive ability to obtain food.

Wellock *et al.* (2003) have made an integrated approach to modelling the effects of several stressors (group size, space allowance, feeder space allowance and mixing) on food intake and growth of pigs. This necessitated quantifying these effects and, rather than using empirical equations derived directly from published data, they have adopted a more basic, biological approach, although parameter values were estimated from experimental data. Food intake was derived mainly from the reduction in potential growth rate caused by the various stressors. Importantly, the effects of multiple stressors are taken as being additive, as demonstrated experimentally with chickens by McFarlane *et al.* (1989) and with pigs by Hyun *et al.* (1998) (see Chapter 18).

Neilsen *et al.* (1995) found no relationship between position in the social hierarchy and any aspects of feeding behaviour or performance when pigs were housed in different group sizes, nor did Dalby *et al.* (1996) when weaned pigs were allowed access to a choice of foods. With ample access to feeder space and adequate environmental conditions, social competition may be less relevant to performance. Social hierarchy is likely to be more stable within a group when there is plentiful feeding space.

Cattle

When heifers are kept with older cows they tend to lose weight, while similar heifers fed separately gain weight, due to limited space at food troughs and dominance of older cows. Similarly, calves at the lower end of the dominance order eat less concentrates and gain weight more slowly. It is better to provide a feeding space for each individual rather than just one long trough. A barrier that separates the heads of adjacently feeding animals is better than one that

just separates the bodies, but a complete head and body barrier is best in allowing subordinate animals to eat.

Miller and Wood-Gush (1991) observed that feeding by dairy cows was more synchronized when they were grazing in summer than when in yard in winter because, even though each cow had her own Callan³ door there were a lot of displacements, usually by a low-ranking cow being displaced by a higher-ranking one. It has also been noted that group-fed cows have a higher intake of a complete food than those fed individually through Callan doors.

As with pigs, social relationships amongst cows during idling are very closely correlated with those at feeding. Low-ranking cows ate less frequently, while middle-ranking ones were ejected most frequently from feeders (Kabuga and Sarpong, 1991). Presumably the lowest learned not to eat when others were eating, whereas ones in the middle did not find replacement as aversive. The frequency of agonistic interactions was 1.4 times higher during feeding periods (especially the first 30 min) than during idling periods, while amicable interactions were more frequent during idling.

Rutter *et al.* (1987) used raw meal data from the LUCIFIR system (see Chapter 2) to test the hypothesis that if one cow replaced another cow at a feeding position within 1 min more times than the second cow replaced the first, then the former was dominant. A matrix of the frequency of competitive replacements was used to generate a social dominance order for a group of 12 cows, and this was found to be almost identical to the social dominance order derived from visual observations of the outcome of all interactions by cows, i.e. it is possible to estimate an animal's position in the 'pecking order' from its feeding behaviour.

Cattle ate faster when there was only one stall for a group of animals than when free access to troughs was allowed (Striklin and Gonyou, 1981). However, the diurnal pattern of eating did not differ between the two situations and dominant cattle did not prevent submissive ones from gaining access to the single feeder.

Dairy cows spend a lot of time visiting concentrate food dispensers and the majority of visits go unrewarded, disrupting the activity of the rest of the herd (Wierenga and Hopster, 1986). When cows were fitted with remote-controlled miniature beepers near the ear to tell them when they could get food, there was a dramatic reduction in the number of unrewarded visits and consequently less disruption.

Bulls are affected by diversions such as heifers or rain. Stags in rut with access to hinds in oestrus eat almost nothing, and therefore show an even more pronounced fall in body condition in the autumn than do hinds, or stags kept in controlled conditions.

Sheep

In hill sheep given blocks of supplementary food, younger ewes have been seen to consume less than older ewes as a result of social competition, probably

³ A door giving access to food that can only be opened by cows wearing the appropriately coded collar-borne device.

because the former kept together as a group, separate from the rest of the flock. Two- and 3-year-old ewes approached the food blocks but were prevented from eating most of the time by the 4-year-old ewes. Thus, social behaviour limits the usefulness of supplementary feeding by causing wide variations in the intake between individual ewes.

Isolated lambs eat less than those in groups but, other than that, the size of the group does not seem to affect daily intake.

The feeding behaviour of sheep can be influenced by the presence and behaviour of other animals, predators being an obvious example. As for interactions between different sheep in a group, when faced with a choice between remaining close to other sheep or moving away to graze, more sociable individuals grazed less (Sibbald *et al.*, 2000). Thus, individual differences in social motivation affect the trade-offs that sheep make when foraging.

Frequency of Offering Food

Lactating and dry cows, given an average of 7 kg of concentrates/day, did not change their silage intake or feeding pattern, irrespective of whether the concentrate was given in two or 22 feeds/day (Gill and Castle, 1983).

Concentrates were given to ewes, increasing from 400 to 600 to 800 over the last 6 weeks of pregnancy, once, twice or thrice daily or mixed with silage (Wylie and Chestnutt, 1992). In weeks 5–6 before lambing, silage intakes were 758 g DM/day for once, 853 for twice/thrice and 996 for mixed, respectively. Three to four weeks before lambing, intakes were 655, 830 and 987 g DM/day, and in weeks 1–2 they were 552, 782 and 876 g DM/day, respectively. These improvements in silage intake are probably due to a more regular flow of nutrients from the concentrates to balance those coming from silage.

Disease

Reduced voluntary food intake is one of the first sign of many diseases. While in some cases this can be attributed to fever, many diseases do not increase body temperature, and some other reason for the reduced intake must be sought. Pair-feeding experiments show poorer performance of infected animals, i.e. anorexia is not responsible for all of the loss of performance, e.g. chickens infected with *Eimeria* spp., sheep with *Strongylus matthei*.

As with other species, a reduction in food intake is one of the first signs of disease in poultry. Decreased weight gains and food intakes are characteristic of infection with the various species of *Eimeria* that cause coccidiosis. Vaccination against Marek's disease has no effect on intake, although it does lead to the production of more extra-sized eggs and a tendency to reduced mortality.

A relatively low level of dosing with *Fasciola hepatica* (liver fluke) for 25 weeks caused a 15% decrease in intake in sheep (Sykes *et al.*, 1980), while large doses severely depressed intake.

Mice force-fed after *Listeria monocytogenes* infection had increased mortality compared with anorexics, and it has been suggested that the purpose of the anorexia is to starve the infecting organisms or stimulate the immune system. Holmes (1993) concludes that: '... present explanations for anorexia in parasitic infections are so rudimentary that this is a most interesting and fruitful field for future study'.

Gastrointestinal parasites in sheep

Infestation with helminths causes a primary depression of food intake in sheep, possibly by the continuous stimulation by the parasites of receptors in the gut wall. The steady decline in intake, which occurs even with a constant level of infestation, is in parallel with the reduction in plasma protein concentration, and it is possible that a deficiency of amino acids is responsible. Plasma levels of CCK increase as intake falls during the course of infestations with *Trichostrongylus colubriformis*, and this is another factor which might be involved in the loss of appetite. A CNS CCK-blocker (Mederantil) given to sheep infected with *T. colubriformis* blocked the intake depression for about 2 h after injection but had little effect in non-infected controls (Dynes *et al.*, 1990).

However, a peripheral CCK-blocker (loxiglumide) had no significant effect in either control or infected lambs (perhaps because the dose was too small or the experiment too short), and it was concluded that CCK produced by nematode infection acts centrally to inhibit food intake. Plasma gastrin levels are also increased in gastric parasitization, and gastrin infusion into the hepatic portal vein depresses intake in sheep (Anil and Forbes, 1980a). Further work is required to elucidate the possible role of gastrointestinal hormones in the anorexic effects of gut infection.

Pair-feeding experiments, to prevent the difference in food intake that would otherwise occur between infested and uninfested animals, show that there is still some loss of production probably as a result of the cost of plasma protein synthesis. Holmes (1993) states that: '... it is still not possible to construct accurate balance sheets of protein synthesis in parasitized animals ...' and '... the cardinal feature of such infections is the loss of considerable quantities of host protein into the gastrointestinal tract and consequent changes in protein synthesis in host tissues'.

Animals on low nutrition, particularly when the food is low in protein content, are more susceptible to the hypophagic effects of parasites, so it is paradoxical that, when fed *ad libitum*, they eat less food than uninfected animals. Infusion of 50 g protein/day into the duodenum of lambs infected with *T. colubriformis* resulted in a food intake depression that was less (22 versus 32%) and worm burdens reduced, compared with non-infused controls (Bown *et al.*, 1989).

Following up the possibility that protein deficiency was responsible for the reduced food intake in infected sheep, Kyriazakis *et al.* (1993b) offered lambs infected with *T. colubriformis* a choice of foods high and low in protein content and found that, relative to uninfected controls, they had reduced daily intake

but increased the proportion of the food high in protein, to give approximately the same daily protein intake as the controls. This increased protein:energy ratio chosen by the infected lambs is presumed to be in response to the increased requirements for protein induced by the parasites. Subsequently, it was shown that this difference in selection for protein between parasitized and unparasitized lambs disappeared once the infected animals had become resistant to the parasite (Kyriazakis *et al.*, 1996). There is further discussion of effects of parasitism on diet selection in Chapter 8.

More recent studies have concentrated on the behaviour of sheep provided with more natural choices of foods at grazing. While the subject of grazing is not covered in this book, it is worth noting that sheep trade off increased risk of being parasitized against the nutritive value of herbage. For example, using *Ostertagia circumcincta*, Hutchings *et al.* (1999) demonstrated that hungry sheep ate more of a nutritious sward even though it was infested with *O. circumcincta*, and those immune to the parasite also chose more of the nutritious infested grass than did non-immune animals. The whole area of trade-off theory in understanding interactions between herbivores and parasites is discussed by Hutchings *et al.* (2006).

Conclusions

Below the LCT, energy requirements increase and food intake normally increases in parallel. In very cold environments, especially with strong winds and heavy precipitation, animals seek shelter and intake may be reduced. In hot environments there is a specific negative effect on intake, with a decline in level of production; the results of short-term experiments can be misleading, however, as acclimatization to hot weather usually gives opportunity for compensatory intake in the cool of the night. In reality, there is an almost continuous negative relationship between environmental temperature and voluntary food intake.

Long daylength stimulates food intake. In poultry this is a primary effect as they do not normally eat at night, but in ruminants it is secondary to the stimulation of growth.

Social facilitation encourages feeding in all farm species, and animals usually eat more when kept in groups than when penned individually. However, if competition for limited feeding space is severe, then feeding behaviour is disrupted (see Chapter 2) and daily food intake can be reduced.

Diseases of most types depress voluntary intake. They are likely to do so by causing abdominal discomfort or by disturbing nutrient requirements in such a way that the food on offer is no longer suitable to meet the new requirements, a situation likely to reduce intake in order to lessen the imbalance. Where a choice of foods is available, animals tend to behave in ways that minimize the parasite burden, but in grazing situations they must often make compromises between obtaining sufficient nutrients for their needs and accepting a certain level of parasitism.

18 Epilogue

The years since the publication of the first edition of this book have seen steady progress in our knowledge of the role of learning in the control of food preferences, but this has not been reflected in any great advancement of our ability to predict voluntary intake. A major limitation is the wide variation in intake and choice between individual animals offered the same food(s) in the same conditions.

Given the general opinion that intake and choice are controlled to meet the animal's requirements, then either there are large differences in the requirements of different animals or the control system is not very precise (or both). By 'requirements' we do not restrict ourselves to nutrient requirements, but we include 'requirements' to avoid undue discomfort, 'requirements' of the social situation in which the animal finds itself and 'requirements' to achieve goals that might be different from those we set for our livestock.

As stated in Chapter 15, there are two approaches to looking at voluntary food intake and diet selection. One is from the point of view of the animal's physiology and seeks to explain food intake and diet selection from measurements of such things as blood levels of hormones and metabolites, and degrees of stimulation of receptors. The other comes from an evolutionary background and posits that animals will evolve to use whatever mechanisms allow them to survive and reproduce.

It has to be said that the first of these has not proved to be very successful or, at least, sufficient entities have not yet been measured in sufficient detail to allow a conclusion as to how intake and selection are controlled. However, the second approach is not fully satisfying either, allowing any observation to be 'explained' on the grounds of evolution without physiological justification.

This chapter brings together some of the various threads that have been running throughout the rest of the book and provides some personal viewpoints and challenges for the future.

Feeding Behaviour

We have seen in Chapter 2 how difficult it is to predict feeding behaviour. Meal size and inter-meal interval seem to be very loosely controlled – indeed, it can be speculated that they are not controlled at all – and Smith (2002), speaking from a lifetime's study of the subject, has said that: 'The apparently simple object – the scientific explanation of the size of a meal – has proven elusive. It has not been attained yet in any animal under any condition.'

While intake and choice of foods over periods of several days are related to animals' nutrient requirements, this is not true for shorter periods, and it raises serious doubts about the validity of trying to simulate feeding behaviour by means of metabolically driven models. For example, the detailed model of Forbes (1980) was induced only to provide realistic meal patterns for sheep by including direct mechanistic control of feeding by rate of absorption of nutrients and, whereas it was described in detail in the first edition of this book, it has not been mentioned in this edition, apart from here. Not the least of the difficulties of accepting a mechanistic model of feeding is the fact that such models generate regular sequences of meals, in contrast to the unpredictable intervals actually observed in many animals (see Chapter 2).

In discussing the difficulty of understanding feeding patterns, Kyriazakis *et al.* (1999), already quoted in Chapter 7, have passed the opinion that: '... the question to be asked in relation to diet selection is not "what time period matters to the animal?" but "how much change or deviation in the internal state is the animal prepared to accept?"'. This still assumes that meal-taking and -selecting are driven by the animal's internal state and not just by external events – but state of what?

Mayer (1953) proposed that the state monitored was the concentration of glucose in the blood of rats, while Booth (1974) suggested that it was rate of supply of energy with an additive contribution from gut distension – we should think of many states at once, not just one or two. What is required is a way of considering feeding behaviour that is multidimensional and not dependent only on minute-by-minute changes in metabolism. The following speculation is presented as a possible way forward in describing how steady changes in physiological variables within the animal can generate the sudden step changes in rate of eating at the start and end of a meal.

The Catastrophe of Feeding

Thom (1975) explores ways of looking at situations in which slow changes in some variables induce very rapid (catastrophic) changes in other variables; a simpler presentation of Thom's ideas is given by Saunders (1980). The multidimensional possibilities of catastrophe theory allow us to use more than one single potential on which feeding depends. In the example that follows only two potentials are used, as this allows pictorial representation in a way that is reasonably easy to understand, although more than two potentials can be incorporated by the use of high-order catastrophes.

The potentials adopted here are: (i) the integration of negative feedbacks, which will vary according to the time since eating last occurred, the rate of digestion of the food, the capacity of the digestive tract and the bulkiness of the food, amongst other things; and (ii) the capacity to utilize nutrients generated by the metabolism of the tissues, varying according to such things as the animal's metabolic rate and its potential to synthesize protein and fat, amongst other things. Figure 18.1 shows Thom's second-order catastrophe which generates a bifurcation, or cusp, diagram.

The sequence of events during a feeding cycle are envisaged to be as follows, with reference to Fig. 18.1.

A-B: start of eating; as the meal progresses capacity starts to fall; negative feedback still weak.

B-C: meal continues; capacity still falling; negative feedback increasing in strength; rate of eating slows.

C-D: meal stops.

D-E: nutrient supply still rising, but more slowly; capacity starts to increase as stomach empties.

E-F: capacity rising; feedback falling.

F-G: capacity rising further; supply falling further.

G-A: next meal starts at M, by catastrophic jump.

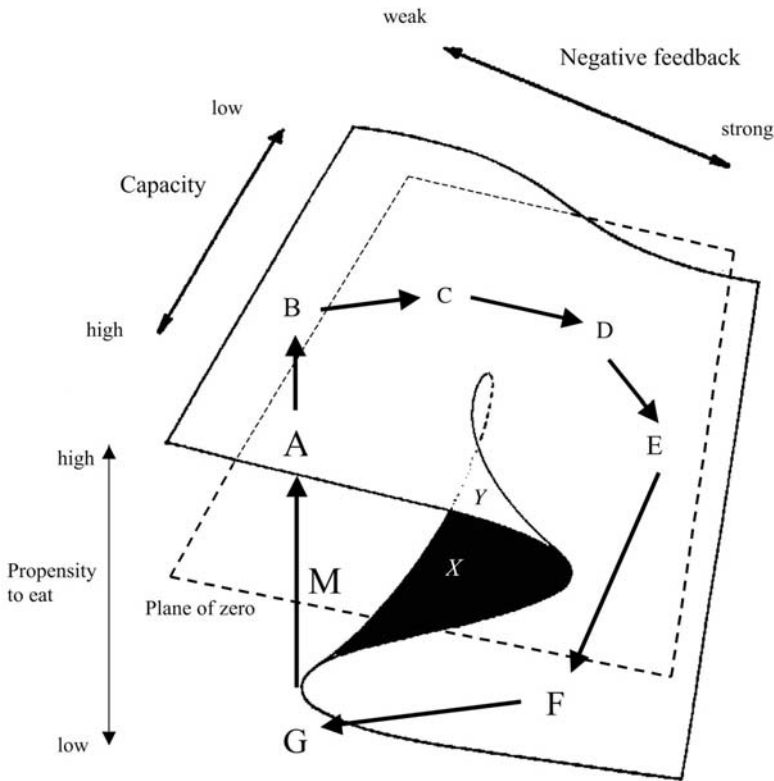


Fig. 18.1. Bifurcation diagram of feeding (see text for explanation).

As the meal starts area X is inaccessible, while area Y is inaccessible later in the meal. The vertical axis is labelled 'propensity to eat', and eating is deemed to start when this potential rises above zero, i.e. at point M midway up the vertical between G and A. Thus, eating starts at the maximum rate, as usually seen, but towards the end of the meal rate of eating slows, as between C and D a commonly observed phenomenon.

With a higher capacity for nutrient utilization, e.g. in lactating animals, the cycle is moved towards the viewer so that segment CD now spans the cusp and eating is predicted to stop suddenly; there is faster initial rate of eating and more rapid movement around the circuit, generating an increase in meal frequency. Low demand for nutrients, on the other hand, moves the cycle away from the viewer, predicting a more gradual start to the meal, lower maximum rate of eating and more gradual slowing towards the end of the meal.

The nature of the two axes is arbitrary, and other factors affecting feeding have been explored, including ease of prehension of food that predicts that grazing animals will fluctuate in their rate of eating during their very long meals. This and other testable outputs of the cusp model can be examined either by scrutiny of past research results or by designing appropriate experiments and measurements.

The 'catastrophe of feeding' has been briefly presented here to stimulate thought and discussion, and it is the author's intention to explore its concepts further and to publish the outcomes.

Minimal Total Discomfort: a Multifactorial Approach

No longer can we look upon the various theories of intake control as alternatives, but rather as complementary and contributing to a multifactorial control system. No single factor is essential for normal food intake, and many manipulations that stay within the physiological range have only small effects that are often statistically non-significant: '... the conventional univariate focus mainly on energy must be replaced with multivariate approaches that recognize multiple biochemical interactions' (Provenza and Immense, 2006). This multiplicity of factors is recognized in the MTD hypothesis in which the sum of squares of deviations of the current supply of each of the resources of interest from their ideal is calculated. While not linear, the addition of the various signals does avoid the introduction of interaction between independent variables and overcomes the problems inherent in multiplicative models that introduce 'non-trivial requirements (usually not met) for model testing' (Pittroff and Soca, 2005).

Like the application of catastrophe theory to feeding described above, the MTD hypothesis is first and foremost an intellectual exercise in which an attempt has been made to incorporate the major factors likely to be involved in the control of food intake and diet selection, including some features of both the physiological and the evolutionary approaches. As discussed in Chapter 10, further development is required before it will be clear whether MTD represents a viable way forward in our understanding, and eventually prediction, of intake and selection.

I suppose the MTD hypothesis is an attempt to bridge the two approaches to food intake control outlined at the start of this chapter. On the one hand, it adopts the commonly held view that there are optimal rates of supply of nutrients and that the animal behaves in such a way as to try to provide these; on the other, while not getting to the level of receptors, it does acknowledge that there is sensory information from the body relaying information on the current mismatch between supply and demand. MTD allows both approaches to be incorporated at once, e.g. effects of short-term infusion of an energy-yielding metabolite can be combined with effects of a long-term change in composition of food.

It is highly unlikely that the MTD approach will ever be 'proved' right or wrong. The idea that we will eventually be able to explain and predict by a reductionist approach alone the behaviour of such a complex system as that controlling food intake and choice is probably wrong. It is certainly worth persisting, however, given the importance of optimal nutrition of farm animals, and we should not reject new hypotheses just because they do not give accurate predictions, which could hardly be expected when we can currently make only crude estimates of some of the important variables in our calculations.

Sensing the Environment, External and Internal

General senses

The first primitive organisms to evolve the capacity to move must also have developed receptors to inform them of the environment in which they found themselves, otherwise they would have no reason to use the new-found ability of locomotion. Initially, the receptors would be likely to sense chemicals to which the proto-animal could respond by moving towards (food) or away from (toxins). Multicellular organisms developed a coelom and eventually a digestive system in which to store and digest food. The contents of the digestive system are outside the body proper and their composition is still sensed, but now a mechanism is required to encourage the ingestion of some substances (food) and to avoid the ingestion of others (toxins). Special senses developed to allow the animal to sense the outside world separately from the world within the digestive tract and to allow it to make decisions about what (and how much?) to eat, based either on innate preferences or on previous experience.

Special senses

In mammals, the taste of potential food is used as a powerful cue to its nutritive value. In some cases (e.g. sugar) the connection between the taste and the nutritive value is close and an innate link can be established. In other cases the nutrient cannot itself be sensed and the animal must learn to rely on some other, proximate, feature of a food source to determine whether it is likely to provide

the nutrient in question. Thus, learned associations between the sensory properties of foods and their nutritive value are likely to be very primitive ones that can function at the subconscious level, such as the ability of the effects of a painful stimulus administered to an anaesthetized animal to become associated with the flavour of the food available when it recovers consciousness (Provenza *et al.*, 1994b).

What are the most appropriate means of differentiating foods for different types of animal? We know that mammals are more sensitive to taste, while vision is more important in birds, but are there particular characteristics that make it easier for animals to learn to associate a food with the metabolic consequences of eating that food? Is a combination of cues, e.g. colour and taste, more effective than one single cue?

Gastrointestinal receptors

Given that the receptors in the wall of the digestive tract are now no longer in direct contact with the external environment, the information they provide cannot be used directly to seek or reject food (except in the case of vomiting). However, their responses can be used as the conditioning stimulus for learned preference or aversion to food with a particular taste, or other characteristic sensory property such as colour. Nausea or other feelings of illness, especially when of abdominal origin, are powerful conditioning stimuli presumably because they presage more serious illness and/or vomiting. Vomiting is innately aversive; also, to expend resources seeking and eating food and then not to obtain any nutritive value from that food is wasteful in the extreme, and waste is minimized by evolution.

The visceral organs of the ruminant are well supplied with receptors for mechanical, chemical and (probably) osmotic stimuli, with afferent information passing to the CNS by the vagal and splanchnic routes. While numerous experiments have been performed in which the natural stimulation of these receptors by digesta has been augmented by balloon distension or introduction of chemicals into the rumen, these have often generated conflicting results. Specifically, how does osmolality exert its effect on food intake via the rumen when it has proved to be so difficult to identify osmoreceptors? Of the three major VFAs, why does butyrate exert least effect on feeding when infused into the rumen while having the greatest effect on chemoreceptors?

Metabolic receptors

The gastrointestinal receptors cannot be expected to guide the animal to eat amounts and mixtures of foods that meet the animal's requirements. Such control must come from within the animal and receptors must exist which monitor the supply in relation to the demand. It is unlikely that there is a specific receptor for each of the 50 or so essential nutrients and, even if there were such prolificacy of receptor types, how would each one know whether the

level of the nutrient it sensed was sufficient or not? Nutrients are essential when they act either as substrates for, or enzymes and cofactors in, essential metabolic pathways, so it would seem sensible to look for ways in which the CNS could be informed about the state of a few critical metabolic pathways. One such appears to be the pathway whereby energy is made available in the liver (see Chapter 4).

The concept of a requirement for a nutrient is difficult to sustain when an animal functions quite well over a range of levels of supply of each nutrient, adapting to an excess by eliminating or storing the unwanted material and to a deficiency by reducing the rate of the pathway in question. The concept 'responses to nutrients' is more meaningful than that of 'requirements for nutrients', and hypothesizes that animals endeavour to eat quantities of nutrients which support maximum growth or milk production or that they eat to optimum efficiency do not seem realistic. Rather, animals eat to achieve the most comfortable situation metabolically which does, in practice, often mean that they eat that amount and proportion of foods which allows them to be most efficient.

Whatever their nature, the signals generated by the animals' metabolism can be used as conditioning stimuli for learned preferences for food, both in terms of quality and quantity. An animal whose metabolism is provided with too much glucose in relation to lysine may attempt to redress the balance by eating more food (to increase the lysine supply), eating less food (to reduce the glucose supply) or eating a different mixture of foods, if it has the choice (to correct the glucose:lysine imbalance). Which of these actions it takes will depend not only on its immediate circumstances (is there a choice of foods available?) but on its nutritional and metabolic history (what has it learned previously about how to cope with the imbalanced situation?).

Despite our appreciation of the importance of learning and our knowledge of receptors in the visceral organs, we are still left with the problem of knowing how animals are able to regulate food intake with reasonable accuracy in relation to their requirements for normal growth, reproduction and fattening. We know, for example, that pigs in the UK used to become very fat if fed *ad libitum*, so they clearly had the capacity to eat, digest and metabolize great quantities of nutrients.

Genetic selection for leanness over the last few decades has produced pigs that have a low level of food intake, so presumably the lower propensity to fatten has caused that lower food intake – intake is responding to demand. Reduced fat synthesis results in reduced uptake of precursors into adipose tissue, and this must lead to metabolic discomfort due to accumulation of these precursors which, in turn, reduces voluntary intake. Is the metabolic discomfort in this case simply an excess of fatty acids available for oxidation in the liver? Or is it a change in the relationship between leptin production by adipocytes and CNS sensitivity to leptin?

A related issue is the ability of animals to select between two foods, a mixture of which provides the most appropriate intake of energy and another nutrient, e.g. protein. Pigs with greater potential rates of lean tissue deposition choose to eat food with a higher protein:energy ratio than do pigs with a

greater propensity to fatten. Again, this is postulated to be related to the ability of the foods to provide metabolic comfort.

How are we to proceed experimentally to unravel the concept of metabolic discomfort?

Central Nervous Involvement

In higher animals, all the capabilities of learning are concentrated in the brain and closely related structures (CNS). The CNS is provided with information by the special senses, gastrointestinal receptors and metabolic sensations and it can use any or all of these as conditioning agents. It may learn, for example, that food with certain sensory characteristics leads to certain unpleasant gastrointestinal consequences and avoid eating it on that basis. Another food may be recognized as one that alleviates a metabolic imbalance and become preferred for that reason.

It is also likely that the CNS is directly sensitive to its own nutrient supply, particularly to energy deficit. However, it is the duty of much of the rest of the body, particularly the liver, to prevent shortages of nutrient supply to the brain (excesses are not so damaging), so the CNS should not normally have to take action to eat food, or avoid eating food, based on its own metabolic status.

The whole concept is summarized in Fig. 18.2, in which the passage of a parcel of food through the GI tract leads to the stimulation of numerous receptors from which signals are relayed to the CNS in a time-related sequence (Forbes, 1999). This information is integrated and used to generate learned associations, e.g. between the sensory properties of the food eaten and its subsequent gut and metabolic effects. As a result, the CNS controls feeding, digestion and metabolism in ways designed to avoid deficiency or toxicity and to provide an optimum supply of nutrients for the various tissues of the body.

These concepts can be visualized as a 'satiety cascade' (Blundell and Halford, 1994), with the information available to the CNS about a particular food item becoming progressively more accurate as the food is seen or smelled in the environment; tasted and eaten; accumulating in the stomach; yielding nutrients in the intestines; providing the body with nutrients via the liver; contributing to the body stores of energy and protein.

There is a continual contention between short- and long-term studies – minute-by-minute changes in behaviour, digestion and metabolism on the one hand – continuous and fairly stable demand for nutrients for maintenance and productive process on the other. It remains to be established experimentally whether there is additivity between effects of rapidly changing internal signals, such as supply of glucose to the liver, and slow-changing indicators of adiposity, such as leptin.

Future Experimentation

Too many experiments have been carried out without it being clear what hypothesis is being tested. Experimentation must go hand-in-hand with theory, or at least be designed to collect data to construct relationships to be used in models.

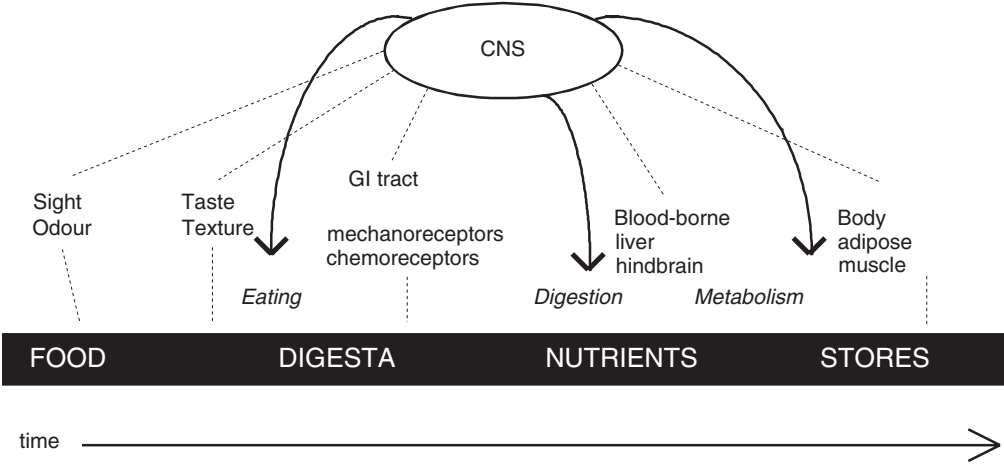


Fig. 18.2. Satiety ‘cascade’. Dotted arrows indicate flows of information to CNS as food goes from being identified in the environment to its nutrients being stored in the body (see text for explanation) (from Forbes, 1999).

Experimental design

Attempts to understand what causes animals to stop eating have often involved injection of putative satiety factors into parts of the digestive or vascular systems, with observation of food intakes during and after the injection period. In a ‘well-designed’ experiment, each animal is given each treatment only once before it is given control and other treatments in a Latin Square design. Thus, the animals are not given the opportunity to learn to associate the effects of the injection with any characteristic of the food and are denied an important route of control that is normally open to them, namely learned associations between the sensory properties of the food, its eventual visceral effects and yields of metabolites. It is postulated that many such experiments have either under- or overestimated the satiating effects of metabolites; some may even have shown no effects of a factor which is, under ‘natural’ circumstances, actually quite important and vice versa.

Consider the dilemma of an experimental animal which, despite continuing to eat the same safe food as usual, suddenly feels ill (or metabolically uncomfortable) due to an infusion of an imbalancing nutrient. The immediate effect of the feeling of illness is to depress food intake, but a longer-term effect might be to render that food aversive, especially if this or a similar treatment is repeated on other days. However, on non-experimental days, or during control infusions, the same food is once again safe. Does the animal learn to associate the presence of the white-coated experimenter with illness and the blue-overalled technician with well-being? Whatever the outcome, it would hardly be surprising if it became very confused and gave results that were difficult to interpret.

If we are to discover the real significance of putative factors involved in the control of food intake, we must give animals a chance to learn about their effects in a much more natural way than the change-over experiments outlined above. During the periods when the animals are exposed to the experimental treatment, they should be given a food with distinctive sensory properties, different from the one they normally eat. The treatment–food pairing should be repeated on several occasions to allow the association to be established and, in addition to recording intake during these treatment periods, the animal should be allowed to demonstrate its feelings for the experimental food, either by recording intake of the stimulus-paired food in the absence of the treatment stimulus or by assessing the animal's preference for this food against another distinctive food which has been paired with a control treatment.

For example, not only does CCK depress food intake in broiler chickens but it also leads to a conditioned aversion for the colour of food on offer after the injection of CCK, relative to a food of a different colour which was available after saline injections (Covasa and Forbes, 1994). Learned aversions to novel foods by farm animals have been demonstrated many times, particularly by Provenza and colleagues and, more recently, learned preferences have also been studied. The development of specific appetites for nutrients, where animals not only avoid eating too much of a substance but also avoid eating too little, are clear evidence that learning to balance the diet is possible.

Experimental complexity and the role of modelling

The complexity of the control of food intake suggests that complex experiments must be performed to advance our understanding of the system. However, the more elaborate the experiment the more likelihood there is of problems occurring where the main parameter to be measured is voluntary food intake, subject as it is to large between- and within-animal variation and to the well-being of the experimental animals. While some complicated experiments may still be necessary, progress can be made by an alternative strategy involving testing of simple hypotheses and linking of ideas and data by simulation models.

Toates and Booth (1974) were the first to adopt this approach for the rat, and their model generated realistic predictions concerning meal size and interval. A similar approach was adopted for ruminants by Forbes (1980), but with the assumption that feeding was inhibited *either* by energy-yielding products of digestion *or* by rumen fill. This approach has been overtaken by several developments in our thinking: (i) the realization that feeding behaviour is not closely controlled by metabolic needs or physical constraints; (ii) the increasing realization of the importance of learning; and (iii) the proposal that the various factors affecting intake do so in an integrated (additive?) rather than an exclusive manner.

Variation between and within individuals

Not only is there considerable variation in feeding behaviour between similar animals, there are also marked fluctuations in intake and choice on successive days in any given animal. This variation has often been overlooked because we tend to assimilate data into means or relationships which we test for statistical significance without necessarily ever looking at the raw data. Variability of feed intake *within* an animal has been postulated in Chapter 10 to enable animals better to manage the relationship between their needs, in terms of nutrient supply, and the food(s) available to them. Variability *between* animals is a necessity for allowing Darwinian evolution to proceed.

Variability in genetic potential, and therefore nutrient demand, also means that giving a single food to a group is not likely to provide optimally for all of the animals. A diet formulated for the needs of the average animal will see some animals over- and others undersupplied with one or more nutrients. Allowing for this by increasing the concentration of a critical component, e.g. protein, to prevent undersupply for the great majority, will see even more wastage as a greater proportion of the population eat a food excessively high in protein. Oversupply leads to increased excretion in faeces and urine, especially critical for the environment in the cases of nitrogen and phosphorus. Will choice feeding provide a practical solution by allowing individuals to compose their own optimum diet?

Practical Considerations Regarding Farm Animals

The reason for our focus in this book on animals of agricultural importance is simple: efficient use of resources, especially food resources, is essential as we tackle the conflict between the increasing number of human beings in the world and the uncertainties of climate, and thus of agriculture, including those due to global warming. While the tone of many parts of this volume is abstract, some of what is written should be of use to those who advise and serve livestock farmers, if not to those farmers themselves.

A balanced diet

Voluntary intake of a single food will be likely to be at an adequate level to meet most closely the animal's 'requirements' when it provides nutrients in a ratio close to that with which the animal uses those nutrients, i.e. a well-balanced food. Where the food is imbalanced, then intake might increase and the animals thereby take in too much energy and become fat, or intake might decrease if the imbalance causes severe metabolic discomfort.

The problem of deciding when a food is balanced is particularly difficult in the case of ruminants, in which considerable modification of some food constituents takes place before absorption. The relative amounts of acetate,

propionate and butyrate produced by ruminal fermentation are unlikely to match exactly the amounts required for the animal's metabolic processes, resulting in a situation of imbalance. While the amount of acetate absorbed from the rumen of a lactating cow offered forage might be adequate to support the synthesis of milk fat, the amount of propionate might be insufficient for gluconeogenesis to support milk lactose synthesis. An increase in voluntary intake to supply the propionate would result in overproduction of acetate and either a return to undereating or an increase in body fat deposition. The practical solution is to supplement the forage with concentrates that provide a higher propionate:acetate ratio, thus balancing the forage and overcoming the imbalance.

It is possible that a ruminal fermentation modifier, by increasing the propionate:acetate ratio, might increase the intake of a forage. However, the forage may well have other imbalances, such as a gross deficiency of protein or an imbalance in the ratio of amino acids, which prevent a higher level of voluntary intake even when the VFA balance is corrected. The problem of amino acid supply is of particular importance in ruminants in which dietary nitrogen sources are considerably metabolized by the ruminal microflora to produce an imbalanced mixture of absorbed amino acids, even when the dietary amino acid mixture was balanced. Hence the importance of providing sources of some essential amino acids that escape ruminal degradation (UDP), as well as sufficient sources of degradable nitrogen so as not to limit microbial activity in the rumen (RDP).

The ruminant nutritionist strives to minimize the cost of a diet (by including cheap, fibrous materials) while ensuring adequate intake of digestible nutrients. Recent research has given us considerable confidence in discussing the importance of learning in animals' adaptation to changes in the food(s) on offer, but we still need to know more about how ruminants trade off the various factors tending to stimulate and inhibit feeding, especially the balance between nutrients and fibre.

Adequate ways of predicting the yields of absorbed nutrients from the composition of the diet and the characteristics of the animal are therefore of the utmost importance and dynamic modelling, supported by appropriate experimentation, provides the best chance of achieving this.

Choice feeding

Chapters 6, 7, 8 and 13 have provided many examples of the ability of animals to correct nutritional imbalances by making appropriate choices from two or more foods. While there is some commercial interest in choice feeding using whole cereal grains for poultry, it is with ruminants that the greatest potential lies, given our relative ignorance of the ability of forage foods to provide a balanced diet in most situations. We have ample evidence that ruminants are capable of making nutritionally wise choices between foods but, as yet, few attempts have been made to develop choice feeding to answer the problems outlined above.

There is a rational fear that, given free access to concentrates, animals would gorge themselves in the short term and eat wastefully large amounts in the long term. However, it may be that offering choices between two forages, or a forage and a by-product such as brewers grains, would actually reduce the need for concentrate supplementation.

It would be a mistake to expect choice feeding to solve all the problems of nutrition of farm animals. We do not yet know the limits to animals' ability to select appropriately in situations where one food is scarce or where one food contains innately aversive compounds, even where these are not toxic. Apparently similar animals can show quite different levels of intake and dietary preference, and it is not known to what extent this is due to differences in their nutritional history and nutrient requirements and to what extent it is inexplicable, random variation.

Welfare

In the wild most animals have access to, and eat from, a variety of food materials. Two of the 'five freedoms' to which farm animals are entitled are 'freedom from hunger and thirst' and 'freedom to indulge in most natural forms of behaviour'. Where a dietary imbalance exists which, according to the discussion above, causes metabolic discomfort, choice feeding is clearly good for the welfare of animals. What is less certain is whether the welfare of animals given a completely balanced diet *ad libitum* can be improved by access to a choice in order to allow them to indulge in the natural behaviour of diet selection and to be given a feeling of some control over their own lives.

If it causes discomfort to eat too much food, or too little, or an imbalance of nutrients, then it should be possible to integrate such food-related discomforts with other discomforts due to an 'imbalanced' environment, e.g. too little space, too hot a temperature. The MTD hypothesis tentatively provides a way of incorporating disparate stressors in the same model (Forbes, 2006a).

It has been shown that multiple stressors increase the heterophil:lymphocyte ratio and plasma corticosterone in chicks in an approximately additive manner (McFarlane and Curtis, 1989). The growth rate of pigs subjected to adverse environmental temperature, stocking density and regrouping in all combinations was depressed according to the sum of the separate effects (Hyun *et al.*, 1998). As the number of stressors increased from 0 to 3, weight gain, food intake and conversion efficiency all decreased linearly (see Fig. 18.3). It seems likely, therefore, that the effects of stressors are additive and that they can be combined with nutrient imbalances by means of the MTD hypothesis.

The following example explores the application of the MTD hypothesis to food- and environment-generated discomforts and uses protein intake, environmental temperature and space allowance (Forbes, 2006a). If each of these is within the optimum range for the animal in question, the place they occupy in 3D space can be considered to be the 'desired' point (see Fig. 18.4).

However, the animal may be currently overeating protein (perhaps because the dietary protein content is high in relation to energy concentration),

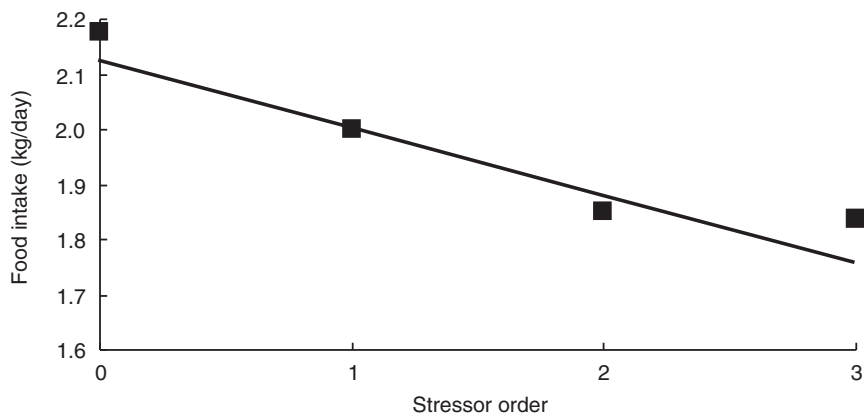


Fig. 18.3. Effect of stressor order on average food intake by growing pigs over a 4-week period (from Hyun *et al.*, 1998).

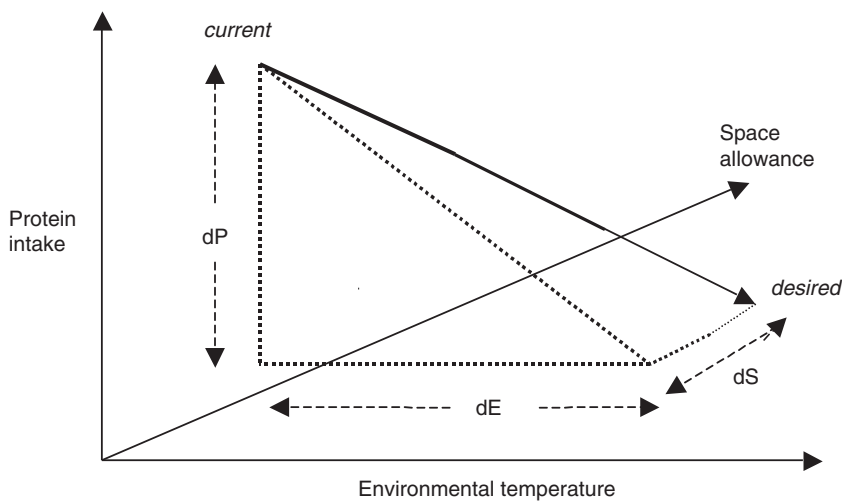


Fig.18.4. Diagram of Pythagorean calculation of distance between current and desired position of an animal in relation to protein intake, environmental temperature and space allowance (from Forbes, 2006a).

is cold-stressed and is allowed less space than it requires for comfort: this is the 'current' position. The shortest route to get from 'current' to 'desired' is along the straight line joining the two, and the length of this can be calculated from the square root of the sum of squares of the three individual deviations, dP , dE and dS (Pythagoras). In order to transform each of the three factors into forms in which they can be combined, it is necessary to put each on a numerical scale and to express the difference between current and desired as a proportion of

the desired value. These proportional differences are then squared, summed and the square root of the sum is obtained as an expression of total discomfort.

Thus:

$$\text{total discomfort} = \sqrt{\sum_{j=1}^i ((d_j - c_j) / d_j)^2} \quad (18.1)$$

where d is the desired value and c is the current value of each of i variables affecting welfare.

In our example (Forbes, 2006a) the current protein intake is 12 g/day and the desired intake is 10 g/day, giving a deviation of 2 g/day, and the proportional deviation is $2/12 = 0.17$, see Chapter 10. For environmental temperature it would be useless to take absolute zero as the starting point of the temperature scale; rather, we can use the minimum at which the animal can survive, say 273°A (0°C), as the low end of the range and then calculate discomfort as the current temperature relative to its optimal temperature, say 303°A. Thus, a temperature of 293°A would give a relative proportional discomfort of $(303-293)/30 = 0.33$.

As far as space allowance is concerned, a minimum realistic space might be the area the animal itself occupies, say 0.1 m², while the optimum might be that space that it is prepared to work to attain, say 1 m². The range from minimal to optimal is thus 0.9 m² and an animal with a space allowance of 0.2 m² has a proportional deviation of $(0.9 - 0.2)/0.9 = 0.77$. Squaring these three deviations and taking the square root gives a total discomfort of 0.854. These calculations suggest that space allowance is having the largest effect on discomfort. Increasing this to 0.55 m² greatly reduces total discomfort to 0.14. This compares with a minimum total discomfort of 0.22 for a situation of mild dietary imbalance (Forbes, 2006b).

This proposal is very speculative and further research will be required before it is known whether it provides any advantage in solving ‘... the problem ... to find the right parameters, variables and indicators and the right solutions using firm biological, psychological and statistical methods’ (Koene, 2006). At least it provides a framework upon which to design relevant research, which is the main function of research models that can themselves never be more than semi-quantitative.

Conclusion

A large part of this book is taken up with simple descriptions of relationships between food intake and the many factors that might affect it, whether these be experimental infusions of hormones or changes in food composition or physiological status. These descriptions are necessary for the completeness of the book, but do not individually give us great insight into how intake and choice might be controlled.

Therefore, other parts of the book are occupied with various theories and integrating hypotheses that are, on the whole, speculative. Such speculation is

also necessary if advances are to be made in understanding and therefore prediction. Precise prediction of food intake and diet selection will then become more useful as a tool in diet formulation, concentrate supplementation and grazing management, although evidence on this last area has not been presented here.

We need to perform well-controlled, critical experiments to clarify individual parts of the jigsaw, but to integrate this with models and to validate the models with other, independent results. Given the key role of learning in the control of food intake and diet selection, future models may benefit from the use of artificial intelligence techniques, but such applications are only just beginning. It may well be that intake control is so complex that it will not be fully understood until we have models as complex as animals themselves, a situation impossible to envisage with current research paradigms.

If some of the experimental results and other observations described here lead others to different hypotheses, and if the approaches to integration adopted here encourage further development then that is all I can hope for. The advances made since the publication of the first edition in 1995 have been considerable and I hope a 'solution' to the mystery of how animals control the amount and mixture of foods they eat is achieved in the useful lifetime of this present volume. I strongly suspect, however, that a single 'solution' will not be found to fit all situations.

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