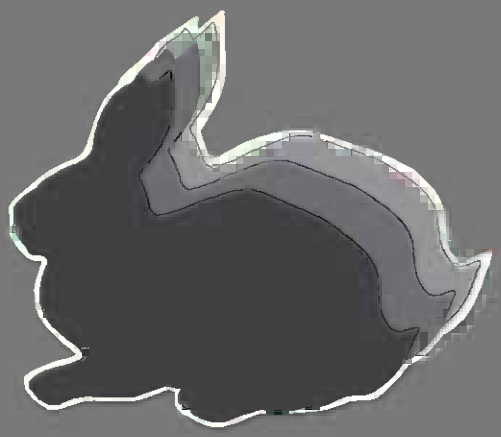
RABBIT FEEDING AND NUTRITION



Peter R. Cheeke

ANIMAL FEEDING AND NUTRITION
A Series of Monographs

RABBIT FEEDING AND NUTRITION

ANIMAL FEEDING AND NUTRITION

A Series of Monographs and Treatises

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Contents

Foreword xi

Preface xiii

1 The Nature of Rabbit Production 1

I. Role of Rabbits and Other Livestock in World Agriculture 1
II. Attributes of Rabbits for Efficient Food Production 4
III. Microlivestock—A New Frontier in Animal Production 7
IV. Factors Limiting Rabbit Production 8
References 9

2 General Principles of Rabbit Nutrition 10

I. Proteins 10
II. Carbohydrates 11
III. Lipids 11
IV. Minerals 11
V. Vitamins 12
VI. Roles of Nutrients 12
VII. History of Rabbit Nutrition Research 13
References 14

3 Digestive Physiology 15

I. Classification Based on Feeding Behavior 15
II. Classification Based on Digestive Tract Physiology 16
III. Comparative Digestive Strategies of Herbivores 19
IV. Anatomy and Functions of the Rabbit Digestive Tract 20
V. Digesta Flow (Transit) in the Gut 28
VI. Microbiology of the Digestive Tract 30
VII. Comparative Digestive Efficiency 31
References 32

4 Protein and Amino Acid Nutrition 34

I. Protein Structure and Synthesis 34
II. Amino Acids in Rabbit Nutrition 39
III. Protein Quality 43
IV. Protein Requirements for Growth and Lactation 46
V. Digestion of Protein 50
VI. Digestibility of Proteins in the Rabbit 51
VII. Nonprotein Nitrogen (NPN) Utilization 54
VIII. Factors Influencing Protein Requirements 57
References 60

5 Energy Metabolism and Requirements 63

I. Energy Categories and Measurement 63
II. Total Digestible Nutrients (TDN) 65
III. Basics of Cellular Metabolism 66
IV. Cellular Metabolism of Carbohydrates 67
V. Factors Influencing Energy Requirements 68
References 75

6 Carbohydrates and Fiber 77

I. Classification of Carbohydrates 77
II. Readily Available Carbohydrates in Rabbit Nutrition 78
III. Digestion of Carbohydrates 79
IV. Fiber in Rabbit Nutrition 87
References 93

7 Fats 96

I. Chemical Characteristics of Fats 96
II. Digestion and Absorption of Fats 98
III. Use of Fat in Rabbit Diets 98
IV. Rancidity of Fats 104
V. Essential Fatty Acids 104
References 104

8 Mineral Nutrition of Rabbits 106

I. Calcium 107
II. Phosphorus 111
III. Magnesium 113
IV. Potassium 114
V. Sodium and Chlorine 115
VI. Manganese 117
VII. Zinc 118

VIII. Iron 119
IX. Copper 120
X. Molybdenum 125
XI. Selenium 126
XII. Iodine 128
XIII. Cobalt 129
XIV. Chromium 130
XV. Some Concluding Comments 130
References 132

9 Vitamins 136

I. Vitamin A 137
II. Vitamin D 144
III. Vitamin E 145
IV. Vitamin K 147
V. B-Complex Vitamins 147
VI. Vitamin C 150
VII. Some Concluding Comments 151
References 152

10 Water: Functions and Requirements 154

I. Properties and Functions of Water 154
II. Water Compartments of the Body 155
III. Water Requirements 155
IV. Nutrients and Toxic Elements in Water 157
References 159

11 Feeding Behavior and Regulation of Feed Intake 160

I. Ingestive Behavior of the Rabbit 160
II. Factors Affecting Feed Intake 160
III. Factors Affecting Feed Conversion Efficiency 170
IV. Feed Restriction 172
References 173

12 Nutrition–Disease Interrelationships 176

I. Enteritis 176
II. Milk Enterotoxemia 188
III. Cecal Impaction (Mucoid Enteritis) 188
IV. Tyzzer's Disease 191
V. Coccidiosis 192
VI. Pregnancy Toxemia 194
VII. Other Diseases with a Nutrition Involvement 195
References 197

13 Feed Analysis **201**

I. Dry Matter 201
II. Crude Protein 202
III. Crude Fiber 203
IV. Ether Extract 205
V. Ash 206
VI. Nitrogen-Free Extract (NFE) 207
VII. Estimation of Feed Energy 207
VIII. Feeding Trials 208
IX. Digestibility Trials 208
X. Measurement of Transit Time 210
References 211

14 Feedstuffs for Rabbits **212**

I. Properties and Classification of Feedstuffs 212
II. Roughages 213
III. Concentrates 246
IV. Protein Sources 254
V. Nonnutritive Feed Additives 265
References 270

15 Toxins in Feeds **276**

I. Natural versus Synthetic Toxins 276
II. Metabolism of Toxins by Animals 278
III. Classes of Natural Toxins 278
References 291

16 Ration Formulation **295**

I. Nutrient Requirements of Rabbits 295
II. Mathematics of Ration Formulation 297
III. Open versus Closed Diet Formulas 300
IV. Quality Control of Diets 300
V. Specific Problems in Rabbit Ration Formulation 301
References 301

17 Feeding Rabbits for Various Productive Functions **302**

I. Nutrient Requirements and Diets for Growth 302
II. Gestation–Lactation Diets 306
III. Complementary Diets 309
IV. Nonpelleted Diets 310
V. Rex Fur Production 311
VI. Angora Wool Production 320

VII. Feeding Rabbits for Exhibition 323
VIII. Feeding Laboratory Rabbits 324
References 326

18 Nutrition of Wild Rabbits and Hares 328

I. Digestive Physiology 329
II. Feeding Behavior and Food Selection 330
III. Nutrient Requirements 334
IV. Nutritional Effects on Reproduction 339
References 340

19 Nutrition of Guinea Pigs 344

I. Nutrient Requirements 345
II. Responses to Dietary Toxins 350
III. Examples of Adequate Diets 351
References 352

20 Nutrition of the Capybara 354

Appendix 1 Table of Feed Composition 359

Appendix 2 Organ Weight in Relation to Body Weight 369

Index 371

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Foreword

This is the ninth in a series of books about animal feeding and nutrition that are written to keep the reader abreast of the many developments in this field that have occurred in recent years. As the volume of scientific literature expands, its interpretation becomes more complex and requires a continuing evaluation, interpretation, and summation in up-to-date books written by distinguished and well-respected authorities.

"Rabbit Feeding and Nutrition" is written by Dr. Peter R. Cheeke, a distinguished scientist who is recognized worldwide for his outstanding work in animal nutrition, and especially in the feeding and nutrition of rabbits. He served as a member of the 1977 National Academy of Science National Research Committee that prepared the publication, "Nutrient Requirements of Rabbits." He has conducted extensive research on the feeding and nutrition of the rabbit and has reviewed pertinent research information throughout the world on this subject. He has also included information on tropical and subtropical feeds, which means the book should be valuable and useful under both temperate and tropical conditions throughout the world.

The book is very well written and documented with numerous tables, figures, and references. The information is presented in a manner useful for animal scientists and students, feed manufacturers, veterinarians, vocational agricultural teachers, extension agents, consultants, and rabbit raisers; it may also be used as a text for courses on this subject.

This book should be especially useful for the developing countries, where a source of animal protein is greatly needed to improve the quality of the human diet. Rabbits can be raised by small farmers and others with simple housing in their backyards and can be fed forages, by-product feeds, and other wastes that otherwise might not be used. Moreover, rabbits are popular for consumers in developing countries who have no refrigeration, since a family can easily consume a rabbit in a meal. Short chapters on the capybara and guinea pig, which may likewise have an important role in food production in developing countries, are also included.

More consideration should be given to the rabbit as a small enterprise for the

poorest-of-the-poor, who greatly need a more nutritious diet. The rabbit can play an important role in the various programs needed to double the world's animal protein production in the next 20 years as a means of improving the human diet. Many world scientists are greatly concerned about the fact that well over one billion people still suffer from chronic malnutrition, with over one-half of them being children under 5 years of age. This malnutrition has carry-over effects in the learning ability, development, and well-being of these children. Even though food production has increased in the developing countries, it has not kept pace with population growth in many of them. Various estimates indicate a world human population increase of 70–90 million yearly, with about 87% of this growth occurring in the countries least able to feed themselves. Therefore, a well-balanced human diet is still a serious problem throughout the world. Proper use of rabbit production, which can be accomplished with limited resources, can play an important role in improving the quality of the human diet, especially in the developing countries.

Tony J. Cunha

Preface

For a number of years I not only have been fascinated by the nutritional peculiarities of rabbits, but also have been frustrated by the challenge of the seemingly simple task of formulating adequate diets for rabbit production. Recent advances in rabbit nutrition research have enlarged our understanding of some of the unique aspects of digestion and nutrient metabolism in rabbits and have reduced or eliminated some of the frustrations associated with diet formulation, particularly as related to dietary influences on enteric diseases. I believe it is now appropriate to assemble what is now known about the nutritional needs of the rabbit into a comprehensive treatise on rabbit nutrition.

"Rabbit Feeding and Nutrition" is intended to be useful to rabbit raisers, animal nutritionists, feed manufacturers, veterinarians, wildlife specialists, and extension agents. I have endeavored to write in a style that will meet the needs of this diverse group. Information on tropical feeds is included, which should make the book useful under both temperate and tropical conditions. Sufficient literature citations are given to allow the specialist to delve deeper into specific areas without being overly technical for a general audience. A chapter on the nutrition of wild rabbits and hares has been included, as many aspects of the nutrition and metabolism of domestic and wild lagomorphs are similar. It is therefore also my hope that the book will be useful to wildlife specialists with an interest in wild lagomorphs. Short chapters on the nutrition of guinea pigs and capybara are included. These species are herbivores with digestive tract physiology similar to that of the rabbit, and they may, like the rabbit, have a role in food production in developing countries.

Much of the information presented in this book has been developed at the Oregon State University Rabbit Research Center. I am most appreciative of the work of my colleague Dr. N. M. Patton and the graduate students who have worked with us. Dr. Patton's spirited discussions on all aspects of rabbit production have led us to a greater understanding and appreciation of the metabolic intricacies and idiosyncracies of the rabbit.

I wish to thank Helen Chesbrough for typing the manuscript and Deloras Martin for assistance with preparation of the figures.

To my family, I express my appreciation for their support and interest and for keeping things going while I'm off on "rabbit trips." I am grateful to what some have termed "the lowly rabbit" for opening doors for me to scientific inquiry and the personal satisfactions I have gained from my associations with "rabbit people."

Peter R. Cheeke

RABBIT FEEDING AND NUTRITION

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1

The Nature of Rabbit Production

Rabbits are raised for a variety of reasons, and are found in virtually every country. Production of rabbits for meat has long been important in western European countries such as France, Italy, and Spain. Rabbits have traditionally been raised by small farmers in these countries to provide meat for the family and supplementary income. In some countries, including Great Britain, Germany, and the United States, raising rabbits for exhibition and showing is a significant activity. Large competitions are held with animals exhibited and judged according to standards set by rabbit breeder associations. Rabbits are extensively used in biomedical research as laboratory animals. The Rex breed has a unique type of fur, with short guard hairs and erect underfur. High-quality coats, gloves, hats, and other garments can be manufactured from Rex pelts. The Angora rabbit produces wool that is used in the manufacture of luxury garments and in handicraft work. Many rabbits are simply raised as pets. Thus there are a variety of purposes for which rabbits are raised, which may influence their nutritional needs and the types of diets required. Not surprisingly, the nutritional requirements for optimal efficiency in raising rapidly growing meat rabbits, Rex rabbits for fur, Angoras for wool, laboratory rabbits kept under maintenance conditions, pet rabbits, and fancy rabbits for exhibition purposes may be quite different.

I. ROLE OF RABBITS AND OTHER LIVESTOCK IN WORLD AGRICULTURE

Domestic animals have been an integral part of farming since the dawn of agriculture. They have provided meat, fiber, milk, work, efficient use of resources, and companionship, and have also contributed to the development of rural stability and an enduring agriculture. In the developed countries, livestock and poultry are primarily raised for production of food and to a lesser extent fiber (wool, mohair). In the developing countries, draft animals (horses, oxen, buffalo) are still extremely important in providing transportation and farm work. The manure is used in soil enrichment and as a fuel. While mechanization

(dependent on nonrenewable fossil fuels) is becoming more widespread, the use of draft animals is expected to be important for many years to come.

Livestock have a major role in world food production. Animal protein (milk, meat, and eggs) is the highest quality food available to humans. The reasons for this are obvious upon reflection. An egg must contain all the nutrients, in the right quantity and balance, to allow the embryo to grow into a baby bird. Milk must contain all the nutrients needed to support the rapid growth of a young animal, as its sole source of food. Meat is animal tissue, and so contains all the nutrients of which an animal is composed. In contrast, a soybean contains the nutrients in the proportion needed to make a soybean plant, while a wheat grain contains the nutrients needed to make a wheat plant. Not surprisingly, then, the nutrient balance in meat and other animal products more closely matches the dietary needs of humans and animals than do plant products.

High-quality plant foodstuffs such as grains, soybeans, and vegetables are used more efficiently when consumed directly by humans than when fed to livestock. There are many reasons why these high-quality feeds are currently fed to animals, relating to economic considerations. A major role of livestock is the conversion of feeds that humans cannot consume directly into high-quality food products such as meat and milk. These feeds include forages and other roughage sources, and agricultural by-products such as grain milling by-products (bran, hulls, etc.). Some feeds such as cottonseed meal contain toxins to which livestock are less susceptible than humans, so that it is advantageous to use these materials as animals feeds. Livestock are particularly important in the utilization of fibrous feeds, which contain large amounts of cellulose. Cellulose is the most abundant organic compound in the world, making up about 50% of the dry weight of all vegetation. Cellulose, though composed entirely of glucose, cannot be digested directly by animals. It is only as a result of fermentation processes in the digestive tract of herbivorous animals that the energy contained in cellulose can be made available as a food to humans as meat and milk. Large areas of the world's surface, consisting of pastures and rangelands, can only be used for food production by the raising of herbivorous animals on the forage (Fig. 1.1). Additionally, most food crops such as grains yield large amounts of fibrous residues that can only be utilized as a food source through animal production. For example, if all the available arable land in the United States were used for cereal production, sufficient straw and stover would be produced to support three times the present population of cattle and sheep (Van Soest, 1982). When grains are cleaned, the screenings—consisting of small shrunken kernels, weed seeds, and other materials—are used in animal feeds. Thus the integration of livestock production with the culture of food crops is integral to efficient use of resources.

Besides the strict considerations of total agricultural efficiency, there are a number of other reasons why livestock production is a desirable component of food production systems. The production of cereals and other seed crops year



Fig. 1.1 Much of the world's land area is unsuitable for growing crops. Livestock production is the primary means of utilizing these areas for the production of food for humans. (Courtesy of the Oregon Agricultural Experiment Station Communications, Oregon State University, Corvallis.)

after year can lead to tremendous erosion problems. The plowing up of grasslands for grain production in the United States has resulted in unprecedented soil erosion. In the 1930s, there was the infamous dustbowl of the Great Plains. Reestablishment of grasslands reduced the erosion problem, but with increased grain production in the 1970s and 1980s soil erosion has again become a major concern. Crop rotation, with grass and legume forage crops grown for livestock production, is the foundation of an enduring agriculture (Fig. 1.2). There are social considerations as well. Livestock production involves a daily, year-round commitment, whereby the farm family is continually working on the land. Care of animals teaches responsibility and good citizenship to the children. The long-term implications of a stable rural population suggest integration of livestock and crop production as the best foundation. Human history confirms this; all stable societies have had such a base.

In the United States, agriculture has become highly mechanized and capital intensive. Less than 3% of the population consists of farmers. Many young people would like to raise animals for a livelihood, but the high costs of such necessities as land, machinery, and buildings preclude their entry into traditional agriculture. Rabbit raising offers an opportunity to engage in commercial livestock production with limited land and financial resources. Additionally, there is increasing interest in "urban agriculture," in part to satisfy innate desires of people to work the land and produce some of their own food. Rabbits are among the most suitable livestock to be a component of urban farming. They can be raised in a small space and be fed vegetable by-products.

Most of the world's human population is fed by the output of small farms (Gallardo, 1984). While population growth is stabilizing in the developed countries, in developing countries populations will at least double before stabilization will occur. To prevent massive famines in these countries, food production will need at least to double. This production will come from increasingly smaller farms, as the expanding populations result in more and more people on the land.



Fig. 1.2 Production of grain crops, especially on hilly land, can lead to severe soil erosion. The use of crop rotations involving forages for livestock production helps to reduce the erosion problem. (Courtesy of Soil Conservation Service, Portland, Oregon.)

All available resouces will need to be utilized efficiently, which will involve crops, livestock, and aquaculture in integrated systems, in which crop wastes are fed to livestock, and livestock wastes are used for crop fertilization.

II. ATTRIBUTES OF RABBITS FOR EFFICIENT FOOD PRODUCTION

The preceding discussion has indicated how livestock production can complement the growing of crops to make most efficient use of resources. Rabbits have a number of characteristics that suggest that they could play a major role in this process, particularly in developing countries (Cheeke, 1986; Owen, 1976). Some of these attributes will be briefly described.

A. Rapid Growth Rate

In the United States and Europe, rabbits in commercial rabbitries exhibit growth rates of 35–40 g/day, and fryer rabbits reach market weight in 8–10

weeks (Fig. 1.3). In tropical countries, the growth rate is lower, in the range of 10–20 g/day, with a correspondingly longer period to reach slaughter weight, but still a very rapid maturity compared to other livestock raised in these environments. The growth rate of rabbits compares favorably with that of broiler chickens. The period taken to reach slaughter weight is much less than for other livestock such as cattle, sheep, and goats.

B. High Reproductive Potential

The reproductive capacity of rabbits is legendary! Does can rebreed within 24 hr of giving birth (kindling), and in fact this is the normal breeding behavior of the wild rabbit. In the United States and Europe, research has established the potential feasibility of postpartum breeding, allowing up to 11 litters per year. Selection for does capable of maintaining this high level of production and development of feeding programs to support intensive production is needed. If adequate nutrition is not provided, does in intensive breeding systems may resorb the fetuses.

The usual breed-back schedule in commercial rabbitries is from 1 to 5 weeks postkindling. This allows production of five to nine litters per year. In developing countries, it is possible to set up a breeding program so that with only four does and a buck in a backyard rabbitry, rabbits can be produced on a year-round

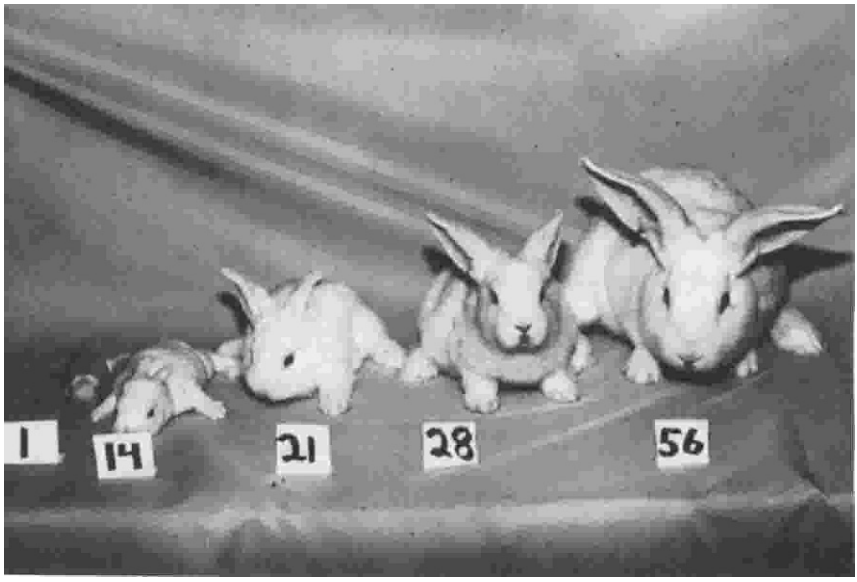


Fig. 1.3 Compared to other types of livestock, rabbits have a rapid growth rate and may reach market weight in 56 days from birth. (Courtesy of D. J. Harris and the Oregon State University Rabbit Research Center, Corvallis.)

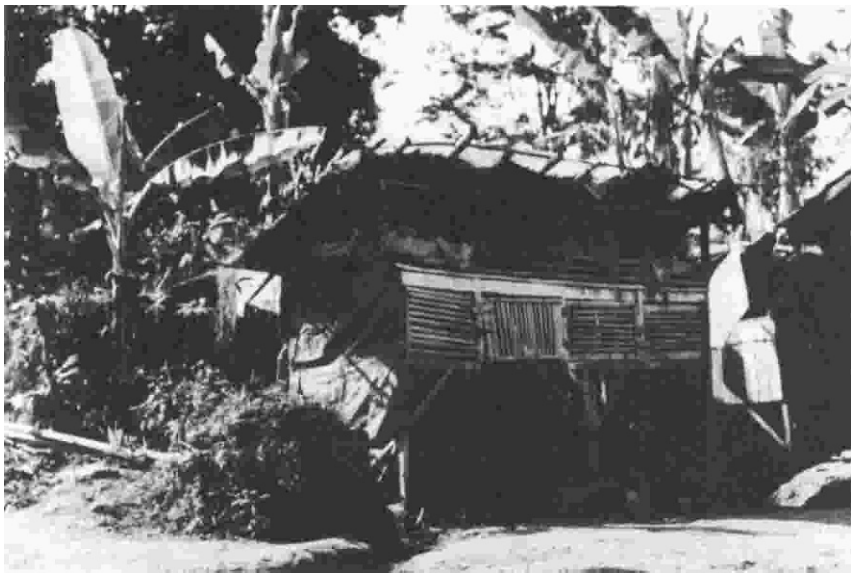


Fig. 1.4 Rabbit production in a village in Indonesia, using cages constructed of locally available bamboo. The pile of forage (lower left), collected daily, is fed to the rabbits along with rice bran, a readily available by-product feed.

basis, with at least one rabbit per week available for consumption by the family. In places like Indonesia, where many families eat meat only a few times a year, such production by rabbits can mean a major improvement in the nutritional status of people (Fig. 1.4).

C. Use of Noncompetitive Feeds

Rabbits can be successfully raised on feeds that are noncompetitive with human foods, such as forages and grain milling by-products. Typical U.S. rabbit diets are composed primarily of alfalfa meal and wheat middlings. In developing countries, rabbits can be fed a variety of forages, such as leguminous tree leaves (e.g., leucaena, sesbania, gliricidia), tropical grass forages (e.g., elephant grass, Guatemala grass), roadside grasses, fruit tree leaves (e.g., banana, papaya, jackfruit leaves), aquatic weeds such as water hyacinth, and by-products such as table scraps, molasses, rice bran, and corn bran.

Rabbits make efficient use of forage proteins. The digestibility of alfalfa meal protein is less than 50% in swine and poultry, whereas it is 70–75% in rabbits. In ruminant animals, alfalfa and other forage protein is largely converted to lower quality microbial protein in the rumen. In rabbits, the forage amino acids are utilized directly, which is significant because leaf proteins have a high quality

(good amino acid balance). The ability of rabbits to use forage proteins efficiently is related to the phenomenon of cecotrophy, in which the animal consumes the cecal contents (night or soft feces). This allows for efficient extraction of protein from dietary ingredients.

D. Small Body Size

In tropical countries, small animals such as rabbits and chickens have a number of advantages over larger animals. In the case of rabbits, only small quantities of forage per day are required, whereas the amount of feed needed for a cow may be unavailable on a small farm. The meat from one rabbit can be consumed by a family in one meal, so refrigerated meat storage is not required (and is not usually available). With large animals, much of the carcass may be lost from spoilage. Small animals like rabbits have simple housing requirements, and are particularly suited to backyard production, because they make no noise and produce little odor (in contrast to chickens and pigs, respectively).

III. MICROLIVESTOCK—A NEW FRONTIER IN ANIMAL PRODUCTION

Vietmeyer (1985) stated: "Livestock for use in developing countries should, like computers, be getting smaller and becoming more 'personal.' Mainframes, such as cattle, cannot solve the widespread shortage of meat because they require too much space and expense for the landless and the poor. Miniframes, such as sheep and goats, could play an increasing role. But tiny, 'user-friendly' species for home use show the most promise—and they are being overlooked." Vietmeyer has termed these small animals "microlivestock." Rabbits are examples. Other small animals that might also be raised for meat production include guinea pigs. In the Andean countries of Peru, Bolivia, and Ecuador, guinea pigs are major meat-producing animals (Fig. 1.5). They are raised right within the home, even in high-rise apartments. They are prolific, tractable, and easy to feed, house, and handle. They have been introduced into western African countries such as Cameroon, where they are raised for meat. Other microlivestock include the grasscutter and giant rat, used as meat sources in West Africa. The capybara is a large rodent being domesticated in Brazil as a meat animal. The blue duiker is a small antelope, about the size of a rabbit, which can be raised domestically (which would also help to prevent its extinction from overhunting). Pigeons, quail, and other small poultry are efficient food producers. These "microlivestock" have great potential as a means of providing protein to the multitudes of low-income people in the developing world.



Fig. 1.5 Microlivestock such as guinea pigs are important sources of food in South America. Here an Ecuadoran farmer displays two of his guinea pigs. (Courtesy of N. Paul Johnston, Brigham Young University, Provo, Utah.)

IV. FACTORS LIMITING RABBIT PRODUCTION

Despite the apparent attributes of rabbits as efficient producers of useful products, utilizing forage-based diets, rabbit production has not become a major segment of animal agriculture. Several factors currently limit the economic viability of rabbit production. A major factor is that rabbits are susceptible to several diseases that reduce production to unprofitable levels in many rabbit herds. Respiratory disease caused by *Pasteurella multocida* is responsible for decreased productivity and high mortality of does. Rabbits are very susceptible to enteric diseases, including enterotoxemia and cecal impaction. These disorders are influenced to a considerable extent by the nature of the diet. Knowledge of nutrient requirements and metabolism is quite limited in comparison to the situation with other livestock. Since feed is the major cost of production, improvements in feeding and nutrition should aid in making rabbit production profitable. Rabbit production is labor intensive. In developing countries, labor is abundant and inexpensive, so this is probably not a limiting factor in those areas. Probably the single most important factor limiting the success of rabbit production is the degree of management skill necessary to obtain the level of productivity of which the animals are biologically capable. Does can readily produce more

than 50 offspring per year, but most rabbit raisers are only getting 30–35 rabbits per doe to market per year.

Rabbits are particularly suited to small-scale backyard production. The incidence of disease is much lower than in large-scale confinement rabbitries, and the TLC (tender loving care) factor seems to come into play. Thus for small-scale home meat production, particularly in developing countries, rabbit raising could assume increasing importance in the future.

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2

General Principles of Rabbit Nutrition

Nutrients can be defined as dietary essentials for one or more species of animals. Not all animals require all nutrients in their diet. In fact, ruminant animals, such as cattle and sheep, have very simple nutritional requirements because the rumen microbes produce animo acids, energy sources, and most of the vitamins. Other animals, such as chickens, require a dietary source of almost all known nutrients. One of the best examples of a nutrient that is not generally required by many animals is vitamin C, or ascorbic acid. It is synthesized in the tissues of most animals; so only humans, other primates, guinea pigs, and a few exotic species have a dietary requirement for this vitamin.

The various nutrients can be classified according to the following categories, which will be briefly described: proteins, carbohydrates, lipids, minerals, and vitamins.

I. PROTEINS

Proteins are essential components of animal tissue. Muscle tissue is largely protein. All enzymes, which facilitate chemical reactions in the body, are proteins. Some hormones are proteins or protein derivatives. Blood proteins have a number of essential functions, including nutrient transport and regulation of fluid balance. The immune system is based on proteinaceous antibodies. Cell membranes contain protein. Thus proteins are basic to animal life. Most of the productive functions of livestock involve protein formation or secretion, including meat, milk, wool, fur, and egg production.

Proteins are composed of small molecules called amino acids. All amino acids contain one or more amino ($-NH_2$) groups. Thus all amino acids (hence all protein) contain nitrogen. The protein content of feeds and tissues is commonly measured by analysis for nitrogen. The provision of adequate quantities of dietary essential amino acids is a major aspect of the nutrition of many kinds of animals.

II. CARBOHYDRATES

Carbohydrates are synthesized by plants using solar energy. The basic reaction of photosynthesis is the formation of glucose from carbon dioxide and water:

$$6CO_2 + 6H_2O \xrightarrow[\text{chloroplasts}]{\text{solar energy}} C_6H_{12}O_6 + 6O_2$$

Glucose is then used by the plant to synthesize other carbohydrates and the carbon-containing part of other constituents of plant tissue.

Carbohydrates serve as the basic energy source of animals, by the reverse of photosynthesis:

$$\underset{\text{carbohydrate}}{C_6H_{12}O_6} + 6O_2 \xrightarrow[\text{metabolism}]{\text{animal}} \text{heat} + \text{chemical energy (ATP)} + 6H_2O + 6CO_2$$

Thus all higher animal life is powered by solar energy, obtained through the metabolism of carbohydrates manufactured by photosynthesis.

Carbohydrates are of two major types: nonfibrous and fibrous. The nonfibrous types, such as starch and sugars, are readily utilized by animals as energy sources. The fibrous types (e.g., cellulose) make up plant fiber, and are responsible for the structural rigidity of plant tissue (e.g., hay, straw, wood). Fiber is utilized only by animals having cellulose-digesting microbes in their digestive tracts.

III. LIPIDS

More commonly known as fats and oils, lipids function mainly as sources of energy for animals. Technically, lipids are constituents of plant and animal tissue that are soluble in organic solvents such as ether. Some lipids, such as cholesterol, have essential functions in animal metabolism. The effect of dietary lipids (saturated and unsaturated fat, cholesterol) on human health (atherosclerosis, cancer) is a controversial area, particularly with respect to meat consumption. Certain aspects of this debate have relevance to the nutritional value of rabbit meat in the human diet.

IV. MINERALS

Minerals are inorganic substances. They can be subdivided into two groups: macrominerals and trace minerals (trace elements). The macrominerals, which

include calcium, phosphorus, sodium, potassium, chlorine, magnesium, and sulfur, are required in relatively large quantities. The trace elements, including copper, iron, iodine, manganese, zinc, iodine, and selenium, are needed in very small quantities, often expressed as parts per million (ppm). Minerals function either in a structural role as a component of tissues (e.g., calcium is a major constituent of bone), in a regulatory role in maintaining osmotic and acid–base balance (e.g., sodium, potassium, and chlorine), or as constituents or activators of enzymes (e.g., selenium, copper, and iron are essential for enzyme activity).

V. VITAMINS

Vitamins are organic substances (composed primarily of carbon and hydrogen) distinct from the other organic nutrients (carbohydrates, lipids, and proteins). They have essential roles in metabolism, so that when they are not present in adequate amounts, characteristic deficiency symptoms develop. They are required in very small quantities in comparison to the other nutrient categories.

Vitamins are classified into two groups: fat soluble and water soluble. The fat-soluble vitamins are A, D, E, and K, while the B complex and vitamin C are the water-soluble group. There are some major differences in nutritional properties of the two groups.

VI. ROLES OF NUTRIENTS

A. Structural Role

Some nutrients are important components of the structure of animal tissues. Protein makes up the structure of muscle tissue. Bone is composed of an organic matrix (mainly protein) that is mineralized with calcium and phosphorus. The skin and hair are composed of protein, while cell membranes are a protein–lipid complex.

B. Sources of Energy

Quantitatively, the greatest nutritional requirement of animals is for energy sources. About 80% of a typical rabbit diet consists of energy sources, primarily carbohydrates. Energy requirements are expressed in calories or joules. The only nutrient categories that can supply energy are carbohydrates, lipids, and proteins. Generally protein sources are more expensive than carbohydrates, so it is desirable to balance rations to minimize the metabolism of protein as an energy source. Energy sources are metabolized by enzymatic reactions in animal cells,

so that chemical energy is released in a form that can participate in energy-requiring chemical reactions. The usual form in which chemical energy is released is as the high-energy substance ATP (adenosine triphosphate). The ATP participates in energy-requiring reactions, such as protein synthesis. Animals require energy sources for the maintenance of body temperature, for maintaining essential biological states (concentrations of ions within cells, etc.), and for the synthesis of new tissue and maintenance of existing tissues.

C. Regulatory Roles

Many nutrients, particularly minerals and vitamins, function in the regulation of cellular metabolism, as constituents or activators of enzymes. The deficiency of a particular nutrient results in deficiency symptoms that reflect the aspect of metabolism that is impaired. For example, the B vitamin thiamin functions in the enzymatic conversion of pyruvic acid to acetyl coenzyme A (acetyl CoA) in cellular metabolism. A thiamin deficiency results in accumulation of pyruvic acid in the blood causing symptoms of polyneuritis due to the effect of pyruvic acid on nerve tissue.

VII. HISTORY OF RABBIT NUTRITION RESEARCH

Although rabbits have been used extensively in biomedical research, and raised for a variety of purposes in many countries, it is remarkable that until the 1970s and 1980s, relatively little knowledge of the nutritional requirements of rabbits was available. This is exemplified by the following quotations from the 1966 edition of the National Research Council (NRC) publication, "Nutrient Requirements of Rabbits":

Protein: "The sensitivity of rabbits to quality of protein is unknown. The fact that rabbits have been successfully raised on relatively simple mixtures of plant products indicates that protein quality may not be of great importance."

Fat: "No specific fat requirements have been established for rabbits."

Minerals: "It is probable that rabbits require the same mineral elements as other animals."

Vitamins: "Although rabbit dietary requirements have been recognized for many of the known vitamins, the extent of the requirement has been estimated for only a few."

Energy: "No specific energy requirements have been established for the rabbit . . ."

Angora wool production: "Recommendations concerning specific nutrient requirements for rabbit wool production are not possible because the necessary information is lacking."

These quotations are sufficient to indicate the inadequacy of information available at that time. The situation was not greatly different 10 years later (NRC, 1977).

Lebas (1980), in his plenary address to the World Rabbit Congress, summarized research publications on rabbit nutrition and feeding during the 20-year period of 1959–1979. There were 250 original articles, with a tendency for the number to increase annually. The principal subject of these papers was nitrogen utilization. Very few reports dealt with minerals and vitamins. Over 80% of the studies were conducted with growing rabbits, rather than animals in the reproductive phase. Lebas also noted that the majority of the studies were conducted with a very small (5–10) number of animals per treatment, resulting in performances that were as much as 15–20% different from each other being statistically equivalent, resulting in a lack of precise requirement figures.

Since the late 1970s, rabbit research on a worldwide basis has expanded considerably, particularly in the area of nutrition. Scientists in Europe, North America, Africa, and Latin America have been conducting significant research, which has considerably expanded the knowledge base of rabbit nutrition and feeding. The World Rabbit Science Association was established in the 1970s, and sponsors a World Rabbit Congress every 4 years, at which scientists from many countries discuss their findings. The first three Congresses were at Dijon, France (1976), Barcelona, Spain (1980), and Rome, Italy (1984).

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3

Digestive Physiology

Probably the major factor influencing an animal's nutritional requirements and the types of feedstuffs that can be employed in its feeding is the nature of its digestive tract. For example, the nutrition and feeding of chickens and beef cattle are very different, largely because of the different functions, properties, and characteristics of their digestive tracts. Animals can be classified on the basis of their feeding behavior and digestive tract physiology. Because the digestive capacities of the rabbit are somewhat unusual in comparison to those of other domestic animals, it is useful to describe briefly the various digestive tract types and feeding behaviors, to understand more fully the unique characteristics of rabbits.

I. CLASSIFICATION BASED ON FEEDING BEHAVIOR

There are three main types of domestic animals in terms of their feeding behavior. These are the carnivores, herbivores, and omnivores. Carnivores (e.g., dogs and cats) have a meat-based diet, consisting of a highly digestible, high-quality food source. As a consequence, they have fastidious nutritional requirements and require a dietary source of nearly all nutrients. They may also have some unique dietary requirements that can be met only by the consumption of meat. Cats, for example, have a dietary requirement for the amino acid taurine and for preformed vitamin A (they cannot convert β-carotene in plants to vitamin A). This is likely a result of their evolutionary history; organisms tend to lose the ability to synthesize substances that are routinely present in their diets.

Herbivores are those animals that normally eat only plant material. These vegetarians include ruminants, like cattle and sheep, and nonruminant herbivores such as rabbits, horses, and guinea pigs. Herbivores have (in most cases) digestive tracts that accommodate a microbial population that is involved in the digestion of plant fiber. An exception is the panda, a specialized feeder that eats bamboo as its primary diet. High levels of feed intake and a fast rate of passage allow the giant panda to meet its nutritional needs without digesting the structural carbohydrates (fiber) of the bamboo (Dierenfeld *et al.*, 1982).

TABLE 3.1

Classification of Herbivores according to Feeding Habit[a]

Class	Ruminants	Nonruminants
Concentrate selectors	Deer, giraffe	Rabbit
Intermediate feeders		
Browse preference	Goats	
Grass preference	Sheep	
Bulk and roughage eaters		
Fresh grass grazers	Cattle	Hippopotamus
Roughage grazers	Hartebeest	Horse, zebra
Dry region grazers	Camel	Kangaroo

[a] Adapted from Van Soest (1982).

Omnivores, such as swine and humans, are cosmopolitan in their eating habits, and consume a wide array of plant and animal foods. Their digestive tracts are intermediate in complexity between those of the carnivores and herbivores.

Herbivorous animals can be further described on the basis of their feeding behavior. Van Soest (1982) has classified herbivores into concentrate selectors, intermediate feeders, and bulk and roughage eaters (Table 3.1). Rabbits are concentrate selectors, selecting low-fiber, high-protein, high-carbohydrate portions of plant material. Observation of wild rabbits reveals a diet of tender, succulent plant parts as the major portion of the diet. Some coarse roughage is consumed, but its function is as a source of indigestible fiber to stimulate gut motility, rather than as a nutrient source.

II. CLASSIFICATION BASED ON DIGESTIVE TRACT PHYSIOLOGY

With some exceptions (e.g., giant panda), herbivores have evolved digestive tracts with anatomical adaptations containing a symbiotic microbial population of bacteria, protozoa, and the like. These microbes often perform digestive functions of which the host is incapable, such as the digestion of cellulose. As a result, herbivores can survive on fibrous feedstuffs that may have very low nutritional value to other animals.

The sites of microbial growth and fermentation are primarily the foregut (stomach) and the hindgut (cecum and colon). Table 3.2 gives examples of herbivores using each type of digestive strategy. Herbivores have anatomical adaptations in these areas that provide a suitable environment for their microbial

populations. The ruminant animals have a compartmentalized stomach, including one compartment, the rumen, which functions as a large fermentation vat. Another unique region is the omasum, consisting of membranous leaves that act as a filter or sieve. Ingested food cannot leave the rumen until it has been reduced to a small particle size. This is accomplished by remastication of the feed (rumination or cud-chewing) and the digestive enzymes of the rumen microorganisms. There are several important nutritional consequences of the rumen. These are worthy of discussion here, because some of the same processes occur in the rabbit digestive tract.

The rumen microbes produce the enzyme cellulase, which can split the cellulose molecule apart into the glucose molecules of which it is composed. The microorganisms ferment the released glucose, and secrete a variety of acids as waste products. These small organic acids are called volatile fatty acids (VFA). The main ones are acetic, propionic, and butyric acids. These constitute the main absorbed energy source of ruminants. Thus cattle and sheep derive their cellular energy from waste products of microbial metabolism. A second important role of rumen microbes is in the synthesis of amino acids and proteins. Although these processes may not all be accomplished by a single type of microorganism, the capacity of the total microbial population is to synthesize from a source of inorganic nitrogen all of the amino acids required by higher animals. These amino acids, incorporated into microbial protein, supply the ruminant with much of its protein needs when the rumen microorganisms are digested in the small intestine. Another important activity of the rumen microbes is that they synthesize all of the vitamins required by ruminants except vitamins A, D, and E. In other words, all the B-complex vitamins and vitamin K are provided to the ruminant from microbial synthesis. To summarize, the following are the major nutritional and feeding contributions of the rumen microorganisms:

1. Rumen microbes digest cellulose and other components of fiber. The end products of this fermentation are the VFA, which are absorbed and provide the

TABLE 3.2

Classification of Herbivores according to Digestive Strategy

Class	Examples
Pregastric fermentation	
Nonruminant	Hamster, kangaroo
Ruminant	Cattle, sheep, goats
Hindgut fermentation	
Cecal fermentation	Rabbit, capybara
Colon fermentation	Horse

animal with energy (calories). Ruminants can thus live on roughages and forages.

2. The rumen microbes synthesize amino acids from inorganic nitrogen. The ruminant meets its amino acid and protein needs to a large degree by digesting the microbial protein. This is of major consequence in feeding ruminant animals. They do not require high-quality dietary proteins, and in fact can survive on nonprotein nitrogen (NPN) sources such as urea.

3. The B-complex vitamins and vitamin K are synthesized by rumen microbes, so that these nutrients are not generally required in the diet of ruminants.

Rabbits are hindgut fermenters. To varying degrees, all of the processes just described for ruminants occur in the rabbit. The specific site of fermentation is the cecum. Muscular contractions in the colon accomplish a separation of fiber particles from the nonfiber components of feeds, with peristaltic contractions rapidly moving fiber through the colon for excretion in the hard feces. Antiperistaltic action moves fluids and small particles in a retrograde manner through the colon to the cecum, where they are retained for fermentation. Bacterial growth results in amino acid synthesis, some fiber digestion, formation of VFA from fermentation of carbohydrates, and synthesis of B-complex vitamins. These products are made available to the rabbit either by direct absorption or by way of the consumption of the cecal contents. At intervals, the cecum contracts, and the cecal contents are expelled through the colon and consumed directly from the anus by the rabbit. This process is known as copropagy (consumption of feces) or, more correctly, cecotrophy (consumption of cecal contents). The consumed cecal contents are referred to as soft feces, night feces, and cecotropes.

The horse is another example of a hindgut fermenter. The main site of fermen-

TABLE 3.3

Gastrointestinal Tract Volume of Various Species[a,b]

Species	Total contents	Stomach	Small intestine	Cecum	Colon and rectum
Ruminant					
Cattle	13–18	10.6–16.3	0.9–2.3	0.8	0.8–1.5
Sheep	12–19	9.8–14.9	1.0–1.6	0.9–1.6	0.5–0.7
Nonruminant					
Rabbit	7–18	2–7	0.6–1.8	2.5–7.8	0.7–1.3
Horse	16.4	1.3	2.6	2.4	8.8
Pig	10.4	3.6	1.9	1.6	3.4

[a] Adapted from Van Soest (1982).

[b] All figures are percentage of body weight.

tation is the enlarged colon. Fiber is digested more efficiently in the horse than in the rabbit, but horses do not normally engage in coprophagy, although they do when fed low-protein diets (Schurg *et al.*, 1977). The comparative sizes of different parts of the digestive tract, reflecting the various sites of fermentation, are shown in Table 3.3.

III. COMPARATIVE DIGESTIVE STRATEGIES OF HERBIVORES

The digestive processes just described represent varying evolutionary adaptations for efficient utilization of herbage. They are different strategies for coping with the inherently low nutritional value of herbage. Ruminants are the most efficient digesters of fiber. The sieve action of the omasum retains feed in the rumen until the fiber has been digested to a small particle size. However, on diets high in low-quality forage, this can be a disadvantage, because rumen fill limits intake. The digestive system of the horse can be advantageous in the use of low-quality roughage, even though the efficiency of fiber digestion is lower than in ruminants, because intake is not limited by the rate of fiber digestion. McNaughton (1985) cited evidence that the colon fermenter zebra in the Serengeti plains of Africa can survive on a diet too low in digestible energy to support a ruminant, because the fast rate of digestive transit allows a high feed intake so the total amount of energy needed can be obtained, whereas rumen fill prevents the ruminant from consuming sufficient forage to meet its energy needs. Thus Janis (1976) concluded that "hindgut fermentation is a superior adaptation for dealing with high fiber herbage, provided that intake is not limited by the actual quantity of herbage available."

The rabbit is also adapted to the use of a high-roughage diet, but it has a different digestive strategy than the ruminant and the colon fermenter. In essence, the digestive strategy of the rabbit is to eliminate fiber from the gut as rapidly as possible, and employ its digestive processes on the breakdown of the nonfiber constituents of forage. Thus, as in the horse, intake is not limited by fiber. Separation of fiber (large particles) from nonfiber components (small particles and solubles) occurs in the colon, with the fluids and small particles moved back into the cecum for fermentation. In this manner, the rabbit concentrates on the proteins and readily fermentable carbohydrates in forage, and simply excretes the fiber without expending resources attempting to digest it. This is probably a reflection of the small body size of rabbits. Small animals have a high rate of metabolic activity per unit of body weight. Thus the separation and rapid excretion of fiber allows the rabbit to utilize herbage without the encumbrance of an overly large gut.

IV. ANATOMY AND FUNCTIONS OF THE RABBIT DIGESTIVE TRACT

A. The Foregut

The general features of the rabbit digestive tract are shown in Fig. 3.1.

The initiation of digestive processes occurs when food is consumed. Rabbits masticate their feed very thoroughly, with as many as 120 jaw movements per minute. The result is that ingested material is broken down to small particle sizes. An exception is the cecotropes, which are consumed whole and remain intact in the stomach for several hours.

The stomach of the rabbit is a thin-walled, pouchlike organ. In the adult the pH of the stomach is very low, from 1 to 2. Smith (1965) measured the pH of the

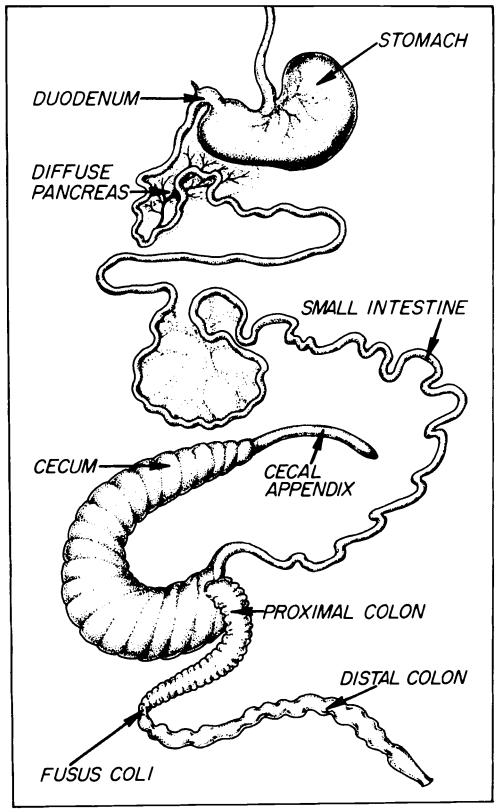


Fig. 3.1 Schematic view of the parts of the rabbit digestive tract.

stomach contents of a wide number of animal species, and found that, compared to the others, the rabbit stomach had an extremely low pH. This very effectively kills bacteria and other microorganisms, so that the rabbit stomach and small intestine are essentially sterile. Brooks (1978) demonstrated that in the suckling rabbit, the stomach pH is higher, from 5 to 6.5, but after weaning it drops to between 1 and 3. One of the reasons that weanling rabbits are highly susceptible to diarrhea is that the stomach pH is not low enough to kill ingested bacteria. On the other hand, this is how they acquire their microbial population in the hindgut.

Secretions into the stomach from glands in the stomach lining include hydrochloric acid (HCl), digestive enzymes such as pepsin (secreted as pepsinogen), and mucus. Henschel (1973) observed that rennin or a renninlike enzyme is secreted in the stomach of the suckling rabbit. The stomach serves as a storage organ, metering ingesta into the small intestine. The stomach is never completely empty in the normal animal, and even after a fast of 24 hr, the stomach is more than half full of digesta (Griffiths and Davies, 1963).

Despite the high acidity of the rabbit stomach, some fermentation occurs. Griffiths and Davies (1963) demonstrated that lactic acid in the stomach arises mainly from the fermentation by bacteria in the cecotropes. The mucuslike membranes around the cecotropes remain intact for at least 6 hr after ingestion, allowing ample time for fermentation within the cecotropes to proceed.

The small intestine is a major site of digestion and absorption. It is divided into three functional areas: the duodenum, jejunum, and ileum. The duodenum is the anterior portion, with digesta moving through the pyloric sphincter from the stomach into the duodenum. The duodenum is the primary area of neutralization of the acid material coming from the stomach, and of mixing by muscular churning action. The bile duct enters into the duodenum near the pyloric sphincter, and the pancreatic duct enters at some distance from the bile duct. The pancreas, located in a loop of the duodenum, is diffuse in the rabbit and difficult to differentiate from supporting tissue. The pancreas is the source of major digestive enzymes involved in carbohydrate, protein, and fat digestion, and is also the source of alkaline secretions (e.g., bicarbonate) that neutralize the stomach acid.

Bile is formed in the liver cells (hepatocytes) and secreted into the small intestine via the bile duct. The major constituents of bile are the bile acids (also called bile salts) and the bile pigments. Bile acids are synthesized in the liver from cholesterol. Cholic acid and chenodeoxycholic acid are the main bile acids synthesized by most mammals. These are referred to as primary bile acids. They are modified by microbial activity in the intestine, producing secondary bile acids such as deoxycholic acid. Bile acids have an important role in fat and vitamin absorption. Because of their detergent properties, they solubilize fats in the aqueous medium of the gut. They accomplish this by forming micelles, which are aggregates of bile acids, triglycerides, fatty acids, and fat-soluble

vitamins. Micelles have a hydrophilic ("water-loving") outer layer, making them water soluble in the intestine.

The bile acids are conjugated with amino acids, increasing their water solubility. Taurine and glycine are the main amino acids involved in bile acid conjugation. There are species differences in the composition of bile acids and conjugates, which are correlated with dietary habits. Ruminants secrete bile acids conjugated mainly with taurine, while rabbits conjugate their bile acids almost exclusively with glycine (Coleman *et al.*, 1979).

The bile pigments, which give bile its characteristic color, are the end products of the liver's metabolism of hemoglobin from the breakdown of old red blood cells. The heme (porphyrin nucleus) in hemoglobin is first converted to biliverdin, a green pigment. Biliverdin is subsequently converted to bilirubin, a reddish orange pigment, by the enzyme biliverdin reductase. Bilirubin is secreted into the bile. In the intestine, the bile pigments are converted by microbial action into a number of compounds called urobilinogens. These compounds give the feces their characteristic color, and some are also absorbed and excreted in the urine, giving it its characteristic yellow color. In rabbits, the reddish orange pigmentation of the urine often observed might be associated in part with bile pigments. Presumably the bile pigments would be retained to some extent in the cecotropes, and would be absorbed following cecotrophy. This suggestion has not been experimentally verified.

As is the case with numerous metabolic processes, the rabbit is somewhat unique in its formation of bile pigments. Most nonmammalian species (birds, amphibians, fish) secrete biliverdin in their bile, while mammals secrete bilirubin. The rabbit secretes mainly biliverdin. Munoz *et al.* (1986) studied bile pigment formation and excretion in the rabbit. Biliverdin constituted 63% of total bile pigment. The liver biliverdin reductase activity was very low, being about 60 times lower than in the rat, for example. The synthesis of bilirubin in the rabbit is apparently limited by the low activity of this enzyme.

Further study of bile pigment metabolism in the rabbit would be desirable, to determine if these pigments are involved in the "red urine syndrome" often observed.

The wall of the small intestine is lined with small projections, called villi, which greatly increase the surface area available for absorption of nutrients. The outer layer of the villi is composed of epithelial cells, which in turn have minute projections called microvilli at their surface (Fig. 3.2). The epithelial cells, or enterocytes, are continually being formed at the base of the villi, in a region called the crypt of Lieberkuhn. As the enterocytes move up the villi, they become functionally mature with maximal digestive–absorptive activity. Cells are extruded off the villi as they are replaced by new enterocytes moving up the villi. These sloughed-off cells are a major component of the endogenous fecal nitrogen fraction.

The microvilli are surrounded by a layer of diffuse material called the glyco-

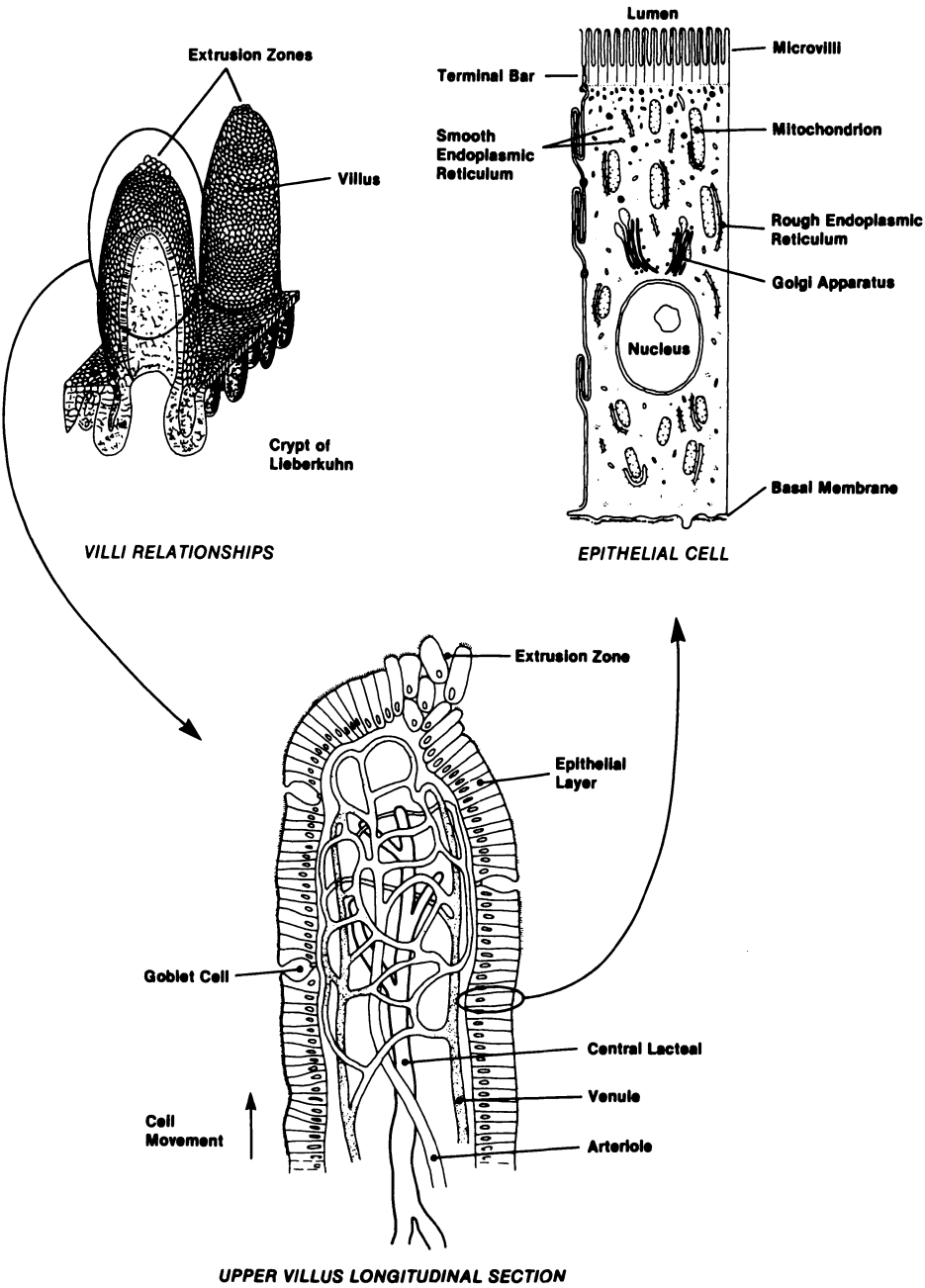


Fig. 3.2 The intestinal villi, showing three-dimensional appearance (top left), longitudinal section of a villus showing enterocytes (bottom), and expanded view of an enterocyte (top right). (Courtesy of E. T. Moran, Jr., University of Guelph, Guelph, Ontario, Canada.)

calyx. The glycocalyx, microvilli, and underlying cellular structure of the enterocytes constitute the "brush border," which is the actual site of digestion and absorption. The glycocalyx is a fine web of polysaccharide fibers, which traps feed particles at the microvilli tip. It can be viewed as a fuzzy layer trapping feed particles, but keeping them from direct contact with the microvilli. Digestive enzymes attached to the surface of the microvilli membrane accomplish digestion, and the subsequent products are actively transported into the microvilli. Pancreatic enzymes produce soluble products that are not absorbed; digestion is completed by the enzymes anchored to the microvilli. Nutrients entering the microvilli are moved through microchannels to the blood and lymph vessels in the villi.

Motility is the process by which feed is moved within the intestine. Segmentation is the type of motility that mixes the intestinal contents; the contents are mixed by being divided into smaller pieces by constrictions of the intestine at intervals. Peristalsis is the type of motility by which the contents are moved along the intestine. It is a moving ring of contraction, pushing material ahead of it. The control of intestinal motility resides with a number of gastrointestinal hormones, including cholecystokinin, somatostatin, and regulatory peptides such as vasointestinal polypeptide (VIP) and substance P.

As digesta moves through the small intestine, mixing and acid neutralization occur in the duodenum, with the jejunum the major site of digestion and absorption.

B. The Hindgut

The hindgut plays important roles in digestion in the rabbit, because of fermentation in the cecum, selective excretion of fiber, and the reingestion of cecal contents (coprophagy).

The ileum enters the hindgut at the ileocecocolonic junction. The ileum ends at the sacculus rotundus, and discharges its contents into the cecum and colon. The colon initiates from an area at the base of the cecum called the ampulla coli.

The cecum of the rabbit is very large, with a spiral fold along its length. It terminates in a blind pouch called the appendix, a lymphoid organ that may have a role in disease resistance.

The appendix secretes an alkaline fluid rich in bicarbonate ions (Williams *et al.*, 1961), which may buffer the VFA produced during cecal fermentation. The enlargement of the appendix when low-fiber diets rich in fermentable carbohydrate are fed (see Fig. 6.2) supports this view. Alternatively, because the appendix is a lymphoid organ, its enlargement may be a reflection of a greater production of microbial toxins when low-fiber diets are fed (see Chapter 12). De Oms and Leffel (1972) observed that surgical removal of the appendix significantly reduced the concentration of vitamin B_{12} in the cecal contents, indicating that the appendix does have an influence on microbial fermentation.

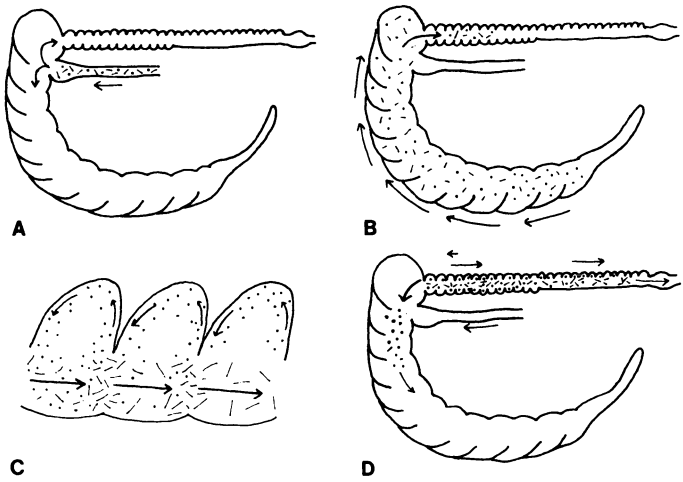


Fig. 3.3 Mechanisms for the selective excretion of fiber and retention of small particles and solubles for fermentation in the cecum. (A) Intestinal contents enter the hindgut at the ileocecal–colonic junction, and uniformly disperse in the cecum and colon. Dashes represent large fiber particles, and dots represent nonfiber particles. (B) Contraction of the cecum moves material into the proximal colon. (C) Peristaltic action moves large fiber particles (dashes) down the colon for excretion as hard feces. Contractions of the haustrae of the colon move small particles (dots) and fluids backwards into the cecum. (D) Small particles and fluids are thus separated from fiber. (From Cheeke *et al.*, 1986.)

Of particular importance in the digestive physiology of the rabbit is the separation of large particles in the colon. The ingesta is discharged into the ceco–colon area, and is fairly uniformly mixed. The cecum is continuously in motion, mixing the contents by rapid contractions back and forth along its length. There is a continual flux of material between the cecum and proximal colon. Separation of large particles from small particles and fluid occurs mechanically. Peristaltic movements move ingesta down the colon. The larger fiber particles, being of lower density, tend to accumulate in the lumen, while small particles and fluids, being more dense, tend to accumulate at the circumference. Contractions of the haustrae (sacculations in the wall of the colon formed by the arrangement of circular muscle fibers) move material in a retrograde manner to the cecum. Thus small particles and fluids are retained for a considerable period in the cecum, where fermentation occurs, while the fiber is eliminated rapidly (Fig. 3.3). The material entering the colon from the cecum is thick and pasty in healthy rabbits. For separation of particles by density to occur, fluid secretion into the proximal colon is necessary. According to Lelkes (L. Lelkes, University of Medicine and Dentistry of New Jersey, Piscataway, personal communication), the dilution of colon contents occurs about 10 cm distal to the cecocolonic junction, during certain periods of the day. During these periods, this region dilates and has a slightly lighter color than the rest of the colon. At these times, it can be visually

TABLE 3.4

Comparative Composition of Cecal Contents, Cecotropes, and Hard Feces

Constituent (%)	Cecal contents	Cecotropes	Hard feces	References
Crude protein	39.9	30.0	—	Eden (1940)
Ash	11.2	11.1	—	
P_2O_5	4.4	4.2	—	
Na_2O	1.9	0.5	—	
K_2O	1.2	1.7	—	
Crude protein	36.4	37.8	14.8	Huang *et al.* (1954)
Fat	1.8	1.5	1.8	
Ash	15.4	14.3	14.8	
Crude fiber	13.4	14.3	27.8	

observed that the material adjacent to the mucosa of the haustrae is thin and liquid while the contents of the central colon are thick and contain larger particles (L. Lelkes, personal communication). Thus, active fluid secretion is an essential part of the cecal–colonic selective excretion mechanism. The production of the hard fecal pellets has been described by Ehrlein *et al.* (1983). Hard feces are produced in the single haustrated colon. Segmental contractions occur, separating the digesta into fecal pellets, while haustral contractions move water back toward the cecum. Thus there is a mechanical separation of water, rather than water absorption, producing the hard fecal pellets.

Coprophagy or cecotrophy is the consumption of the cecal contents. A comparison of the composition of soft feces, cecal contents, and hard feces suggests that the soft feces (cecotropes) are of cecal origin (Table 3.4), showing a higher protein and water and lower fiber content than the hard feces (Table 3.5). The soft feces are surrounded by a mucilaginous membrane, secreted by mucus-secreting (Goblet) cells in the colon. They appear as a cluster (Fig. 3.4), rather than as the single pellets typical of the hard feces. The cecotropes are consumed as discrete clusters and continue to ferment in the stomach for several hours after they are consumed. Their mucus coating protects them against being digested in the stomach. The terms *day feces* and *night feces* are sometimes used for hard and soft feces, respectively, although excretion of the cecotropes also occurs during daylight hours.

Cecotrophy is an integral part of a rabbit's digestive physiology. It is necessary for maximum digestibility of both high-fiber (low-energy) and low-fiber (high energy) diets (Robinson *et al.*, 1985; Thacker and Brandt, 1955). It is particularly important in the efficient digestion of protein. The cecotropes are also rich in B vitamins (Table 9.5).

The excretion of hard and soft feces is related to feeding, which in turn shows

TABLE 3.5

Comparative Composition of Hard Feces and Cecotropes

Constituent (%)	Hard feces	Cecotropes	References
Crude protein	9.2	28.5	Eden (1940)
Ether extract	1.7	1.1	
Crude fiber	28.9	15.5	
Nitrogen free extract	52.0	43.7	
Ash	8.2	11.2	
Phosphorus	1.3	2.2	
Sodium	0.11	0.22	
Potassium	0.57	1.80	
Dry matter	52.7	38.6	Fekete and Bokori (1985)
Ash	13.7	15.2	
Crude fiber	30.0	17.8	
Crude protein	15.4	25.7	
Gross energy (kcal/kg)	4350	4540	
Crude protein	14.8	37.8	Huang *et al.* (1954)
Fat	1.8	1.5	
Ash	14.8	14.3	
Crude fiber	27.8	14.3	
Crude protein	18.7	37.4	Thacker and Brandt (1955)
Ether extract	4.3	3.5	
Ash	13.2	13.1	
Lignin	12.3	7.5	
Cellulose	46.6	27.2	
Other carbohydrates	4.9	11.3	
Cell wall constituents	78.1	45.1	Uden and Van Soest (1982)
Cellulose	35.8	20.3	
Hemicellulose	31.1	19.1	
Acid detergent fiber	47.0	26.0	
Lignin	11.0	5.8	

a circadian rhythm (Jilge, 1974; Ruckebusch and Hornicke, 1977). Hard feces are excreted during the first 4 hr after feeding, followed by cecotropes over the next 4 hr (Ruckebusch and Fioramonti, 1976). The fusus coli apparently acts as a pacemaker to control contractions for the excretion of the two types of feces. The arrival of the cecotropes at the anus triggers a neural response, resulting in the rabbit licking the anal area and consuming the cecotropes. Keeping rabbits in wire cages has no effect on cecotrophy; in fact, if the cecotropes are discharged and drop from the anus, the rabbit will not consume them. Coprophagy can be prevented for experimental purposes by fitting the animal with a collar (Fig. 4.8).

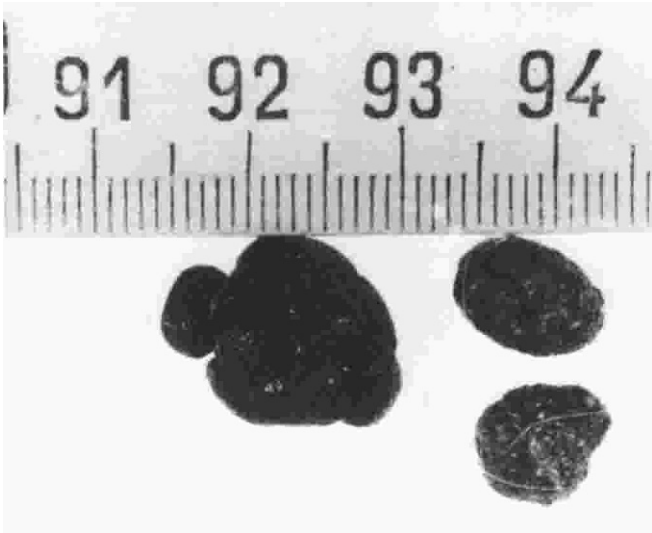


Fig. 3.4 The soft feces or cecotropes (left) are excreted as a cluster surrounded by a mucilaginous membrane, whereas the hard feces (right) are excreted as individual pellets. (Courtesy of S. Fekete, Budapest, Hungary, and *The Journal of Applied Rabbit Research.*)

The composition of both the hard and soft feces is influenced by the diet. Proto *et al.* (1968) noted that fibrous feeds raise the fiber content of both types of feces in about the same proportion, so that the crude fiber content of the cecotropes is in the range of 50–70% of that of hard feces over a wide range of dietary fiber levels (Fig. 3.5). In contrast, a low dietary protein level has less effect on reducing the protein content of the cecotropes than of the hard feces, so that when dietary protein is low, the rabbit becomes increasingly efficient in conserving nitrogen. On low-fiber diets, cecotrophy is reduced because of hypomotility of the hindgut, and a prolonged retention time of material in the cecum (de Blas *et al.*, 1986). Hypomotility of the hindgut is involved in diarrhea (enteritis) and cecal impaction. The role of fiber in preventing these disorders appears to involve stimulation of motility, either by a scabrous effect or by pressure (bulk). This is discussed in further detail in Chapter 12.

V. DIGESTA FLOW (TRANSIT) IN THE GUT

Digesta flow through the rabbit digestive tract can be very rapid, but conversely, some material may be retained for extensive periods. Liquid markers placed in the stomach reach the cecum rapidly; Pickard and Stevens (1972) found that

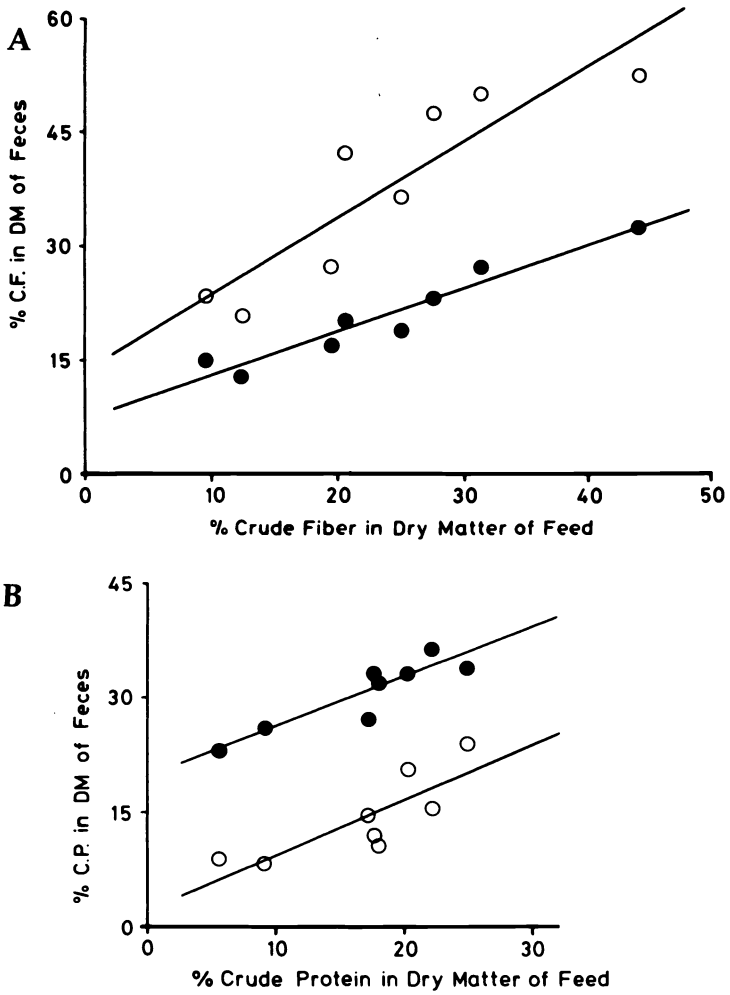


Fig. 3.5 The composition of the hard (○) and soft feces (●) is influenced by the composition of the diet. Fibrous feeds raise the fiber content of both types of feces, with the relative difference in fiber content remaining about the same (A). With a low dietary protein level, the protein content of the soft feces is reduced to a lower degree than for the hard feces (B), indicating that the separation of protein into the cecotropes is more efficient at low protein levels. (From Hornicke and Bjornhag, 1982, courtesy of MTP Press, Ltd., Lancaster, England.)

32% of a liquid marker reached the cecum in 1 hr, and 80% had reached it by 12 hr. Liquids were retained for prolonged periods in the cecum. Solid markers reached the cecum from the stomach in about 4 hr. Liquids and small particles are retained in the cecum for considerable periods. Some particles may have several transits through the gut as a result of cecotrophy.

VI. MICROBIOLOGY OF THE DIGESTIVE TRACT

Smith (1965) studied the microbial flora of the digestive tract of 15 species of mammals, including all the common livestock and laboratory animal species. All had similar types of microorganisms present, with the exception of the rabbit, which had a markedly different microbial population. No microorganisms were detected in the stomach and small intestine, while the flora of the hindgut was almost entirely *Bacteroides* species. He attributed the virtual sterile condition of the stomach and small intestine to the very low pH of the rabbit stomach (Table 3.6) and the thorough mixing of gastric contents. More recent studies have confirmed the unusual microbiology of the rabbit gut. Gouet and Fonty (1979) found that the rabbit microflora was characterized by the dominance of strict anaerobes, particularly nonsporulated gram-negative bacilli (*Bacteroides*). However, these authors found microorganisms through the entire tract, although the hindgut had the highest populations. The number of spore-forming anaerobes was 100–1000 times lower than for *Bacteroides*, and consisted mainly of numbers of the genera *Endosporus*, *Clostridium*, and *Acuformis*. The common gut bacteria *Escherichia coli* and *Lactobacilli* spp. appear to be generally absent in healthy rabbits. Emaldi *et al.* (1979) reported that the hindgut bacterial population had ammonia and urea utilizing capability, and proteolytic activity (degradation of intact proteins). Thus the cecal and colonic population has the capability of hydrolyzing urea and utilizing NH_4^+ as a nitrogen source. Cellulolytic activity was observed, probably associated with *Bacteroides* species.

The development of the fecal microflora with age was studied by Smith and Crabb (1961) in a number of animal species. The initial flora was predominantly *E. coli* and *C. perfringens*, with *Bacteroides* and *Lactobacilli* developing shortly

TABLE 3.6

pH of Various Segments of the Digestive Tract in Several Species[a]

Species	pH				
	Stomach[b]	Duodenum	Ileum	Cecum	Colon
Rabbit	1.9	6.0	8.0	6.6	7.2
Guinea pig	4.5	7.6	8.2	7.0	6.7
Horse	5.4	6.7	7.9	7.0	7.4
Pig	4.3	6.0	7.5	6.3	6.8
Rat	5.0	6.5	7.1	6.8	6.6
Monkey	4.8	5.6	6.0	5.0	5.1
Cow	6.0	6.7	7.9	7.0	7.4

[a] Adapted from Smith (1965).
[b] Anterior portion of the stomach.

after. With increasing age, a characteristic pattern for each species developed, which in the rabbit involved a conversion to primarily *Bacteroides* species. Gouet and Fonty (1979) studied gut flora changes in age in rabbits. They noted three major characteristics of the gut flora:

1. Bacteria became established very irregularly for the first 3 weeks. This was attributed to the presence of an antibioticlike factor in rabbit milk. This has been identified by Canas-Rodriguez and Smith (1966) as octanoic and decanoic fatty acids.
2. The facultative anaerobic microflora have a very simple composition. Up to day 14, *Streptococci* are dominant, after which there is a progressive change to *Enterobacteria*. *Lactobacilli* were never found.
3. The dominant flora was nonsporulated strict anaerobes. *Endosporus* before weaning and *Acuformis* after weaning, along with *Bacteroides*, were the dominant cecum and colon bacteria.

Diet can affect the bacterial population of the hindgut. Morisse *et al.* (1985) found that with a high-fiber, low soluble carbohydrate diet, the cecal microbes were primarily *Bacteroides* and *Sphaerophorus*. With a diet high in soluble carbohydrates, *Clostridia* and *E. coli* were predominant. This has implications in rabbit diarrhea, as will be discussed in Chapter 12.

The protozoal population of the rabbit gut has not been well described, and their significance in cecal fermentation, if any, is not known. Experiments with defaunated rabbits, similar to those conducted with ruminants, would be of interest to determine if the metabolism of protozoa-free rabbits differs from those with a normal microbial population. Lelkes and Chang (1987) reported that protozoa are present in the rabbit cecum, with about 10 million protozoa per milliliter of normal cecal contents. A typical species are elongated and ciliated, measuring 15–20 μ long and 4–6 μ wide. A pronounced drop in the numbers of protozoa occurs with the onset of mucoid enteritis (Lelkes and Chang, 1987).

In summary, the rabbit digestive tract is unusual in the absence of *Lactobacilli* and general absence of *E. coli*, and the predominance of a simple population of *Bacteroides* species.

VII. COMPARATIVE DIGESTIVE EFFICIENCY

In comparison to other nonruminant herbivores such as the guinea pig (Slade and Hintz, 1969) and the horse (Table 3.7), the rabbit digests fiber inefficiently, and as a result derives less digestible energy from roughages than do other herbivores and ruminants. It is apparent from the data in Table 3.7 that the use of the rabbit as a "pilot animal" in studies of horse nutrition is not advisable.

TABLE 3.7

Comparison of Digestive Efficiency in Horses and Rabbits[a]

Item	Diet 1		Diet 2		Diet 3	
	Horse	Rabbit	Horse	Rabbit	Horse	Rabbit
Dry matter	70.0	47.4	60.4	54.3	63.4	61.8
Crude protein	53.0	80.2	74.0	73.7	74.1	65.9
Crude fiber	—	—	34.7	16.2	—	—
Cellulose	—	—	—	—	51.2	25.5
Starch	—	—	—	—	98.0	96.8
Acid detergent fiber	47.5	25.0	—	—	—	—
Neutral detergent fiber	68.9	36.7	—	—	—	—
Energy	79.9	49.3	56.9	51.8	—	—

[a] Given as percentage. Diet 1, whole corn plant pellets (Schurg *et al.*, 1977); diet 2, pelleted alfalfa meal diet (Slade and Hintz, 1969); diet 3, complete pelleted diet (Wolter *et al.*, 1980).

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4

Protein and Amino Acid Nutrition

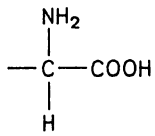
Protein is commonly regarded by livestock producers as the most important component of feed, with a high-protein feed being viewed as superior to a lower protein one. While this is not entirely correct, it is true that there is usually a good relationship between protein content and nutritive value. Also, one nutrient is not really more important than another; it is necessary to supply all nutrients in adequate quantities. On a quantitative basis, energy sources are needed in larger quantity than protein. Nevertheless, there is no question that provision of adequate quantity and quality of dietary protein is of major concern.

All proteins contain nitrogen because they are made up of amino acids, which contain nitrogen. On the average, proteins contain 16% nitrogen. The protein content of feeds is determined by digesting the feed with acid, and analyzing for the amount of nitrogen (as ammonia) present. This assumes, fairly accurately, that all the nitrogen in the feed is associated with protein. By definition, the crude protein (CP) content of a feed is 6.25 times the nitrogen (N). The factor of 6.25 arises from the fact that protein averages 16% N: 16 g of N are derived from 100 g of protein; therefore, 1 g of N is derived from 100/16 = 6.25 g. Thus each gram of N measured corresponds to 6.25 g of protein.

I. PROTEIN STRUCTURE AND SYNTHESIS

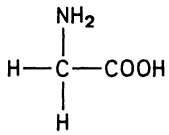
Proteins are made up of "basic units" called amino acids. The relative proportions of different amino acids and their sequence when joined together determine the characteristics of the protein.

All amino acids important in animal nutrition contain the following structure:

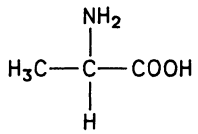


Because the amino group is on the alpha (α) carbon atom (the second from the terminal end) they are called α-amino acids. Amino acids differ in the chemical

group that is bonded to the α-carbon. For example, note the difference between glycine and alanine:



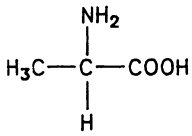
glycine



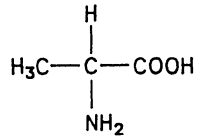
alanine

These are the two simplest amino acids in structure. The others (Fig. 4.1) are of greater complexity.

These chemical structures are a diagrammatic way of representing a three-dimensional object. Each amino acid except glycine has an asymmetric α-carbon, meaning that four different chemical groups are attached to this carbon. Compounds with an asymmetric carbon can exist as two isomers, which differ in how they reflect polarized light (dextrorotary, to the right; levorotary, to the left), so they are designated the D-and L-isomers. These isomers can be illustrated as follows:



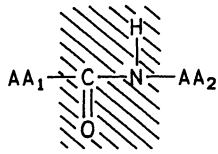
L-alanine



D-alanine

Only L-isomers of amino acids are used metabolically in the synthesis of proteins. In some cases, animals can convert the D- to the L-form. For example, DL-methionine is used as a feed additive, because D-methionine can be converted to L-methionine. On the other hand, DL-lysine is not used as a feed supplement, because D-lysine cannot be metabolized. L-Lysine is the form produced as a feed additive.

The fundamental structure of proteins is a string or chain of amino acids linked together by chemical bonds between their amino (NH_2) and carboxyl (COOH) groups. These are called peptide bonds:



A tripeptide synthesized from glycine, alanine, and methionine is shown to illustrate the arrangement of amino acids in a protein:

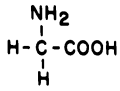
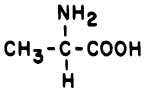
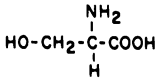
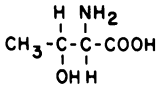
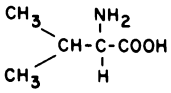
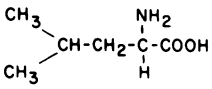
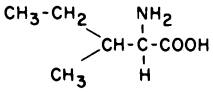
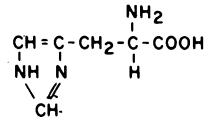
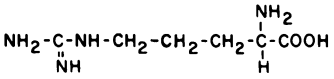
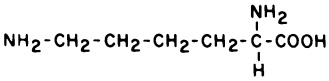
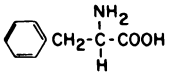
Amino acid	Formula	Structure
Aliphatic		
Glycine	$C_2H_5O_2N$	
Alanine	$C_3H_7O_2N$	
Serine	$C_3H_7O_3N$	
Threonine	$C_4H_9O_3N$	
Valine	$C_5H_{11}O_2N$	
Leucine	$C_6H_{13}O_2N$	
Isoleucine	$C_6H_{13}O_2N$	
Basic		
Histidine	$C_6H_9O_2N_3$	
Arginine	$C_6H_{14}O_2N_4$	
Lysine	$C_6H_{14}O_2N_2$	
Aromatic		
Phenylalanine	$C_9H_{11}O_2N$	

Fig. 4.1 Names and structures of amino acids. (Courtesy of C. T. Robbins, Washington State University, Pullman.)

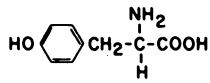
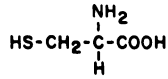
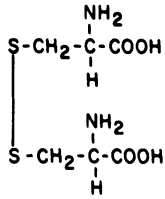
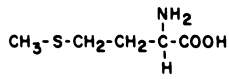
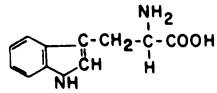
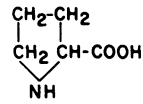
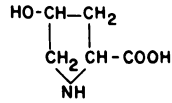
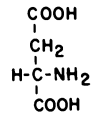
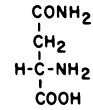
Amino acid	Formula	Structure
Tyrosine	$C_9H_{11}O_2N$	
Sulfur-containing		
Cysteine	$C_3H_7O_2NS$	
Cystine	$C_6H_{12}O_4N_2S_2$	
Methionine	$C_5H_{11}O_2NS$	
Heterocyclic		
Tryptophan	$C_{11}H_{12}O_2N_2$	
Proline	$C_5H_9O_2N$	
Hydroxyproline	$C_5H_9O_3N$	
Acidic		
Aspartic acid	$C_4H_7O_4N$	
Asparagine	$C_4H_8O_3N_2$	

Fig. 4.1 (*Continued*)

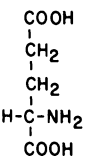
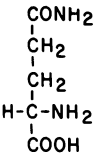
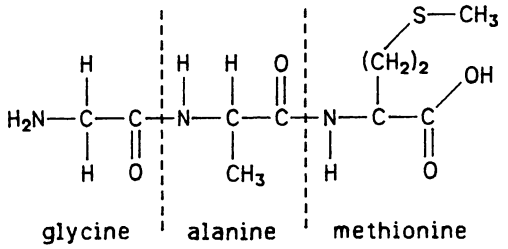
Amino acid	Formula	Structure
Glutamic acid	$C_5H_9O_4N$	
Glutamine	$C_5H_{10}O_3N_2$	

Fig. 4.1 *(Continued)*



A group of amino acids linked together in this way is called a polypeptide. A protein molecule is simply a very large polypeptide, usually consisting of hundreds or even thousands of amino acids joined together in a polypeptide chain. The properties of a protein are determined by its amino acid composition and the sequence in which the amino acids are joined together. Various types of bonds can be formed between nonadjacent amino acids in the chain, causing the protein to have a particular shape. It may be spherical, as are globulins (a class of blood proteins), or may be a more or less straight chain, as are muscle proteins. Occasionally, mutations occur in which an incorrect amino acid becomes incorporated at a particular site. For example, in sickel cell anemia of humans, one amino acid (glutamic acid) is replaced with another (valine), a seemingly simple change in a protein containing 574 amino acids, but the substitution changes the shape of the hemoglobin molecule, and interferes with the proper function of the red blood cells.

The control of the synthesis of protein is a fundamental process of all life, and is regulated by the DNA of the nucleus. DNA is the chemical basis of heredity, and consists of two strands of nucleic acid-containing nucleotides. The sequence of nucleotides contains a code of genetic information. The two strands making up

DNA are not identical, but during cell division, when the strands separate, each strand is coded to synthesize the other strand (i.e., it serves as a template on which a new strand is put together). DNA also serves as a template for the synthesis of RNA. There are three types of RNA: messenger RNA (mRNA), transfer RNA (tRNA), and ribosomal RNA (rRNA). The genetic code exists in the nucleotide sequence of mRNA. The code consists of a specific sequence of three nucleotides for each amino acid. Protein synthesis occurs in a part of the cell called the ribosomes, in which the code for amino acids contained in the mRNA is translated into the sequence of amino acids in the protein. The mRNA interacts with the rRNA, so that mRNA associated with the rRNA has a nucleotide sequence that attracts complementary nucleotides on tRNA. The tRNA is coded for amino acids. Each particular sequence of three nucleotides in tRNA is specific for one amino acid. The amino acids are attracted to the correct binding site on tRNA, and the tRNA transfers the amino acid to the ribosomes by being attracted to a particular nucleotide sequence on mRNA attached to the ribosome. Thus the genetic information in the nucleus, contained in the nucleotide sequence in DNA, controls the nucleotide sequences in mRNA, tRNA, and rRNA, with the result that amino acids are joined together in the ribosomes in the correct sequence to form protein molecules.

These events have been presented in a simplistic but hopefully understandable manner. The determination of the control of the genetic code is one of the outstanding scientific achievements of the twentieth century, and has opened the door to genetic manipulation. Gene splicing to repair defective genes, and gene modification are now practical. It will be possible to correct metabolic diseases arising from genetic defects. It is also possible to insert genes into bacteria to cause them to synthesize proteins such as insulin and growth hormone. These are exciting times in biology; possible future developments in biotechnology stagger the imagination. It may even be possible to duplicate DNA from extinct animals and recreate them, in cases where tissues are available. These include museum specimens and bodies found frozen in ice, such as the long-extinct wooly mammoth.

II. AMINO ACIDS IN RABBIT NUTRITION

About 20 amino acids are used by animals in the synthesis of their proteins. Those amino acids that cannot be synthesized by animals, and thus are required in the diet (or synthesized by gut microflora), are called essential amino acids, while those that can be synthesized are referred to as nonessential amino acids. These terms refer to the need for them to be provided in the diet; metabolically, they are all essential. While the number of essential amino acids varies somewhat

among species, in general the following are considered the dietary essential amino acids of most animals:

Arginine	Lysine
Histidine	Methionine
Isoleucine	Phenylalanine
Leucine	Threonine
Tryptophan	Valine

Adamson and Fisher (1971) demonstrated that these amino acids are nutritionally essential for the rabbit, and that dietary glycine is required for maximum growth rate. These requirements were demonstrated by feeding a purified diet with the protein provided by a mixture of amino acids. The effect of deletion of each of the amino acids was assessed by measuring growth rate. Weight loss occurred with each deletion of an essential amino acid, while the control group showed a normal weight gain. When glycine was omitted from the amino acid mixture, growth rate was about half of that of the control group. Thus rabbits require the same amino acids in the diet as do most other nonruminant animals.

The specific requirements for amino acids for growth and productive functions (lactation, Angora wool production, Rex fur production) have not been well studied. Specific requirement figures are desirable for use in ration formulation. Adamson and Fisher (1973) reported requirements for growth, using a purified diet containing crystalline amino acids. Their study was the primary basis for the NRC requirement figures, while the French rabbit nutritionist, F. Lebas, has provided estimates based on European work and practical experience (Table 4.1).

A number of studies have been conducted on requirements of lysine, methionine, and arginine. Lysine and methionine are of interest because these are usually the limiting amino acids in nonruminant nutrition. Arginine has been studied by several investigators (Adamson and Fisher, 1976; Cheeke, 1971; Colin, 1975b; Gamen and Fisher, 1970; Spreadbury and Davidson, 1978), probably because the first report on amino acid requirements of rabbits involved arginine (McWard *et al.*, 1967). Estimates of the arginine requirement for growth by various investigators are provided in Table 4.2. In the study of Spreadbury and Davidson (1978), a growth rate of 42 g/day was achieved with an arginine level of 0.56%, suggesting that this level is adequate for a high growth rate.

Arginine is synthesized in many animals by the enzymatic reactions of the urea cycle, as an intermediate in the formation of urea from ammonia. Arginine formed via the urea cycle can enter the metabolic pool of amino acids and reduce the dietary arginine requirement. Poultry do not have a functional urea cycle, cannot synthesize arginine, and have a high dietary arginine requirement. They excrete uric acid rather than urea as the main excretory product of protein

TABLE 4.1

Essential Amino Acid Requirements of Rabbits

Amino acid	Percentage requirement in diet			
	Growth			Does and litters fed one diet[b]
	NRC[a]	Lebas[b]	Lactation[b]	
Methionine + cystine	0.6	0.5	0.6	0.55
Lysine	0.65	0.6	0.75	0.7
Arginine	0.6	0.9	0.8	0.9
Histidine	0.3	0.35	0.43	0.4
Leucine	1.1	1.05	1.25	1.2
Isoleucine	0.6	0.6	0.7	0.65
Phenylalanine + tyrosine	1.1	1.2	1.4	1.25
Threonine	0.6	0.55	0.7	0.6
Tryptophan	0.2	0.18	0.22	0.2
Valine	0.7	0.7	0.85	0.8
Glycine[c]	—	—	—	—

[a] National Research Council (1977).
[b] Lebas (1980).
[c] Quantitative requirement unknown, but dietary need demonstrated.

metabolism. Cheeke and Amberg (1972) found that uric acid was a negligible component of urinary nitrogen in the rabbit. These observations indicate that the rabbit has urea cycle enzymes and can synthesize arginine, and that its arginine requirement is lower than originally thought.

Several studies, including those of Colin *et al.* (1973) Colin (1975a, 1978a,b) and Spreadbury (1978), indicate that a level of about 0.65% sulfur amino acids (methionine + cystine) is adequate for normal growth. Colin (1978b) demonstrated that cystine can supply 35–65% of the total sulfur amino acid requirement. Using an alfalfa–wheat mill run diet, with no other source of protein,

TABLE 4.2

Estimates of the Dietary Arginine Requirement of Growing Rabbits

References	Arginine requirement (% of diet)
McWard *et al.* (1967)	1.0
Cheeke (1971)	0.88
Adamson and Fisher (1973)	1.0
Spreadbury and Davidson (1978)	0.56

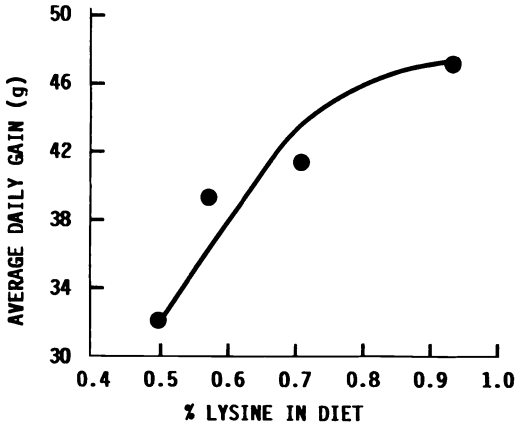


Fig. 4.2 Growth response of weanling rabbits to various dietary lysine levels. (Adapted from Spreadbury, 1978.)

Sanchez *et al.* (1984) observed no response to supplemental methionine. Raharjo *et al.* (1986), using similar diets, observed no response of does to methionine supplementation, indicating that simple forage–cereal by-product diets may contain adequate sulfur amino acid levels.

Reports of Adamson and Fisher (1973), Cheeke (1971), Colin (1974), Colin *et al.* (1975), Colin and Allain (1978), and Spreadbury (1978) suggest that the lysine requirement for growth is about 0.9% of the diet. A typical growth response to supplementary lysine is shown in Fig. 4.2. Lysine appears to have a growth-depressing effect when fed in excess of the requirement (Cheeke, 1971; Sanchez *et al.*, 1984).

Specific requirement figures for other amino acids for commercial meat production have not been established experimentally.

The expression of amino acid requirements is influenced by the dietary energy level. The feed intake of rabbits and other animals is controlled to a large degree by the caloric content of the feed. Animals must consume more of a low-energy diet to meet their energy needs. The concentration of protein, amino acids, and other nutrients necessary to meet metabolic needs, when expressed as a percentage of diet, is higher in high-energy diets, because feed intake is less. Conversely, with low-energy diets and a high feed intake, amino acid requirements as a percentage of the diet are reduced. Ideally, amino acid requirements should be expressed as amount per kilocalorie of digestible energy (DE). Colin and Allain (1978), for example, suggested a lysine requirement for growth of 2.4 g per 1000 kcal DE (2.4 mg/kcal). They observed higher rates of gain of fryers fed low lysine levels with 17.5% crude fiber diets than with low-fiber diets (Fig. 4.3) because of the higher intake of the high-fiber diets.

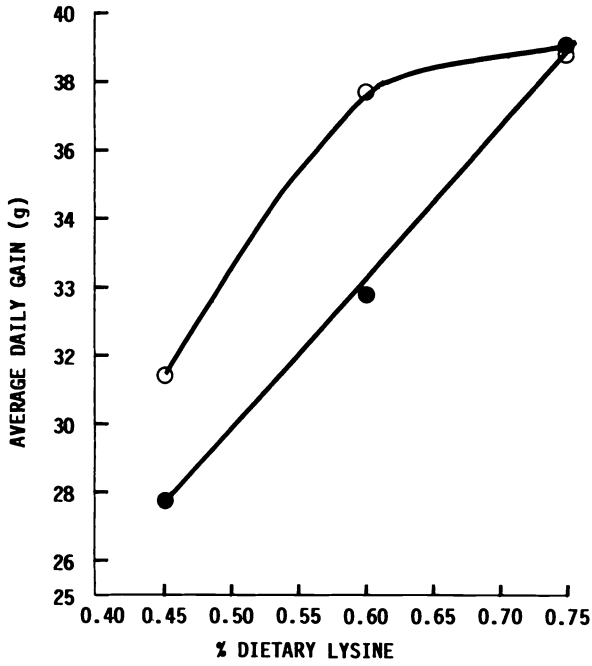


Fig. 4.3 The lysine requirement as a percentage of diet is lower with high-fiber diets, because of the higher feed intakes. Crude fiber content 10% (●); 17.5% (○). (Adapted from Colin and Allain, 1978.)

III. PROTEIN QUALITY

The quality of a protein refers to how well its amino acid composition matches the requirements of the animal to which it is being fed. Because of the bacterial protein synthesis in the cecum, it has often been assumed that protein quality is not important in rabbit nutrition. However, as the previous discussion has indicated, rabbits do have dietary essential amino acid requirements, so protein quality is important. Cheeke (1971) compared the growth of rabbits fed a high-quality protein (casein) with those fed very low-quality proteins (zein and gelatin). The average total weight gain over a 20-day period was 751 g for the casein group, 11 g for the gelatin group, and a weight loss of 79 g for the zein-fed group, indicating that bacterial protein synthesis in the cecum cannot compensate for severe amino acid deficiency. In a subsequent trial (Cheeke and Amberg, 1972), cottonseed meal was shown to give poorer gains than soybean meal or fish meal, and normal growth was achieved when the deficient amino acids were provided (Table 4.3).

While protein quality is important, it is apparent that rabbits can meet their

TABLE 4.3

Effect of Amino Acid Supplementation on Growth Response to Different Protein Sources[a]

Dietary protein source	Average daily gain[b] (g)
Soybean meal	37.6*[b]
Fish meal	34.4*
Cottonseed meal	24.6**
Cottonseed meal + amino acids[c]	34.8*

[a] From Cheeke and Amberg (1972).

[b] *Different from ** ($p < 0.01$).

[c] Amino acids provided were 0.45% lysine and 0.21% methionine.

amino acid needs on quite simple diets based on forage and grain by-products. Sanchez *et al.* (1984) compared the growth response of fryer rabbits fed diets based on alfalfa meal and wheat mill run, with varying levels of soybean meal supplementation. The results (Table 4.4) show no reduction in gain as a result of reducing the soybean meal level to 3% of the diet, and no response to supplemen-

TABLE 4.4

Growth of Weanling Rabbits Fed Diets Varying in Level of Soybean Meal Supplementation[a,b]

Protein supplement	Average daily gain (g)
21% Soybean meal	36.8
21% Soybean meal + MHA[c]	39.4
15% Soybean meal	36.5
15% Soybean meal + MHA	39.9
9% Soybean meal	39.1
9% Soybean meal + MHA	38.9
3% Soybean meal	38.1
3% Soybean meal + MHA	37.3

[a] From Sanchez *et al.* (1984).

[b] The diets contained 54% alfalfa meal and 20, 26, 32, and 38% wheat mill run for the 21, 15, 9, and 3% soybean meal levels, respectively.

[c] 0.3% Methionine hydroxy analog.

TABLE 4.5

Performance of Growing Rabbits Fed Diets with or without a Protein Supplement[a]

Diet	Average daily gain (g)	Feed/gain
54% Alfalfa		
21% Soybean meal	34.4	3.51
0% Soybean meal	33.9	3.81
0% Soybean meal + 0.3% MHA	33.5	3.79
74% Alfalfa		
21% Soybean meal	32.6	3.76
0% Soybean meal	31.9	3.86
0% Soybean meal + 0.3% MHA	34.1	3.91

[a] From Sanchez *et al.* (1984).

tation with 0.3% methionine hydroxy analog (MHA). In a subsequent experiment the soybean meal supplement was removed entirely, and no growth depression occurred (Table 4.5). Thus a simple diet of alfalfa meal and wheat mill run appears to be of adequate protein quality for the growing rabbit.

Three of the diets used by Sanchez *et al.* (1984) were tested with does in production over a 1-year period. No significant differences in production were observed (Table 4.6). Raharjo *et al.* (1986) studied the effect of total removal of the soybean meal on reproductive performance (Table 4.7). No differences were noted. These studies indicate that a simple mixture of 54% alfalfa meal and 41% wheat mill run provides an adequate amount and quality of dietary protein for growth and reproduction of rabbits.

TABLE 4.6

Reproductive Performance Achieved with Diets Varying in Quantity of Protein Supplement[a]

Performance parameter	Level of dietary soybean meal (%)		
	21	15	9
Total kits born per litter	9.4	9.2	8.6
Born alive (%)	78.9	75.6	86.4
Total litter live birthweight (g)	517	542	478
Total litter weight at 21 days (g)	2690	2780	2550
Total litter weight at 28 days (g)	4120	4380	3990
Average daily gain, 4–8 weeks (g)	38.8	39.0	38.5

[a] From Sanchez *et al.* (1985).

TABLE 4.7

Reproductive Performance with and without a Protein Supplement[a,b]

Performance parameter	Level of dietary soybean meal	
	21%	0%
Total kits per litter	9.11	8.67
No. kits born alive	8.47	7.86
Total litter birthweight (g)	519	461
Total litter weight at 21 days (g)	2550	2350
Total litter weight at 28 days (g)	3920	3660
Average daily gain, 4–8 weeks (g)	41.4	41.1

[a] From Raharjo *et al.* (1986).

[b] Diets contained 54% alfalfa meal, 20% wheat mill run, and 21% soybean meal (21% SBM diet) and 54% alfalfa meal and 41% wheat mill run (0% SBM diet).

IV. PROTEIN REQUIREMENTS FOR GROWTH AND LACTATION

Animals have no specific requirement for protein; rather, they require the amino acids from which body proteins are synthesized. For practical purposes, however, it is useful to express a crude protein requirement based on good-quality dietary protein.

Numerous studies have been conducted for the determination of optimal dietary protein levels for growth and lactation. Since it is not a common practice in the rabbit industry to use separate grower and lactation diets, a protein level that is adequate for both functions is usually needed.

Spreadbury (1978) and Omole (1982) have studied dietary protein requirements under temperate and tropical conditions, respectively. Their results are shown in Fig. 4.4. A level of 18% crude protein was optimal under tropical conditions, while about 16% protein was the optimal level in a temperate climate. The difference in performance observed in the two studies, with a maximum average daily gain of 35–40 g for temperate conditions and 20–25 g for tropical areas, is typical. In a study conducted in Spain (de Blas *et al.*, 1981), the optimal crude protein level for growth was 16% (Fig. 4.5). In this study, three crude fiber levels (7, 11, 15%) were used. With lower protein levels, gain was reduced to a greater extent with the low-fiber diets. This reflects a greater feed intake on the high-fiber lower energy diet, resulting in a greater daily protein intake at the same dietary protein level.

Because feed intake varies with the DE content of a diet, it is desirable to

express the CP requirement as the milligrams CP per kilocalorie DE. The optimal protein/energy ratio is about 55 (Fig. 4.6). de Blas *et al.* (1984) have provided estimates of the amount of crude protein required per day by fryers for different rates of gain (Table 4.8).

The optimal level of dietary crude protein for lactating does appears to be somewhat higher than for growth of fryers. Sanchez *et al.* (1985) recommended a level of 19% crude protein for maximum production of both lactating does and growing fryers, but differences between 17.5% and 19% protein were slight. Under tropical conditions, Omole (1982) found that 18% protein gave maximum litter size and weaning weight (Fig. 4.7). Partridge and Allan (1982) measured milk production of does fed diets with 13.5, 17.5, and 21.0% crude protein, with litter size adjusted to eight kits per doe. The total 28-day milk yields were 3.89, 4.82, and 5.27 kg for does fed the 13.5, 17.5, and 21.0% protein levels, respectively, indicating that at least 21% protein is required for maximum lactational performance. In a subsequent study, Partridge *et al.* (1983) observed that does fed a high-energy diet with 19% crude protein were in positive nitrogen balance, indicating that their dietary protein status was adequate.

Raharjo *et al.* (1986) found that there were no significant differences in re-

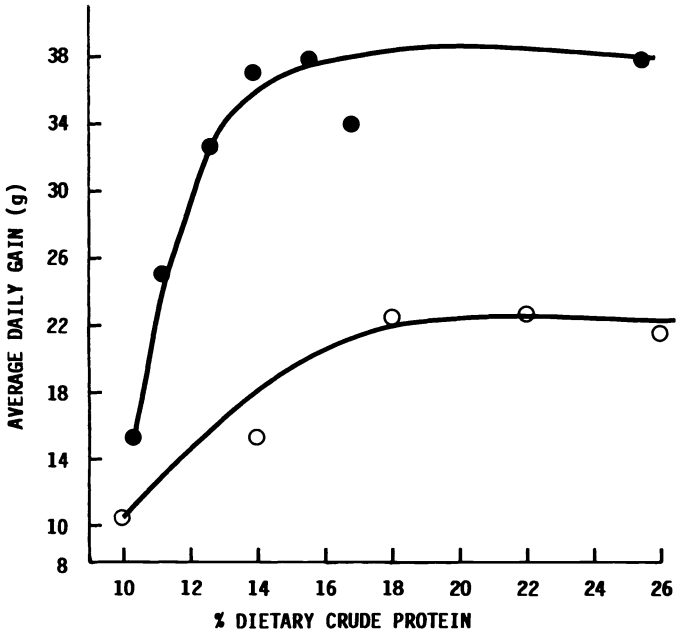


Fig. 4.4 Effect of dietary crude protein levels on average daily gains of fryers under temperate (●) and tropical (○) conditions. (Temperate data from Spreadbury, 1978; tropical data from Omole, 1982.)

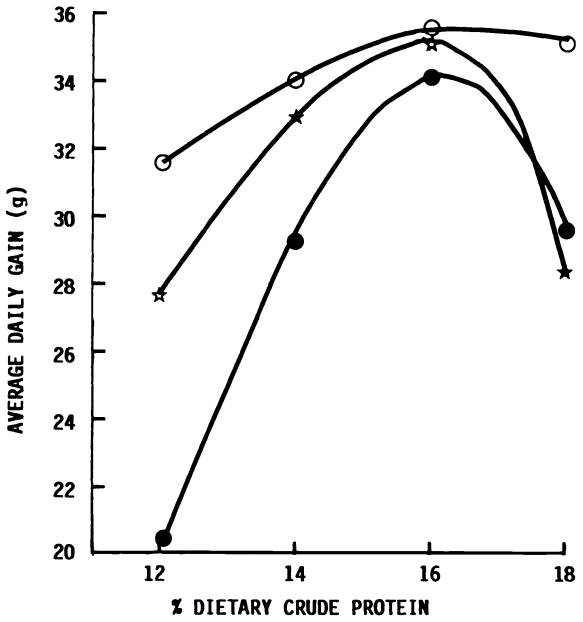


Fig. 4.5 Growth response to various dietary crude protein levels with different crude fiber levels (☆, 7%; ●, 11%; ○, 15%). With low-protein diets, gains are greatest when fiber levels are high, because of increased feed intake. (Data from de Blas *et al.*, 1981.)

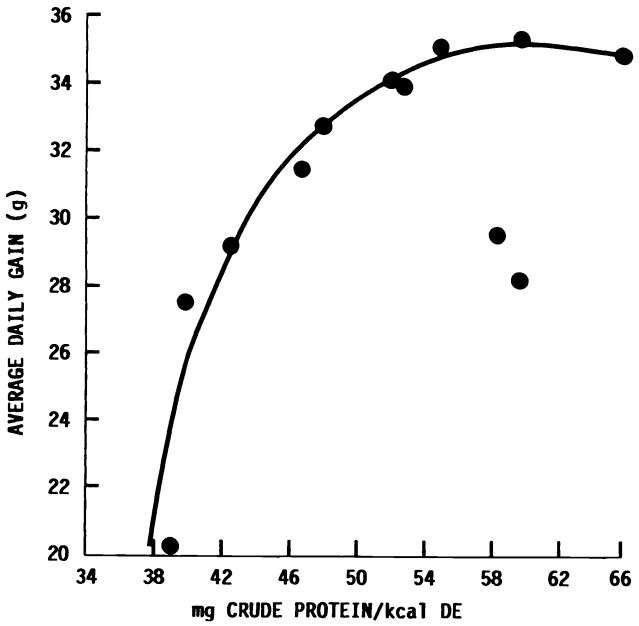


Fig. 4.6 Growth rates of fryer rabbits fed diets with varying protein to digestible energy (DE) ratios. (Data from de Blas *et al.*, 1981.)

TABLE 4.8

Digestible Crude Protein (CP) Requirements of Fryer Rabbits for Various Rates of Gain and Slaughter Weight[a,b]

Market weight (kg)	Average daily gain (g)			
	30	35	40	45
2.00	9.93	10.66	11.40	12.13
2.25	11.18	11.80	12.43	13.06
2.50	11.46	12.03	12.60	13.17

[a] From de Blas *et al.* (1984).
[b] Given as grams CP per day.

productive performance between does fed a diet with a protein supplement of 21% soybean meal, and a group with the soybean meal removed. The levels of dietary crude protein were 21.0 and 16.0%, respectively. Feed intake was not measured, but was probably higher on the lower energy (16% protein) diet, which had wheat mill run substituted for soybean meal. A higher feed intake could compensate for the lower protein level.

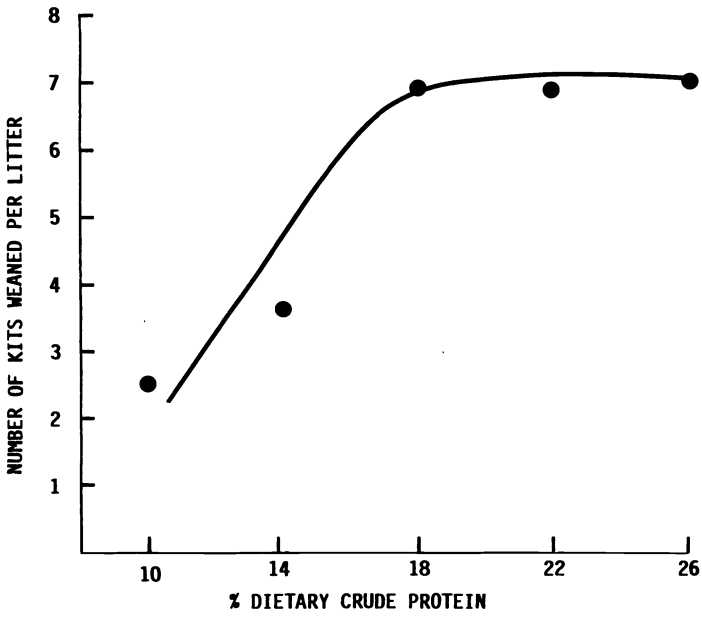


Fig. 4.7 Effect of dietary protein level on number of kits weaned per litter. (Data from Omole, 1982.)

TABLE 4.9

Effect of Different Dietary Protein Levels on Performance of Angora Rabbits[a]

Item	Dietary crude protein				
	25.4%	21.2%	19.3%	13.8%	10.2%
Initial body weight (g)	3020	2930	3100	3130	3060
Body weight after 3 months (g)	3160	3190	3210	3490	3260
DM feed consumed per day (g)	87	94	113	110	107
Digestible protein consumed per day (g)	19.2	15.4	17.5	11.5	6.2
Wool production in 3 months (grams per animal)	73	76	88	82	78
N balance (grams per animal per day)	1.0	0.5	1.5	0	−4.9

[a] From Lall *et al.* (1984).

Because of the relationship between energy level and feed intake, a protein requirement as a percentage of the diet cannot be given precisely, but in general, 17–18% dietary crude protein should be adequate for a diet fed to fryers and lactating does.

Very little research has been conducted on the protein requirements for Angora wool or Rex fur production. Lall *et al.* (1984), in India, evaluated the effects of five diets (25.4, 21.2, 19.3, 13.8, and 10.2% crude protein) on wool production of Angora rabbits. Pertinent data on performance are shown in Table 4.9. The wool production was not affected over a 3-month period by the dietary protein level, but the lack of positive nitrogen balance in the groups fed the 10 and 13% protein levels indicates that wool production may have been at the cost of tissue breakdown, which could have adverse long-term consequences. The authors suggested 20% dietary crude protein as an optimal level for Angora wool production.

V. DIGESTION OF PROTEIN

Proteins must be digested to release the amino acids of which they are composed before they are of nutritional value to an animal. The amino acids are absorbed and used in the tissues for the synthesis of proteins characteristic of the particular animal. The digestion can be accomplished either by digestive enzymes the animal secretes, or by enzymes produced by microorganisms in the gut. Protein digested by microbes is converted to ammonia, which may be absorbed, and to microbial protein. The host animal derives benefit when it digests the microbial cells, and utilizes the microbially synthesized amino acids. In some animals, including swine, poultry, and humans, most of the digestive

processes are accomplished by the animal's own enzymes, and microbial action is of minor importance. In others, such as the ruminants (cattle, sheep, etc.), the microbial processes are of major importance. In rabbits and other nonruminant herbivores, both processes are important (Slade and Robinson, 1970). It is not known if protozoa are of significance as gut microbes in rabbits. It will be assumed for this discussion that bacteria constitute the major physiologically significant component of the intestinal flora.

Some protein digestion occurs in the stomach and small intestine. The very acid stomach of the rabbit probably results in some hydrolysis of protein. Proteolytic enzymes in the small intestine, such as trypsin and chymotrypsin, are important in protein breakdown. The activity of these enzymes in the intestine increases rapidly as the baby rabbit begins consuming solid feed, because of a rapid growth in size of the pancreas (Alus and Edwards, 1976). The extent of digestion of protein in the small intestine of the rabbit has not been fully documented, but presumably, with readily digestible protein concentrates like soybean meal, the major part of protein digestion occurs in the small intestine. Wolter *et al.* (1980) studied the partial digestion of protein in the various parts of the rabbit digestive tract, but interpretation of the results is difficult because of the secretion of proteins (digestive enzymes) into the gut and their subsequent digestion farther down the tract. These authors reported the digestibility of protein in the different segments as follows: stomach, +6.1%; duodenum, −78.5%; jejunum–ileum, −50.4%; cecum, −103.6%; colon, +56.8%. In other words, more protein (or nitrogen) is being secreted into the small intestine and cecum than is being absorbed, because of secretion of enzymes, and secretion of ammonia into the cecum. If the nitrogen contributions of these secretions could be subtracted, then positive digestibility of protein in the intestine and cecum would undoubtedly be seen.

VI. DIGESTIBILITY OF PROTEINS IN THE RABBIT

Some generalities about protein digestion are that the digestibility of typical plant proteins (soybean meal, cottonseed meal, etc.) is similar to what it is in other nonruminants such as swine, but the digestibility of forage proteins is much higher. Protein digestibility coefficients for a number of feedstuffs are shown in Table 4.10.

Robinson *et al.* (1985) proposed that the ability of rabbits to digest forage proteins efficiently is a consequence of the selective retention of nonfiber components in the cecum. Cecal fermentation with subsequent cecotrophy (coprophagy) is a digestive strategy that extracts protein from forages with high efficiency. This is likely to be particularly true of the rabbit in its natural habitat, in which its diet is composed of leaves and other succulent plant tissues. Drying of

TABLE 4.10

Digestibility in the Rabbit of the Crude Protein of Various Feedstuffs

Feedstuff	Digestibility of crude protein (%)	References
Alfalfa hay	72–83	Voris *et al.* (1940)
Barley, grain	85	
Corn, yellow	84	
Cottonseed meal	84	
Linseed meal	86	
Oats	79	
Soybean meal	90	
Wheat	85	
Wheat bran	83	
Alfalfa meal	64	Maertens and DeGroote (1984)
Oats	73	
Wheat shorts	75	
Rapeseed meal	76	
Soybean meal	79	
Sunflower meal	76	
Full-fat soybeans	88	

TABLE 4.11

Effect of Coprophagy on the Digestibility of Crude Protein in the Rabbit[a]

Dietary protein source	Coprophagy[b]	Nitrogen digestibility (%)	Nitrogen retention (g/day)
Alfalfa meal	+	64.9	1.10
Alfalfa meal	−	50.8	0.93
Soybean meal	+	76.9	0.78
Soybean meal	−	64.0	0.65
Fresh grass	+	77.6	0.78
Fresh grass	−	67.6	0.44

[a] From Robinson *et al.* (1985).

[b] +, Coprophagy allowed; −, coprophagy prevented by a collar.



Fig. 4.8 For studies on the effect of cecotrophy (coprophagy) on nutrient utilization, rabbits can be fitted with a collar that prevents them from consuming the cecotropes.

forages, in the curing of hay or preparation of alfalfa meal, tends to reduce protein availability by denaturing soluble proteins and stimulating the binding of protein to plant cell wall components.

Besides having an influence on the digestibility of protein (Table 4.11), coprophagy can have an effect on essential amino acid requirements and the utilization of poor-quality proteins. Synthesis of amino acids by cecal microorganisms could perhaps overcome dietary amino acid deficiencies. Kennedy and Hershberger (1974) determined the effect of coprophagy on the utilization of a very poor-quality protein (gelatin), which almost totally lacks tryptophan and is very low in methionine. When coprophagy was prevented, rabbits fed gelatin as the protein source were in negative nitrogen balance, indicating that because of

TABLE 4.12

Effect of Coprophagy on Utilization of Poor-Quality Protein[a]

Diet protein source	Coprophagy	Nitrogen digestibility (%)	N Balance (mg/day $W^{0.75}$)[b]	Apparent BV[c]	Weight change (g/day)
Casein	−	88.3	236.1	26.8	6.8
Gelatin	−	70.7	−186.2	−48.6	−12.5
Casein	+	96.1	458.3	37.8	36.3
Gelatin	+	87.9	89.4	12.8	4.5

[a] From Kennedy and Hershberger (1974).

[b] $W^{0.75}$, or "metabolic body size," is defined in Chapter 5, Section V,A.

[c] Biological value (BV) is a measure of the use of absorbed amino acids for protein synthesis. The lower the BV, the lower the effeciency of use of the protein.

the amino acid deficiencies, they were catabolizing tissue proteins. Animals permitted to consume their soft feces showed a positive nitrogen balance and a body weight gain (Table 4.12), indicating that bacterial protein synthesis had compensated for part of the dietary amino acid deficiencies.

These results of Kennedy and Hershberger (1974) demonstrate that with a severe amino acid deficiency, cecal fermentation followed by coprophagy can alleviate the deficiency. Under practical conditions, however, the significance of coprophagy in meeting essential amino acid needs is uncertain. Spreadbury (1978) estimated that about 10% of the absorbed amino acids in fryer rabbits originated from bacterial protein, suggesting that coprophagy is of minor importance in the protein nutrition of the young rabbit. For adult animals, such as were used by Kennedy and Hershberger (1974), coprophagy might make a greater contribution to protein requirements. Jecsai *et al.* (1985) and Teleki *et al.* (1985) studied the effect of cecotrophy with diets with a high (16.7%) or low (12.8%) crude protein content on nitrogen metabolism in Angora rabbits. On the low-protein diet, cecotrophy improved nitrogen utilization as assessed by nitrogen balance, blood urea, and serum amino acids. In rabbits fed the higher protein diet, cecotrophy did not influence nitrogen metabolism.

VII. NONPROTEIN NITROGEN (NPN) UTILIZATION

Synthesis of bacterial protein in the cecum and subsequent consumption of the cecal contents by coprophagy would suggest an ability of rabbits to utilize nonprotein nitrogen (NPN) sources such as urea. The advantages of such use would be primarily economic, because urea is a cheaper source of nitrogen than are protein supplements. Urea-hydrolyzing (ureolytic) bacteria are present in the

rabbit cecum (Crociani *et al.*, 1984), as are organisms that can utilize ammonia for amino acid synthesis. The ureolytic activity in the cecum is located mainly in microorganisms closely associated with the cecal mucosal lining (Hill, 1983). According to Forsythe and Parker (1985a), the cecum is the major site of urea hydrolysis in the rabbit digestive tract. However, Candau *et al.* (1979) found that most dietary urea is hydrolyzed in the stomach, and only a very small fraction of dietary urea reaches the cecum directly. Urea is secreted into the cecum from the blood (Forsythe and Parker, 1985b; Knutson *et al.*, 1977; Vialard, 1984), which may help to maintain an adequate nitrogen supply for bacterial metabolism.

In spite of these capabilities, it appears that urea is of very limited value as a nitrogen source for fryer rabbits. Several studies (Table 4.13) have shown little or no growth response when urea or other NPN sources were used to supplement a low-protein diet.

Adult rabbits under maintenance conditions might be able to utilize sufficient NPN to meet maintenance needs. However, in most cases this is not of practical importance, because does in a commercial rabbitry should be in production. It is possible that a diet for Angora woolers (mature animals kept for wool production) could be developed using urea to provide part of the nitrogen needs, although Teleki *et al.* (1983) found that when urea was used to replace 16% of the crude protein in the diet of adult Angora rabbits, nitrogen balance was reduced, indicating inefficient utilization of urea.

Salse (1985a) developed an artificial cecum to study fermentation processes in the rabbit. Wheat bran with a nutrient solution containing urea as the nitrogen source was used as the substrate. Bacterial protein synthesis was demonstrated. Bran fermented in this manner was shown to be of high nutritive value to growing rabbits, supporting a growth rate and nitrogen retention equivalent to that obtained with a mixture of soybean meal and wheat bran providing the same

TABLE 4.13

Response of Fryer Rabbits to Dietary NPN Sources

References	Diet	Average daily gain (g)
Cheeke (1972)	Basal (12% CP)	20.0
	Basal + urea	22.8
	Basal + biuret	24.0
	Basal + diammonium citrate	22.1
	Basal + fish meal	29.4
King (1971)	Basal (low protein)	22.7
	Basal + urea	21.5
Lebas and Colin (1973)	Basal (low protein)	20.4
	Basal + urea	21.1

TABLE 4.14

Affect of Age and Cecotrophy on Utilization of Urea by Rabbits[a,b]

Dietary treatment and age of animal[c]	Cecotrophy	ADG	Digestibility (%)		N Retention
			DM	N	
Low protein (basal)					
Adult	+	29.9	56.4	72.1	0.98
Adult	−	6.1	50.9	53.0	0.38
Fryer	+	39.0	53.7	69.6	1.37
Fryer	−	24.9	49.2	50.5	0.95
Basal + soybean meal					
Adult	+	17.1	58.2	70.9	1.12
Adult	−	−2.4	52.3	56.7	0.61
Fryer	+	29.7	57.6	70.7	1.39
Fryer	−	25.1	53.3	58.2	1.25
Basal + urea					
Adult	+	6.6	55.5	77.5	0.75
Adult	−	−19.4	49.0	64.1	0.04
Fryer	+	31.0	55.1	78.5	1.26
Fryer	−	11.9	47.5	59.7	0.83

[a] Adapted from Robinson *et al.* (1986).

[b] ADG, Average daily gain (g); DM, dry matter.

[c] +, Cecotrophy allowed; −, cecotrophy prevented.

dietary protein level (Salse, 1985b). These results suggest that cecal fermentation produces bacterial protein of adequate quality to support normal growth of the rabbit.

Robinson *et al.* (1986) studied the effect of age and cecotrophy on the utilization of urea by rabbits. A basal diet with 13.6% crude protein provided mainly by wheat mill run was used, and supplemented with either urea or soybean meal to provide 16% dietary crude protein. Prevention of cecotrophy reduced growth rate of fryers by 36, 16, and 62% for the basal, basal plus soybean meal, and basal plus urea treatments, respectively (Table 4.14), indicating that cecal synthesis of bacterial protein was of greatest significance in the diet with urea. Similarly, prevention of cecotrophy reduced nitrogen retention by 31, 10, and 34% for the same respective treatments. The growth and nitrogen retention results indicate that effective utilization of urea required cecal bacterial protein synthesis and cecotrophy, as also noted by Hoover and Heitmann (1975). Interestingly, urea utilization appeared to be more efficient in fryers than in adults. When cecotrophy was prevented, adult does had a marked loss of weight and almost zero nitrogen retention when fed the diet with urea (Table 4.14). Nitrogen retention was reduced by 61, 46, and 95% for the basal, basal plus soybean meal, and

basal plus urea treatments when cecotrophy was prevented. Thus, any utilization of urea by adult rabbits requires the involvement of cecal fermentation and cecotrophy.

Biuret is hydrolyzed more slowly than urea and thus might be more likely to reach the cecum to serve as a bacterial substrate. Proto and Gioffre (1986) compared urea and biuret as NPN sources in rabbits and found that retention of ingested nitrogen was 36.9% with biuret and 20.6% with urea, indicating that biuret was much more effectively utilized.

VIII. FACTORS INFLUENCING PROTEIN REQUIREMENTS

A. Dietary Energy Level

As previously discussed, the expression of protein requirements as a percentage of the diet has the limitation that the optimal percentage changes depending on the energy level. An animal requires a specific amount of protein per day. As an example, assume that a 6-week-old rabbit requires daily intakes of 19.2 g of CP and 350kcal DE for maximum growth. Compare the protein and energy intakes when high- and low-energy diets are used (Table 4.15). With the low-energy diet, the rabbit eats 140 g of feed per day, to consume its requirement of 350 kcal DE (140 g feed × 2.5 kcal/g = 350 kcal). On the high-energy diet, a rabbit would need to eat only 109 g to take in 350 kcal. Thus, on the high-energy diet, the 19.2 g of protein required has to be in the 109 g of feed, while the low-energy diet can contain the 19.2 g of protein in 140 g of feed. The 19.2 g in 109 g is equivalent to 17.6% protein (19.2/109 × 100), while in the low-energy diet the percentage is 13.7% (19.2/140 × 100). When expressed on a protein/calorie basis, each feed contains 55 mg CP/kcal DE (176,000 mg/3200 kcal = 55; 137,000 mg/2500 = 55).

It is apparent that if diets widely divergent in energy level are used, expression

TABLE 4.15

Example of Relationship between Protein and Energy Contents of Rabbit Diets

Item	High-energy diet (3200 kcal/kg)	Low-energy diet (2500 kcal/kg)
Daily feed intake (g)	109	140
Daily energy intake (kcal DE)	349	350
Crude protein in diet (%)	17.6	13.7
Daily protein intake (g)	19.2	19.2
mg protein/kcal DE	55	55

of the protein requirement as a percentage of the diet is not accurate. High-energy diets require a higher level of protein, whereas low-energy diets can have a lower level. By providing a standard amount of protein per unit of energy (e.g., 55 mg protein/kcal DE), the protein requirement is met regardless of what dietary energy level is used. The example used is a hypothetical one, to make the calculations easy, but the principle demonstrated holds true for practical conditions.

B. Dietary Fiber Level

With most animals, an increase in dietary fiber level increases the fecal loss of nitrogen, because of an increased content of sloughed-off intestinal cells (endogenous nitrogen) due to the abrasive or scabrous effect of fiber on the microvilli of

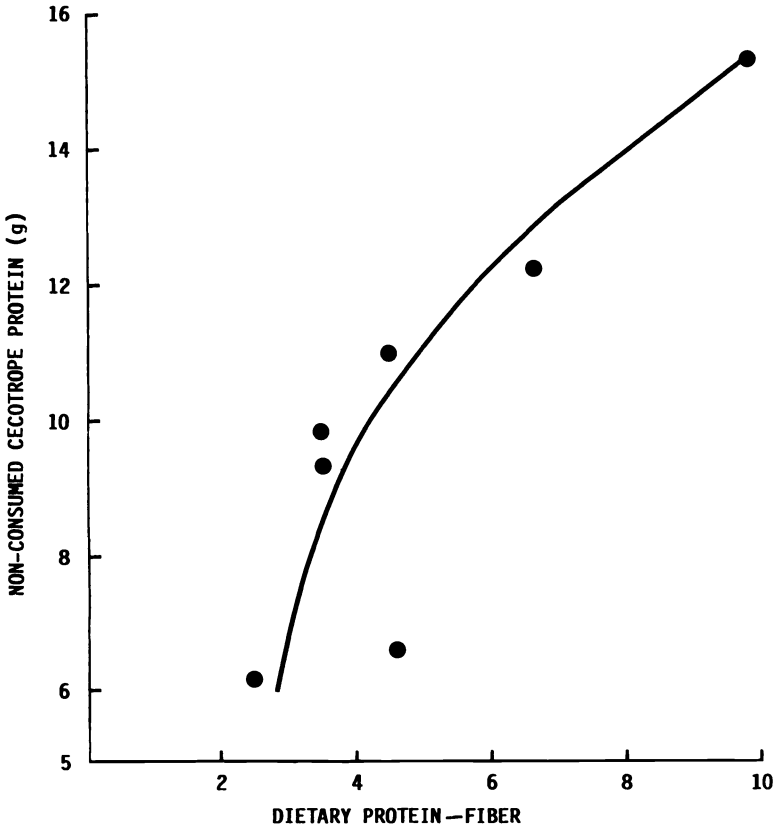


Fig. 4.9 The amount of cecotrope protein that is not consumed increases when there is a relative surplus of dietary protein over dietary fiber. When the fiber content is high, the increased excretion of endogenous protein is compensated for by an increased consumption of cecotropes. (Data from Fekete and Bokori, 1985.)

the intestine. With increasing fiber levels, the dietary protein requirement increases, and the apparent digestibility of protein decreases in most animals. In rabbits, high dietary fiber levels do not adversely affect the digestibility of crude protein (Fekete and Bokori, 1985). These authors demonstrated that the quantity of soft feces (cecotropes) consumed by rabbits was voluntarily regulated to balance the protein intake. When the dietary fiber level was increased, rabbits consumed a greater quantity of cecotropes, to compensate for the higher losses of endogenous protein (Fig. 4.9). Diets were formulated to contain varying levels of crude protein and crude fiber. The "protein minus fiber" is simply the percentage of dietary protein in excess of dietary fiber. These diets were fed to rabbits, and the feces collected and separated into hard feces and cecotropes. It was observed that as the protein level relative to fiber increased, the rabbits ate less of the cecotropes, so more nonconsumed cecotropes were discharged beneath the cage. Thus when there is a need to conserve nitrogen, the rabbits eat more of the cecotropes, and compensate for the higher endogenous nitrogen excretion caused by high dietary fiber levels.

C. Environmental Conditions

Environmental temperature affects feed intake. When the temperature is low, more feed must be consumed to meet the animal's increased energy requirements needed to maintain body temperature. The protein requirement is not significantly increased by a lower environmental temperature. Therefore, under cold conditions, a lower percentage protein level can be used in feeds, because of the increased feed intake. Conversely, at high temperatures, feed intake is reduced. In order to continue meeting the protein requirement from a lower feed intake, the percentage protein in the diet should be increased.

In areas of consistent climatic conditions, such as prolonged hot summers or cold winters, modification of the dietary protein level to compensate for seasonal changes in feed intake is probably economically warranted.

D. Excess Dietary Protein

It is undesirable to have a higher level of protein in the diet than necessary. Protein sources are usually among the most expensive feed ingredients. Excess protein is metabolized as an energy source, with the nitrogen excreted as urea in the urine. It is usually more expensive to use protein as a source of energy than carbohydrates, so in ration balancing, the amount of protein used should closely match the animal's requirements for protein synthesis.

Besides adding unnecessary costs, feeding excess protein can have some other undesirable consequences. When the extra protein is used as an energy source, increased nitrogen is excreted in the urine. Bacterial action in the manure converts the urea in urine to ammonia, which is given off as a gas. Thus the source

of ammonia in the air in a rabbitry is from excretion of nitrogen from excess protein in the diet. It is not possible to formulate a diet that so closely meets the animal's needs that no urea will be excreted, but the greater the level of excess dietary protein, the greater the amount of ammonia that will be released into the rabbitry. An additional factor is that urea in the urine requires dilution with water, so that the more urea excreted by a rabbit, the greater the urine volume and water intake. The extra water excretion contributes to a higher humidity. As the humidity increases, more ammonia is dissolved in the water in the air, leading to higher air ammonia levels. Further, as the rabbits breath, the dissolved ammonia attacks the mucous membranes of the nasal passages, allowing infection by bacteria, resulting in respiratory disease (snuffles).

There is some evidence that excess dietary protein can contribute to enteritis problems, by increasing the amount of nitrogen (as NH_4^+, the ammonium ion) in the cecum. According to Morisse *et al.* (1985), elevated ammonia levels in the cecum cause increased cecal pH (lower acidity), allowing pathogenic bacteria such as *Escherichia* and *Clostridia* species to proliferate.

Thus, excess protein in the diet will generally increase feed costs, and may be involved in provoking respiratory disease and enteritis.

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5

Energy Metabolism and Requirements

Energy-providing nutrients make up the major part of human and animal diets. The concept of feeds providing energy is not always easy to grasp, although most people are at least vaguely familiar with the term "calorie," one of the basic units of energy measurement.

I. ENERGY CATEGORIES AND MEASUREMENT

In the United States and several other countries, feed energy is measured in terms of calories. Some of the basic definitions are given below:

1 calorie	=	the amount of heat energy required to raise the temperature of 1 g of water by 1°C, measured from 14.5°C to 15.5°C (the room temperature of the European laboratories in which the original work was conducted)
1 kilocalorie (kcal)	=	1000 calories
1 megacalorie (mcal)	=	1000 kcal

For expression of energy requirements of rabbits, kilocalories are most commonly used. In many countries, and in much of the scientific literature, a different unit of energy measurement, the joule, is used:

1 calorie	=	4.184 joules
1 kcal	=	4.184 kj
1 kj	=	0.239 kcal

The energy content of feeds is measured by burning a sample of the feed in an instrument called a bomb calorimeter, and observing the amount of heat released. The heat is measured by the change in temperature of a known weight of water in a vessel surrounding the combustion chamber. From the definition of a calorie, one can appreciate that the caloric content can be calculated if you know the sample weight, weight of water, and the temperature change of the water when the sample is burned.

The total heat energy released when a feed sample is completely burned in a bomb calorimeter is the gross energy. Most feedstuffs have similar gross energy contents. However, animals cannot completely "burn" feeds. Therefore, it is necessary to measure the various energy losses that occur after a feed is consumed, to find the proportion of the gross energy that can actually be metabolized by the animal. The main losses of energy are indigestible material, which simply passes through the digestive tract, and loss of energy as heat.

The gross energy content of a feed is of little value as an estimate of feed energy. It is only a starting point. For example, wheat straw and wheat grain have about the same gross energy content, but they obviously are not comparable at all as far as providing calories to animals is concerned.

To determine the useful or productive energy content of a feed, the various energy losses that occur are subtracted from the gross energy value. The first loss encountered is the energy associated with the excretion of indigestible material in the feces. This correction yields digestible energy (DE):

$$\text{DE} = \text{gross energy} - \text{fecal energy}$$

To calculate DE content of a rabbit feed, the following procedure is employed. Rabbits are housed individually in metabolism cages, allowing for separate collection of feces and urine. The test diet is fed, and the feed intake and feces output measured. Then a sample of each of the feed and feces is burned in a bomb calorimeter. From this, the number of calories consumed and the calories excreted in the feces are calculated. Subtraction of the fecal energy excreted from the gross energy consumed yields the digestible energy value.

A further correction for energy lost in the urine can be made by collecting the urine, drying it, and measuring its energy content. This correction yields the metabolizable energy (ME):

$$\text{ME} = \text{DE} - \text{urine energy}$$

ME values are the unit of choice for poultry, because birds excrete their urine and feces together. For rabbits, however, it is much more cumbersome to collect and dry the urine, so DE values are commonly used for expression of rabbit energy requirements. There is no particular advantage, except with poultry, in using ME, because DE and ME are highly correlated, and similar in magnitude. Only a small amount of energy is lost by way of the urine.

There is one other major energy loss that has not been accounted for in these calculations, and that is the loss of heat energy. As animals metabolize nutrients, the chemical reactions that occur give off heat. This heat is taken up from the tissue cells by the blood, and brought to the body surface and released. Thus all warm-blooded animals are continuously losing heat to the environment. This heat loss is of no nutritional benefit (except in cold conditions) to the animal, so

represents an energy loss. The heat loss is determined by keeping an animal or human subject in a calorimeter chamber, in which the loss of heat is measured. Some chambers are surrounded by a water bath, and the temperature of the water is carefully monitored. By knowing the temperature change of a known weight of water, the amount of heat released by the animal to cause that change can be calculated. Correcting for heat loss gives net energy (NE):

$$NE = ME - \text{heat loss}$$

The NE thus represents the fraction of the gross energy that is actually utilized by the animal for productive purposes. While NE is the most precise estimate of a feed's energy value, it is not commonly used for rabbits because of the difficulty of measuring heat losses. DE values are the most commonly used in rabbit nutrition because of the relative ease of determination.

The three nutrient categories that can serve as energy sources are carbohydrates, fats (lipids), and protein. As a general rule of thumb, purified proteins and carbohydrates yield about 4 kcal DE per gram, while fat yields about 9 kcal per gram.

II. TOTAL DIGESTIBLE NUTRIENTS (TDN)

The TDN system has been used for many years as an estimate of the DE content of feeds. It is based upon the assumed equivalence of carbohydrate and protein as energy sources, and the higher energy content of fat. Fat is commonly measured as the "ether extract" portion of the feed. Since only those nutrients that are absorbed can yield energy, the digestibility of the carbohydrate, protein, and ether extract fractions of the feed is determined in a metabolism trial, or estimated from "book values." The formula for percentage TDN of a feed is as follows:

$$\%\ \text{TDN} = \%\ \text{digestible crude protein} + \%\ \text{digestible NFE} + \%\ \text{digestible crude fiber} + 2.25\ (\text{digestible ether extract})$$

The NFE is the nitrogen-free extract, corresponding to starch, sugars, and other readily digestible carbohydrates. The ether extract is multiplied by 2.25 to account for its higher energy content than protein or carbohydrate (9 kcal/g divided by 4 kcal/g = 2.25).

The accompanying table gives examples of some typical TDN and DE values for rabbit feedstuffs.

As these representative values indicate, grains and protein supplements have a higher energy value than roughages such as alfalfa and grass meals.

Ingredient	% TDN	DE (kcal/kg)
Alfalfa meal	53	2350
Barley grain	75	3330
Beet pulp	70	3080
Bermuda grass	43	1890
Corn grain	83	3790
Cottonseed meal	67	3090
Oats	65	2950
Soybean meal	82	3770
Timothy hay	32	1420
Wheat grain	79	3680
Wheat bran	64	2610

III. BASICS OF CELLULAR METABOLISM

The mechanisms by which animals derive energy from feeds form the foundation of the science of biochemistry. Literally thousands of biochemical reactions occur in animal tissues as absorbed nutrients are metabolized. A brief description of cellular metabolism will be given, bearing in mind that the subject is extremely complex.

Animals are composed of cells. Most cells contain common entities, such as a nucleus, mitochondria, lysosomes, endoplasmic reticulum, and several other subcellular organelles. The nucleus contains the genetic material, the DNA, and so can be regarded as the "nerve center" of the cell. The nucleus directs the synthesis of proteins within the cells. The mitochondria constitute the "powerhouse" of the cell. Much of the oxidation of nutrients to release energy occurs in the mitochondria. The lysosomes are the"disposal system" of the cell. They contain digestive enzymes, and break down worn-out cellular components such as enzymes that have lost their activity. The endoplasmic reticulum is a network of tubular vesicles in which protein synthesis occurs.

Cells are arranged so that they can receive nutrients from the blood and dispose of waste products to the blood. Cells that produce secretions, such as hormones, usually secrete these substances into the blood. An animal cell is very unstable in thermodynamic terms. A great deal of energy is required to maintain it in the living state. Movement of nutrients into and within the cells requires energy. Thus a major part of the dietary energy consumed by an animal is required for maintenance of existing tissues in the living state.

The basic metabolic machinery of the cell is concerned with carbohydrate metabolism. The net result is the reverse of photosynthesis. The solar energy that plants used to synthesize carbohydrates is potentially available to animals when they metabolize those carbohydrates. Energy is given off in two forms in animal

metabolism. One form is as heat, which is wasted energy, except for what is needed to maintain body temperature. The other form is as useful chemical energy. This biochemical energy is tranferred to a compound called adenosine triphosphate (ATP), which serves as an energy-providing substrate in biochemical reactions. For example, when glucose is metabolized as an energy source, it undergoes a number of chemical reactions in which it is converted to smaller molecules, and along the way, energy is transferred from glucose to ATP. The complete metabolism of glucose results in its conversion to carbon dioxide and water, and transfer of some of its energy to ATP. The ATP then fuels other reactions, like protein synthesis.

IV. CELLULAR METABOLISM OF CARBOHYDRATES

Carbohydrates are absorbed in two main forms. These are the simple sugars, such as glucose, and the volatile fatty acids (VFA) produced as end products of bacterial fermentation in the rabbit cecum. Generally, the simple sugars constitute the major source of absorbed energy in rabbits, and of these, glucose is the primary sugar metabolized.

All cells in the body metabolize glucose as an energy source. Two series of reactions, called metabolic pathways, are involved in glucose oxidation. One is called glycolysis. In the glycolysis reactions, glucose undergoes a series of enzymatic reactions, resulting in it being split into two molecules of pyruvic acid. In the process, about 20% of the energy that the cell will drive from glucose oxidation is liberated in the form of ATP synthesis. The glycolysis reactions, also known as anaerobic fermentation, occur in almost all living organisms. Glycolysis occurs in the bacteria that live in the cecum of the rabbit. The bacteria convert the pyruvic acid to waste products, the VFA, which they excrete. These organic acids, while waste products to the bacteria, can be used as an energy source by the host animal. Yeasts also ferment sugars by glycolysis, and convert the pyruvic acid to ethanol (alcohol). If bacteria contaminate the brewing process, vinegar (acetic acid—one of the VFA) is produced.

The enzymes in animal cells that accomplish the glycolysis reactions are located in the cytoplasm or soluble portion of the cell contents. The pyruvic acid is taken up by the mitochondria, where the remainder of glucose metabolism occurs. The reactions in the mitochondria are referred to as the Krebs cycle or citric acid cycle. In these reactions, the remainder of the energy obtained from glucose is released associated with ATP, and the waste products of carbon dioxide and water are produced. In the Krebs cycle reactions, certain cofactors containing vitamins play a role. These include NAD (contains the vitamin niacin) and FAD (contains the vitamin riboflavin). These cofactors are reduced (gain hydrogen) in the Krebs cycle reactions, and then are oxidized by another set of

enzymes called the cytochrome system. During the process, ATP is produced. In the final step of the oxidation process, the hydrogen is given up by the cofactors, and reacts with oxygen to produce water.

The VFA absorbed from the cecum are mainly acetic, propionic, and butyric acids. These are metabolized by the Krebs cycle reactions, which involve the oxidation of acetic acid by a series of enzymatic steps, releasing energy as ATP.

Amino acids and fats can also be used as sources of energy. They enter the pathways of carbohydrate metabolism. Fats contain fatty acids, which are metabolized by a process called β-oxidation, to produce acetic acid. ATP is produced both during β-oxidation, and when the acetic acid is further metabolized in the Krebs cycle.

Amino acids that are not used in protein synthesis are used as energy sources. The first step in this process is the removal of the amino group (deamination) in the liver. The nitrogen is released as ammonia, which then is converted to urea by the urea cycle enzymes. Urea is secreted into the blood, and excreted in the urine. After deamination, the remainder of the amino acid molecule can be converted to intermediates of glycolysis or the Krebs cycle, and used for ATP production.

V. FACTORS INFLUENCING ENERGY REQUIREMENTS

Several factors influence the energy requirements of animals. These include productive function (growth, lactation, maintenance, etc.), age, sex, body size, and environment (temperature, humidity, air movement). The study of animal energetics was a leading aspect of animal nutrition in the first half of the twentieth century. Among the leaders in bioenergetics were Dr. Samuel Brody at the University of Missouri and Dr. Max Kleiber at the University of California. Since the 1950s bioenergetics has received less attention in nutrition research. In part this may be because the level of energy in the diet, within a fairly wide range, is not critical to animal performance, since voluntary feed intake is regulated according to energy need. Thus while we may list requirements for other nutrients as a percentage of the diet, there is not a comparable fixed requirement for the dietary energy level.

In the following discussion, it should be borne in mind that energy requirements, heat production of an animal, and voluntary feed intake follow similar trends, and generalizations made concerning one of these items apply to the others. Heat production is a measure of energy requirements, because the waste heat given off by an animal is a function of its total energy metabolism. The amount of feed consumed is regulated quite well by animals, so that they eat sufficient feed to meet their energy requirements. It is often said that animals eat to meet their energy needs. If they did not, there would be great variations in

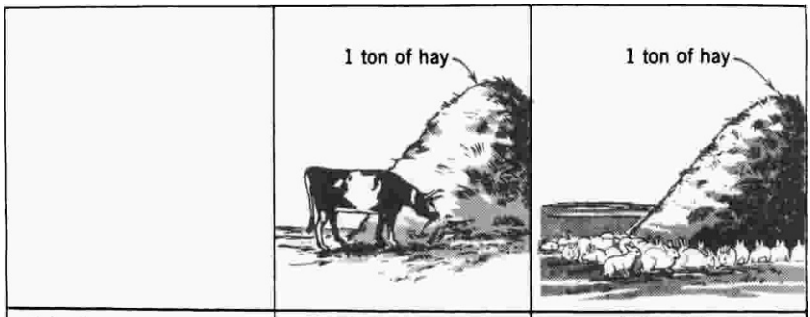
body weight on a daily basis, with energy being stored (as fat) or mobilized from body fat to maintain energy metabolism.

A. Body Size and Energy Requirements

The heat production and energy requirements of animals change with body weight. A pound of cow is not the same metabolically as a pound of rabbit. The smaller the animal, the greater its relative energy requirements. The smallest mammal, the shrew, weights about 1 g and eats about 1 g of feed per day. Shrews are voraciously hungry because they have to eat almost constantly to maintain their high rate of metabolism. If all animals had the same rate of metabolism, we could extrapolate and state that a 10-lb rabbit eats 10 lb of feed per day, a 150-lb man eats 150 pounds of food per day, and so on. We know that this is not true. Brody (1964), at the University of Missouri, studied the metabolic rate of animals ranging in size from a mouse to an elephant, and found that there is a relationship between heat production and body size. As the size increases, the metabolic rate per unit of body weight decreases. With a 100% increase in body weight, there is about a 75% increase in metabolic rate. This relationship is used to calculate "metabolic body size," which is $W^{0.75}$. The metabolic rate of different animals per $W^{0.75}$ is similar, so this unit can be used for comparing animal species of widely differing size. For example, a mouse and an elephant have a similar metabolic rate per unit of metabolic size, but a greatly different metabolic rate per unit (e.g., per gram) of weight.

Using these relationships, it is apparent that the relative feed intake of rabbits is greater than for sheep, and for sheep is greater than for cattle. It takes less feed to maintain 1000 lb of cow than to maintain 1000 lb of sheep, and it takes a lot more feed to maintain 1000 lb of rabbits. This has important implications in rabbit production. If rabbits require more feed per unit of weight than other livestock, can they be competitive as meat animals?

Kleiber (1961) posed this question, and answered it with Fig. 5.1. The higher relative feed requirements of rabbits are balanced by their more rapid growth rate. However, it is very important to appreciate the high relative maintenance costs for rabbits. If animals are being kept in a nonproductive state, it is much more expensive to keep rabbits than larger animals. One hundred 10-lb rabbits eat much more feed per day than does one 1000-lb cow. Thus, it is critical in commercial rabbit production that high productivity be maintained. Does should be kept in gestation and lactation. Palpation is necessary to ensure that does are pregnant. The high energy cost of maintenance for rabbits means that whenever a rabbit is just being kept, without being productive, it is very expensive to keep. One of the major problems in the rabbit industry is the lack of productivity (30 fryers per doe per year instead of 60), with the resultant inefficient utilization of feed because of the high feed intake per unit of body weight for maintenance.



Animals	1 steer	300 rabbits
Total body weight	1300 lb	1300 lb
Food consumption per day	16⅔ lb	66⅔ lb
Duration of 1 ton of food	120 days	30 days
Heat loss per day	20,000 kcal	80,000 kcal
Gain in weight per day	2 lb	8 lb
Gain from 1 ton of food	240 lb	240 lb

Fig. 5.1 The effect of body size on feed utilization. (From Kleiber, 1961; courtesy of John Wiley and Sons, Inc.)

B. Productive Function and Energy Requirements

The energy requirements of an animal are influenced by its state of production and productivity. The term basal metabolic rate (BMR) is used to describe the lowest rate of metabolism of an animal in a state of complete rest, in a thermoneutral environment, in a postabsorptive state. The work of Brody (1964) and Kleiber (1961) led to the following equation for estimation of BMR:

$$\text{BMR (kcal/day)} = 70.5\ W^{0.75}\ \text{kg}$$

Using this equation, the BMR of a 10-lb (4.54-kg) rabbit can be calculated:

$$\begin{aligned}\text{BMR} &= 70.5\ (4.54^{0.75}) \\ &= 70.5 \times 3.1 = 219\ \text{kcal/day}\end{aligned}$$

Thus, a 10-lb rabbit would require a minimum of 219 kcal energy intake per day for the basic energetic reactions involved in remaining alive. The BMR is useful primarily as a base or starting point for estimating energy requirements.

The maintenance metabolic rate (MMR) is the energy expenditure under conditions of no net weight gain or loss, under normal conditions of activity, environmental temperature, and so on. The maintenance requirements must be met before any productive functions are accomplished. The MMR is about twice the BMR. Partridge *et al.* (1983a) have estimated the maintenance requirement of New Zealand White does as about 96 kcal ME/kg $W^{0.75}$ or 300 kcal for a 10-lb rabbit. In another study, Partridge *et al.* (1986a) determined ME values of 79

kcal/kg $W^{0.75}$ for nonpregnant and pregnant does, and 114 kcal/kg $W^{0.75}$ for lactating and concurrently pregnant and lactating does.

The energy requirements for productive functions in rabbits have not been well defined. Lebas (1975) reported that 9.5 kcal of DE were required per gram of body weight gain. At levels below about 2500 kcal DE/kg diet, feed intake may not be adequate to provide sufficient DE intake for maximum gain. Reid *et al.* (1980) estimated the DE requirements of body tissue gains as 5.32 kcal/g for protein tissue and 9.76 kcal/g for fat. The maintenance requirement for 4- to 8-week-old New Zealand White fryers was estimated at 49 kcal/day by Reid *et al.* (1980). About 45% of the dietary DE was retained as carcass energy gain, whereas Dehalle (1981) reported energy retention as 25% of DE intake.

Daily energy intakes to support a high growth rate (45 g/day) are shown in Table 5.1. Pote *et al.* (1980) reported an average figure of about 350 kcal DE/day for the 4- to 8-week period. Lebas (1975), with rabbits over the period of 6–12 weeks of age, observed a daily DE intake of 400–430 kcal. The maintenance requirement as a percentage of the total energy requirement tends to increase with age, so the gain is energetically less efficient at higher body weights. This is a consequence of the slowing of the growth rate as mature weight is approached.

Energy requirements are greatest for lactation, and are estimated at three, four, or more times the maintenance requirement at peak lactation (Lang, 1981). Partridge *et al.* (1983) noted that does were in negative energy balance in lactation, with mobilization of body tissue. These authors estimated that a doe yielding 300 g of milk per day at peak lactation would have a daily ME requirement of 815 kcal for milk production, which along with a maintenance requirement of 277 kcal ME would give a total daily caloric requirement of 1092 kcal ME. With typical commercial diets of about 2300 kcal ME/kg, a feed intake of 475 g/day would be required to meet this requirement. This exceeds the feed intake capacity of a New Zealand White doe. The development of high-energy lactation diets for rabbits would appear to be warranted.

TABLE 5.1

Daily Energy Requirements of the Growing Meat Rabbit Gaining 45 g/day[a]

Live weight (kg)	Age (weeks)	Maintenance ME (kcal)	Production ME (kcal)	Total daily ME requirement (kcal)
1.0	6.0	151	139	290
1.5	7.5	191	167	358
2.0	9.0	229	194	423

[a] Adapted from Davidson and Spreadbury (1975).

Reproductive efficiency is influenced by daily energy intake. With livestock in general it is observed that conception rate is much higher in females that are gaining weight at the time of mating than in those that are in poor condition or losing weight. For this reason it is common with animals such as sheep to increase the energy intake of the females before breeding (this practice is known as "flushing"). It is likely that the high conception rate of rabbits mated 1–7 days postpartum is because the does are gaining weight at this time as a result of going from restricted feeding prepartum to *ad libitum* feeding postpartum. By about 10 days postpartum, milk production reaches a peak (see Chapter 17) and the does are in negative energy balance. In this period, until the litter is weaned, conception rate declines because the does are in negative energy balance. In simple terms, the hormonal system of the female depresses reproduction because a negative energy balance provides a "signal" that it is not a good time to reproduce. In the ancestral wild rabbits, a negative energy balance would occur with poor feed conditions, so reproduction would likely be unsuccessful. Domestic animals have retained this ecologically significant metabolic regulation. Thus, under intensive commercial rabbit production, the use of high-energy lactation diets to minimize negative energy balance may be a means of increasing reproductive efficiency. Raharjo *et al.* (1986) noted in does bred 1 day postpartum that doe weight declined with increasing number of parities, suggesting a continued decline in body condition because of the high energy requirements during lactation. High-energy diets would probably prevent this trend, and increase longevity of does in the breeding herd.

While the use of high-energy lactation diets appears to be beneficial, high-energy diets should not be fed to nonlactating pregnant does. If high-energy gestation diets are fed, does become obese and a high rate of kit mortality is observed (Cheeke, unpublished observations; Partridge *et al.*, 1986b). Partridge *et al.* (1986b) attributed the high neonatal mortality to increased kit birth weights and a buildup of fat deposits in the abdominal cavity of the doe, impeding movement of fetuses through the reproductive tract.

C. Environmental Temperature and Energy Requirements

Mammals produce heat as a waste product of energy metabolism, and have a physiological need to maintain a constant body temperature. Under warm conditions this necessitates efficient dissipation of heat, while in cold environments, metabolism must be increased to produce sufficient waste heat to maintain body temperature.

The environmental temperature at which there is minimum need for thermoregulation is called the thermoneutral zone or comfort zone. According to

Brody (1964), the zone of thermal neutrality for the rabbit is 21°–25°C (69°–77D°F). Above the comfort zone, special mechanisms must be brought into play to remove heat. These include sweating, panting, increasing the surface area, and dilation of the blood vessels at the body surface. In rabbits, rapid breathing, stretching out to increase body surface, and dilation of blood vessels in the ears are obvious responses to heat stress. Rapid breathing increases water evaporation from the lungs; water evaporation removes heat. Above the critical temperature, body temperature begins to rise, until death from heat stress occurs. In rabbits, pending death from heat stress is noted by very rapid breathing, bluish mucous membrances, and moisture exuding from the nose and mouth. Does near kindling are highly susceptible to heat stress. Animals can often be saved by plunging them into a bucket of cold water. Rabbits are very sensitive to heat stress. Their body temperature begins to rise at a lower environmental temperature than is true for other livestock like cattle. The two major routes of heat elimination are evaporation of water from the lungs, accounting for 20–40% of the heat loss, and radiation of heat from the body to the environment. This is faciliated by increasing the surface area by stretching out, and by the large surface area of the ears. The jackrabbit (a hare) has evolved very long ears and a large body surface area, adaptations that improve its ability to dissipate heat in its hot desert environment (Fig. 5.2).

As the environmental temperature decreases below the comfort zone, heat production must be increased to maintain body temperature and the loss of heat must be minimized. Heat loss is minimized by reducing the surface area (assuming a hunched posture with the legs under the body, etc.) and shunting the blood away from the body surface and extremities. Animals huddle together to reduce their collective surface area. Heat production is increased by changes in metabolism, induced by hormones such as thyroxine and epinephrine. Increased physical activity and shivering are other mechanisms of increasing muscle activity and heat production. The lower critical temperature is the point at which the animal can no longer maintain its body temperature, and death from cold follows.

The small body size of the rabbit compared to other livestock is a disadvantage in cold and hot environments. The smaller the body size, the greater the relative surface area. This is a disadvantage in cold environments, because of the greater heat loss. In hot environments, a small body has less "thermal inertia" than a large body. As an analogy, consider a large rock, and the same rock broken up into small pieces. In a hot environment, the small pieces will become hot much more rapidly than the intact rock. Similarly, a small animal gains heat more rapidly from the environment because of its large surface area, and the body temperature will rise more rapidly because there is less mass to heat than is the case with a large animal.



Fig. 5.2 The jackrabbit has anatomical features such as large ears and a large body surface area relative to body weight, which aid in the efficient dissipation of heat. (Courtesy of B. J. Verts, Oregon State University, Corvallis.)

D. Energy Toxicity

Almost all nutrients are toxic when consumed in excessive quantities. Long-term deleterious effects occur when excess calories are consumed, so the term "energy toxicity," while not commonly used, may be appropriate. The animal body has no mechanisms for excreting energy consumed in excess of requirements. Excess calories, whether consumed as carbohydrate or fat, are not excreted but rather are stored in adipose tissue as body fat. The net result of consumption of excess calories is obesity. In rabbits this may occur when nonpregnant or nonlactating adult animals are given unrestricted access to feed. For this reason it is necessary to restrict the feed of these animals (e.g., show rabbits) to keep them in desirable body condition.

There is a widespread misconception that high-energy diets are "hot" and cause animals to "burn out." For example, the following quotation is taken from a 1986 article in a rabbit magazine:

> To molt an animal, hot feeds should be given. This means that the feed is not temperature-wise hot, but that the ingredients of the feed heat the animal's body temperature causing the old fur to fall out. Barley is a hot feed and is what loosens the coat. Don't feed the barley for more than 10 days as you could burn out the animal. Sunflower seeds heat up the body and bring on a molt. Caution should be used however not to over-feed sunflower seeds as it will overheat the blood.

This statement is well-meant and offers some sound advice to rabbit raisers, but the rationale is incorrect. Barley and sunflower seeds do not heat up the animal and "overheat the blood" causing the hair to fall out. As discussed in Chapter 17, the hair growth cycle is responsive to energy intake. The period of time from the formation of hair in the hair follicle until it has reached maturity and falls out (sheds), known as the anagen, catagen, and telogen phases, is the hair growth cycle. Restricted feeding, thus restricted energy intake, prolongs the length of this cycle and the period in which the coat is in "prime" condition. As the caloric intake increases, the turnover rate of hair is faster. Thus it is difficult to keep the coat of a full-fed rabbit in prime condition because of the rapid growth and shedding of hair. Barley, being a high-energy (for rabbits) ingredient, thus stimulates the fur growth cycle and minimizes the prime period. The same is true for sunflower seeds. Thus, the advice to "go easy" on the barley and sunflower seeds is sound. However, the explanation that the animals will "burn out" if this advice is not followed is irrational. If the term *burn out* has any validity at all, it is in reference to a low-energy diet which cannot support adequate production. For example, a doe fed a low-energy diet cannot consume enough energy to support lactation, and so she will use body fat as an energy source. This will cause her to become thin, lose body condition, become emaciated, and burn out. It is not because she is being fed a "hot feed" but because she is starving and is able to provide milk for her litter only by metabolizing her own tissues. Thus, the terms *burn out* and *hot feed* have no scientific validity and serve only to cause confusion.

To summarize, the consumption of excess energy by rabbits will shorten the hair growth cycle, will cause obesity, and will adversely affect reproductive performance. Because of the high-energy requirements for growth and lactation, it is difficult to overfeed calories to rapidly growing fryers and lactating does. Alternatively, it is readily possible to provide replacement (junior) does and nonlactating does with excess energy, resulting in obesity and subsequent poor reproductive performance. The feed intake of these animals should be restricted to maintain the desired body condition.

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6

Carbohydrates and Fiber

I. CLASSIFICATION OF CARBOHYDRATES

Carbohydrates are substances in plant tissue arising from the products of photosynthesis. The simple sugars, such as glucose, fructose, and ribose, are the basic unit of carbohydrate structure. Some of the more important carbohydrates in nutrition will be briefly described.

A. Simple Sugars (Monosaccharides)

These commonly contain five (pentose) or six (hectose) carbon atoms. Glucose and fructose are hexoses, while ribose is a pentose. Glucose is the major carbohydrate in animal metabolism. It is the carbohydrate that is referred to in the term "blood sugar." Glucose is synthesized by plants from carbon dioxide and water in the process of photosynthesis:

$$6CO_2 + 6H_2O + \text{solar energy} \rightarrow C_6H_{12}O_6 + 6O_2$$

Photosynthesis occurs in the chloroplasts, where the chlorophyll traps solar energy from sunshine to form ATP. Other carbohydrates and the carbon-containing portion of amino acids and fats are synthesized by plants from glucose. The formation of glucose in photosynthesis provides the basic "fuel" for all forms of higher life.

Another simple sugar is fructose. It occurs in honey, and along with glucose is a consistuent of table sugar. Ribose, a five-carbon sugar, is found in RNA and DNA (as deoxyribose).

B. Disaccharides

These contain two simple sugars. The most widely known is sucrose, or table sugar, consisting of glucose and fructose joined together.

C. Polysaccharides (Complex Carbohydrates)

These contain a large number of simple sugars joined together. They make up the major part of the carbohydrates in plant tissue. An important polysaccharide

is starch, a storage carbohydrate or energy reserve in plant seeds and tubers. Starch consists of a large number of glucose molecules joined together, either in a straight chain (amylose) or in a branched structure (amylopectin). The cereal grains (wheat, corn, barley, milo, oats) are major sources of starch, as are tubers such as potatoes and cassava. The Jerusalem artichoke is unusual in that the tubers contain inulin, a storage polysaccharide made up of fructose units joined together as glucose is in starch. Forages also contain fructosans, or polymers of fructose.

The other major types of polysaccharides are those that make up plant fiber. These are mainly cellulose and hemicellulose. Cellulose consists of glucose units joined together, as in starch. However, the chemical bond joining the glucoses is different in cellulose and starch. This seemingly simple difference has profound nutritional implications, because no animal produces the enzyme cellulase, which breaks the bonds in cellulose. As a result, animals can only use cellulose as an energy source if their digestive tract is inhabited by bacteria that produce cellulase (celluloytic bacteria).

Hemicelluloses contain a variety of simple sugars, including xylose, arabinose, and glucuronic acid. Common types of hemicellulose include xylans (containing xylose,) β-glucans (containing polymerized β-glucose), and a variety of pentosans (containing mixtures of pentoses). The hemicelluloses tend to have a higher digestibility in most animals than cellulose. Pectins are similar in structure to hemicelluloses, and serve in plant tissue as the "glue" cementing plant cells together.

A significant but often overlooked source of carbohydrate is the mucopolysaccharides secreted into the gut as mucus. Goblet cells in the intestinal and cecal mucosa secrete large quantities of mucus, especially in rabbits affected by mucoid enteritis. Secretion of mucus into the digestive tract provides lubrication for passage of ingesta and protects the mucosa from damage. The mucopolysaccharides are digested in the hindgut by bacteria.

Although plant fiber consists mainly of carbohydrate, rabbit raisers tend to refer to carbohydrates and fiber as two distinct entities, whereas fiber is in fact just one type of carbohydrate. It is convenient in rabbit nutrition to distinguish two categories: readily available carbohydrates (sugars, starch, hemicellulose) and fiber (cellulose and lignin). These will be discussed separately.

II. READILY AVAILABLE CARBOHYDRATES IN RABBIT NUTRITION

The main carbohydrate of concern in this group is starch, which is the major component of cereal grains. Corn, milo, and wheat have the highest starch content of common cereal grains (Table 6.1), while oats and barley are lower in

TABLE 6.1

Carbohydrate Composition of Cereal Grains[a]

Item (%)	Grain				
	Corn	Milo	Wheat	Barley	Oats
Crude fiber	2.5	2.7	2.1	6.3	12.2
NFE[b]	81	80	83	76	67
Total sugars	1.9	1.5	4.1	2.5	1.5
Starch	72	71	67	65	41

[a] Adapted from Church (1986).

[b] NFE, Nitrogen-free extract, a measure of the total readily available carbohydrate.

starch and have a higher content of pentosans and cellulose. Starch is aggragated into starch granules, which in some cases (e.g., potato starch) are resistant to digestion. Moist heating causes a rupture of starch granules and a change in crystal structure of the starch (gelatinization). This process improves starch utilization by animals. Starch is important in rabbit nutrition because it provides energy, and on the negative side, may be involved in provoking enteric diseases.

Other readily available carbohydrates important in rabbit nutrition are sucrose and hemicelluloses. Sucrose occurs in rabbit feed mainly as a component of molasses, a by-product of sugar refining. Sucrose and molasses are highly palatable to rabbits, and they increase diet acceptability. Molasses is also useful in reducing dustiness and fines, and improving pellet quality. Hemicellulose is a component of forages and grain by-products such as wheat bran and wheat mill run. Lactose (milk sugar) is the main carbohydrate of animal origin, and is a major constituent of milk. Rabbit milk has an unusually low lactose content.

III. DIGESTION OF CARBOHYDRATES

A. Foregut

Carbohydrates are absorbed in the form of simple sugars such as glucose. Carbohydrate digestion involves the degradation of complex carbohydrates into the simple sugars of which they are composed.

Digestive enzymes are secreted by the pancreas gland into the small intestine, and also by cells in the intestinal mucosa. Some of the enzymes involved in carbohydrate digestion are listed here:

Carbohydrate	Enzyme	End product of digestion
Starch	Amylase	Glucose
Sucrose	Sucrase	Glucose and fructose
Lactose	Lactase	Glucose and galactose

The activity of most carbohydrate-digesting enzymes is low in newborn animals, with the exception of lactase activity, which is highest in the neonatal period. Alus and Edwards (1976) studied the development of digestive enzyme secretion in the rabbit from birth to weaning. Examination of stomach contents revealed total dependence on milk up to day 10, consumption of a small amount (about 5% of total intake) of solid feed by day 15, and by day 20, coprophagy was taking place and solid feed constituted the major portion of feed intake. From days 25 to 30, only traces of milk were consumed and coprophagy was fully developed. From days 20 to 30, the levels of intestinal sucrase and maltase increased by 27- and 14-fold, respectively. Lactase decreased gradually from birth to 30 days. Pancreatic amylase increased slowly from birth to 15 days, and then increased by over 60-fold in the next 15 days. Thus the ability to digest carbohydrates in feeds changed in parallel with the change in diet from milk to solid feed (Fig. 6.1).

Catala and Bonnafaus (1979) studied the secretion of amylase in rabbits. Maximum amylase activity was observed in the duodenum, with weak (3% of duodenal activity) activity in the lower tract. Activity in the duodenum was 392

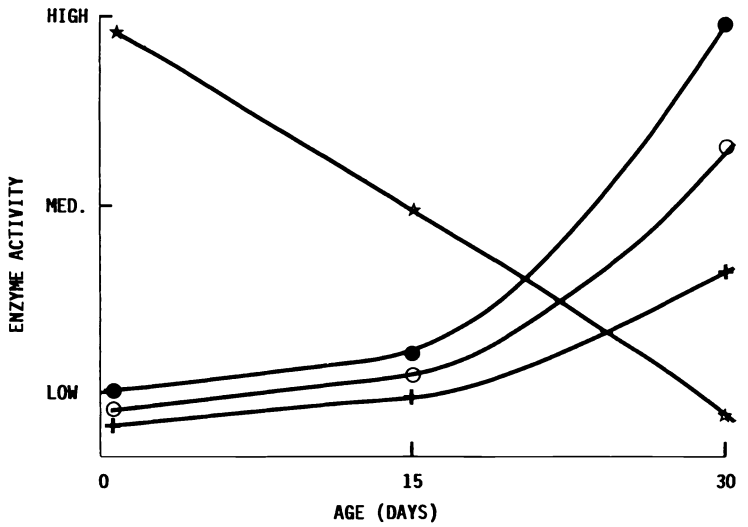


Fig. 6.1 Changes in activity of carbohydrate-digesting enzymes with age in the young rabbit. Lactase (☆); amylase (●); sucrase (○); maltase (+).

μmol maltose produced per gram per minute. Wolter *et al.* (1980) studied the digestibility of starch in various parts of the digestive tract of rabbits. The cumulative percentage digestibility of starch was as follows: stomach, 31%; small intestine, 82%; cecum, 86%; colon, 92%; feces, 97%. In other words, 82% of the starch was digested by the time digestive contents had passed through the small intestine, while 97% had been digested at the point of fecal excretion. Unfortunately, the source of starch used in this study was not specified.

Cheeke and Patton (1980) proposed that with diets high in starch, carbohydrate overload of the hindgut may occur, provoking enteritis. The results of Wolter *et al.* (1980) do not seem to support this hypothesis. However, the rate of passage of digesta through the small intestine could be a factor, and in conditions that precede enteritis, it is possible that passage rate through the small intestine may be rapid, leading to incomplete duodenal digestion of starch. It is also likely that the passage of 18% of the ingested starch to the hindgut could be sufficient to cause carbohydrate overload. In other nonruminant animals, such as swine, the digestibility of starch in the small intestine appears to be higher than in rabbits. Cunningham *et al.* (1963) observed that 96% of ingested corn starch was digested prior to the terminal end of the small intestine in pigs.

The source of starch may influence the site and extent of its digestibility. The digestibility of starch is influenced by its composition and physical form, protein–starch interactions, the cellular integrity of the starch granules, antinutritional factors (e.g., tannins, amylase inhibitors), and the physical form of the ingredient. In general, cereal starches are more readily digested than root and tuber starches, while legume starches (e.g., beans, lupines, peas) have intermediate digestibility. Starch granules can be imbedded in a protein matrix in the endosperm, reducing their digestibility. This is especially true of corn and sorghum starch. Gelatinized starches may form complexes with proteins that reduce the digestibility of both starch and protein.

Little work has been conducted with rabbits to evaluate digestion of starch from different cereal grains. Although it is not well documented with research data, it appears that corn (maize) may tend to provoke enterotoxemia in rabbits, by promoting carbohydrate overload of the hindgut (see Chapter 12). A proposed mechanism to account for this effect is that corn starch (that in grain, not isolated corn starch) may be digested more slowly in the small intestine than starches from other grains, resulting in a higher percentage of corn starch reaching the hindgut than is the case with other grains such as oats and barley. This, coupled with the higher starch content of corn as compared to other grains (Table 6.1), would provide a greater pool of starch in the cecum to serve as a substrate for bacterial growth, leading to a proliferation of starch-digesting bacteria, and a high level of acid production. This in turn may lead to a shift in microbial populations, with growth of pathogens such as *Escherichia coli* and *Clostridium* spp. (see Chapter 12). In ruminant animals, starch in corn is less rapidly fer-

mented in the rumen than starch from other cereal grains (Orskov, 1986), supporting the suggestion that corn starch may be less degradable than starch from other grain sources. Further studies with rabbits would be desirable, to compare starch digestibility in the small intestine and cecum for various grains. Assuming that starch from corn is more likely than starch from other sources to cause carbohydrate overload of the hindgut in rabbits, processing methods such as steam rolling, popping, and extrusion should be beneficial in allowing a use of higher dietary levels of corn without inducing enteritis. The digestibility of starch is improved by cooking. Lee *et al.* (1985) studied the *in vitro* digestibility of various raw and cooked starches using rabbit amylase, and *in vivo* response in New Zealand White rabbits as assessed by blood glucose and insulin levels. The hydrolysis of starch was markedly increased by cooking. Serum glucose and insulin levels were increased when cooked starches were fed, whereas raw starch caused no elevation, suggesting more rapid digestion with the cooked starch. These results suggest that feed processing procedures involving heat treatment might be effective in increasing starch digestion in the small intestine of the rabbit, thus avoiding carbohydrate overload of the hindgut.

B. Cecal Fermentation

In ruminant animals, volatile fatty acids (VFA) produced as end products of microbial fermentation in the rumen are absorbed across the rumen wall into the portal blood, and constitute the primary absorbed energy source. On diets high in fiber, acetic acid is the major VFA produced in the rumen, while on high-concentrate diets, propionic acid production is increased. Butyric acid generally is produced only in small quantities of about 5–10% of total VFA. Butyrate is metabolized during absorption to ketone bodies and β-hydroxybutryate in ruminants.

The VFA are also produced as end products of bacterial fermentation in the rabbit cecum. Use of VFA as a source of energy has been estimated to provide 12% (Hoover and Heitmann, 1972), 30% (Parker, 1976), and 40% (Marty and Vernay, 1984) of the maintenance energy requirements. Marty and Vernay (1984) demonstrated that VFA are a major energy source for metabolism of the hindgut tissues. Because of the use of energy-requiring reactions in the absorption of electrolytes and other nutrients in the rabbit colon, considerable energy is needed by hindgut tissues. Butyric acid (butyrate) is the preferred fuel for hindgut metabolism, followed by propionate and acetate.

The production and blood distribution of VFA are different in rabbits than in ruminants. In contrast to ruminants, in which butyric acid is produced in much lower quantity than acetate and propionate, in the rabbit butyric acid is usually produced in considerably higher quantities than propionic acid (Table 6.2). This is probably a reflection of the unusual microbial population of the rabbit cecum,

TABLE 6.2

Proportion of VFA in Cecal Contents of the Rabbit

Diet	References	Proportion of total VFA (%)		
		Acetate	Propionate	Butyrate
Low fiber	Pote *et al.* (1980)	65	10	25
Medium fiber		69	9	22
High fiber		69	12	19
Low fiber	Hoover and Heitmann (1972)	78	9	13
High fiber		84	8	8
Low fiber	Morisse *et al.* (1985)	70	7	23
Medium fiber		73	7	20
High fiber		72	18	10
Commercial type	Wolter *et al.* (1980)	69	12	19
Unspecified	Vernay and Raynaud (1975)	73	7	20
3% Crude fiber	Champe and Maurice (1983)[a]	71.4	13.3	9.7
6% Crude fiber		72.7	11.7	9.5
9% Crude fiber		72.2	9.5	13.6
12% Crude fiber		69.2	9.9	17.1

[a] Isobutyrate, isovalerate, and valerate were included in the total VFA content.

dominated by *Bacteroides* species, which often are butyrate-producing organisms (Vernay and Marty, 1984). Lactobacilli, which are propionate producers, are negligible in the rabbit cecum. Thus the unusual pattern of VFA production in rabbits is probably a consequence of the unusual bacterial flora.

Vernay *et al.* (1984) and Vernay (1986a) studied the absorption of electrolytes and VFA in the rabbit hindgut. During the excretion of cecotropes, the rabbit colon conserves water, sodium, and chloride and secretes potassium. During the excretion of hard feces, secretion of water and bicarbonate occurs in the proximal colon and absorption of water, VFA, sodium, potassium, and chloride occurs in the rest of the colon. By this mechanism, the excretion in the hard feces of substances with nutritional value is minimized. The adrenal hormone aldosterone plays a role in these processes by stimulating fluid secretion in the proximal colon and increasing the rate of fluid absorption in the other colon segments.

In the rumen epithelium, butyrate is more than 80% metabolized to ketone bodies, whereas in the rabbit cecal-colonic tissue, only negligible amounts of ketone bodies are produced (Vernay and Marty, 1984). As previously mentioned, butyrate is the major substrate of energy metabolism in the hindgut tissue, as it is for the rumen wall of ruminants. In ruminants, diets that reduce rumen butyrate production lead to greater digestive problems, such as rumen

wall abscesses and clumping of papillae. As discussed in Chapter 12, low cecal butyrate levels may be associated with enteritis in rabbits. Propionate and butyrate are efficiently removed from the portal blood during its passage through the liver, so acetate is the main VFA in the peripheral circulation. Propionate is metabolized by the methylmalonate pathway in the liver, producing succinyl CoA, a constituent of the citric acid cycle. Acetate is principally used for fatty acid synthesis in liver tissue, and is metabolized in peripheral tissues to CO_2 (Vernay and Marty, 1984).

Lactic acid is rapidly metabolized in the cecum of the rabbit to acetate and possibly propionate (Parker and Mould, 1976). Lactate found in the blood arises primarily from fermentation in the stomach (Vernay, 1986b). Griffiths and Davis (1963) demonstrated that lactic acid production in the stomach occurs in the cecotropes or soft feces. The cecotropes are surrounded by a mucilaginous membrane that remains intact for at least 6 hr after the soft feces are consumed. The cecotropes contain bacteria that continue to grow and ferment starch, producing lactic acid as an end product. The cecotropes have sufficient buffering capacity to maintain the pH at about 6.0, even though the external medium of the stomach is highly acidic. The D(−)-lactate isomer is produced in greater quantities than the L(+)-lactic acid.

Griffith and Davies (1963) observed that bacteria within intact cecotropes in the stomach excrete amylase into the stomach lumen. The bacterial amylase was adapted to acid conditions, retaining 88% of its activity at pH 5.0, whereas salivary amylase was only 30% active at that pH. During fermentation within the cecotropes, phosphate is released from the soft feces, increasing the pH of the stomach (Griffiths and Davies, 1963). This explains the observation of Alexander and Chowdhury (1958) that fermentation within the rabbit stomach producing lactic acid results in an increase in the stomach pH.

The production of VFA is greater when high-starch diets are fed as compared to diets high in cell wall constituents (Pote *et al.*, 1980; Morisse *et al.*, 1985), as shown in Table 6.3. In the work of Morisse *et al.* (1985), the *Bacteroides* population was greatest on the 18.5% starch diet, which on a percentage of total VFA basis had the lowest butyrate production. This is inconsistent with the suggestion of Vernay and Marty (1984) that *Bacteroides* are the major source of butyrate.

Champe and Maurice (1983) noted that with increasing dietary crude fiber, the butyrate/propionate ratio increased, so that as fiber level increased, the proportion of butyric acid produced was higher. The higher cecal butyrate levels could help to explain the protective effect of fiber against enteritis (see Chapter 12). However, most other reports (see Table 6.2) indicate that the proportion of butyrate is decreased with high-fiber diets. Champe and Maurice (1983) also measured the five-carbon VFA, valeric acid, and the branched-chain VFA, iso-

TABLE 6.3

Effect of Diet on Cecal VFA Production in Rabbit

Diet	References	Acetate	Propionate	Butyrate	Total VFA
High starch	Pote *et al.* (1980)[a]	36.3	5.7	13.6	55.6
High fiber		24.0	4.3	6.3	34.6
18% Starch, 17% crude fiber	Morisse *et al.* (1985)[b]	24.7	6.2	3.3	34.2
20% Starch, 14% crude fiber		61.3	5.8	16.6	83.7
35% Starch, 10% crude fiber		52.4	5.2	17.3	74.9

[a] μmol/ml.
[b] mmol/kg.

butyrate and isovalerate. Isobutyrate was 2–3% of total VFA, while valerate and isovalerate were each about 1.5% of the total.

Morisse *et al.* (1985) suggested that the higher VFA production on low-fiber, high soluble carbohydrate diets helps to prevent growth of pathogenic microbes involved in enteritis by maintaining an acid cecum (pH 5.8–6.0). They also suggested that toxin production by toxigenic *Clostridia* species only occurs when the cecal pH is less acid than normal. Rolfe (1984) observed that cecal VFA, and particularly butyric acid, reduces the colonization of the hamster gut by *Clostridium difficile*. The effect of VFA and butyrate on *Clostridium spiroforme*, the main organism responsible for enterotoxemia in rabbits, should be determined.

Mucopolysaccharides are secreted into the small intestine, cecum, and colon from goblet cells in the mucosa. The cecotropes are surrounded by a mucilaginous layer of these compounds; thus mucopolysaccharides are consumed via cecotrophy. Digestion of mucus is accomplished by bacterial activity, with the mucus serving as a significant carbohydrate source for cecal fermentation. *Bacteroides* spp., a major type of cecal microbe in rabbits, ferment mucopolysaccharides (Salyers *et al.*, 1977).

Dehalle (1981) examined the effect of diet composition on the weights of different parts of the digestive tract, using two high-energy and two low-energy diets (Table 6.4). The two high-energy diets contained 23 and 29% cornstarch and 5.0 and 4.5% wheat straw, whereas the low energy diets had 18 and 14% corn starch and 20.5 and 20% wheat straw. The weights of the stomach tissue and stomach contents were higher on the high-fiber diets, whereas the cecal weight was greater on the high-starch diets (Table 6.4). This demonstrates the importance of the cecum in fermentation of soluble carbohydrates. Thus, in contrast to what might be expected, a low-fiber diet results in a greater cecal size than does a high-fiber diet. Champe and Maurice (1983) and de Blas *et al.* (1986)

TABLE 6.4

Effect of Diet on Weight of the Digestive Tract Contents[a]

Results	Diet[b]			
	1	2	3	4
Slaughter weight (g)	2036	2083	1974	2029
Empty stomach (g)	22.3[c]*	22.6*	19.3**	19.6**
Stomach contents (g)	72.0*	69.1*	53.7**	54.9**
Empty cecum (g)	29.3*	30.4*	38.1**	34.7**
Cecal contents (g)	96.3	96.5	105.1	103.0
Empty stomach (as % of empty cecum)	78.2*	76.2*	56.9**	57.9**
Stomach (as % body weight)	1.1	1.1	1.0	1.0
Cecum (as % body weight)	1.4	1.5	1.9	1.7

[a] From Dehalle (1981).

[b] Diet 1, low energy (2280 kcal DE/kg), low digestible protein (11.5%); diet 2, low energy (2240 kcal DE/kg), high digestible protein (12.8%); diet 3, high energy (2610 kcal DE/kg), low digestible protein (12.7%); diet 4, high energy (2670 kcal DE/kg), high digestible protein (14.2%). *Note:* Low and high digestible protein are with respect to dietary energy level (i.e., low and high protein/kilocalorie ratios).

[c] *Different from ** ($p < 0.05$).

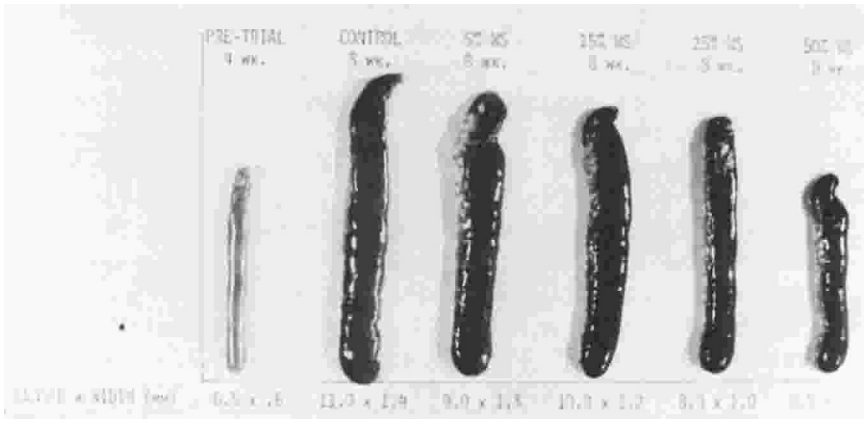


Fig. 6.2 The addition of wheat straw (WS) to a low-fiber diet (control) reduced the size of the cecal appendix. The appendix is a lymphoid organ, and its enlargement on a low-fiber diet suggests a greater production of bacterial toxins with this type of diet. Another possible explanation for the enlargement of the appendix is that it secretes bicarbonate ions, which may buffer VFA in the cecum (see Chapter 3). (Courtesy of W. A. Schurg, University of Arizona, Tucson.)

observed similar trends, with cecal enlargement on low-fiber diets. The cecal enlargement is probably the result of hypomotility with low-fiber diets, and while it may facilitate fermentation, it also predisposes the animal to diarrhea. The higher weight of the stomach in the animals fed the high-fiber diets may reflect the greater feed intake on the low-energy diets, and the physical effect of fiber in stimulating an increased thickness of the stomach wall.

Schurg and Reid (1979) reported that feeding high levels of wheat straw (25 and 50%) reduced the size of the cecal appendix, and the appendix was virtually empty (Fig. 6.2). In contrast, rabbits fed low-straw, high-grain sorghum (low-fiber, high-starch) diets had enlarged appendices, containing large amounts of ingesta. The appendix is a lymphoid organ, and may play a role in immunity to toxins. These observations support the postulated role of high-starch diets in promoting production of bacterial toxins (see Chapter 12).

IV. FIBER IN RABBIT NUTRITION

As discussed in Chapter 3, the digestive strategy of rabbits involves the selective retention of small particles in the cecum, and the rapid excretion of larger particle sizes, mainly fiber, in the feces. It is an apparent contradiction that rabbits are herbivorous, forage-consuming animals and yet digest fiber very inefficiently. However, as previously discussed, this apparent anomaly is in fact an effective digestive strategy for the efficient use of roughages.

A. Chemical Nature of Fiber

Fiber is a very broad term, encompassing the structural components of plant tissue. Its chemical composition varies according to the specific plant material involved. The fiber of forages consists mainly of cellulose, hemicellulose, and lignin, which make up the cell walls of plant tissue. Lignin is an indigestible phenolic compound found in association with cellulose. These two compounds, often referred to as lignocellulose, provide structural rigidity to plant tissue, and the content increases as the plant matures. With increasing maturity, the percentage of lignin increases (lignification), resulting in decreasing digestibility of fiber with increasing plant maturity. Straw, the residue of mature forages and grains, has a very low feeding value because of its high degree of lignification. Pectins and hemicelluloses are involved in cementing the cell wall and "gluing" plant cells together.

For many years, the major method of fiber analysis was the determination of crude fiber. Crude fiber is still used on feed tags in the United States, as the legal measure of fiber content. However, it is widely recognized that the crude fiber determination does not accurately measure fiber. The crude fiber fraction as

measured in the laboratory does not contain all of the plant fiber, and contains nonfiber components. For this reason, other methods of fiber analysis have been developed. The most widely accepted, particularly for forage analysis, is the fiber analysis scheme developed by P. J. Van Soest of Cornell University. This system measures acid detergent fiber (ADF) and neutral detergent fiber (NDF). The ADF consists primarily of cellulose and lignin, while NDF also includes hemicellulose. Hemicellulose is estimated as the difference between ADF and NDF.

In rabbit nutrition, the main interest in fiber is related to its apparent role in protecting against enteritis. For this role, indigestible fiber seems to be involved. The best measure of indigestible fiber is ADF, or the indigestible lignicellulose complex. There is not, unfortunately, a good correlation between ADF and crude fiber for feeds in general, although within a feed category (e.g., alfalfa meal) there is a better correlation. The crude fiber content of alfalfa hay is about 9 units less than the ADF (e.g., 34% ADF is equivalent to about 25% crude fiber).

B. Fiber Digestibility in Rabbits

Voris *et al.* (1940) noted that "the digestibility of the crude fiber fraction of forages is remarkably low. This observation is not new, having been made by Von Knieriem as early as 1898. . . ." Data in Table 6.5 further illustrate the general low digestibility of fiber in rabbits.

As discussed in Chapter 3, the muscular activity of the hindgut propels fiber rapidly through the colon, while nonfiber components are moved in a retrograde manner by reverse peristalsis into the cecum for fermentation. The digestibility

TABLE 6.5

Comparison of Digestibility of Whole-Plant Corn Pellets in Rabbits and Horses[a]

Pellet component	Apparent digestibility (%)	
	Rabbits	Horses
Dry matter	47	70
Crude protein	80	53
ADF	25	48
NDF	37	69
Ether extract	94	99
Ash	36	31
Gross energy	49	80

[a] Adapted from Schurg *et al.* (1977).

TABLE 6.6

Bulk Density, Water-Absorbing Capacity, and Swelling Capacity of Common Feedstuffs

Feed	Bulk density (g/100 ml)	Water absorbed (ml/100 g)	Increase in volume when saturated with water (%)
Alfalfa meal	53	630	160
Beet pulp	61	870	380
Canola meal	56	280	60
Corn	62	180	20
Ground barley	60	340	100
Oats	42	240	20
Rice hulls	45	260	40
Soybean meal	70	400	200
Wheat mill run	48	380	120

coefficients for crude fiber vary considerably depending on the feedstuffs involved. Feeds high in cellulose and lignin (alfalfa meal, grass meal) generally have a crude fiber digestibility of less than 15% in rabbits, whereas for nonlignified material (e.g., beet pulp), crude fiber digestibility can be as high as 60% (Maertens and DeGroote, 1984; Voris *et al.*, 1940). The digestibility of crude fiber of grain milling by-products such as rice bran and wheat mill run is quite high, giving these products a higher DE for rabbits than for swine and poultry.

Processing procedures can influence fiber digestibility. A number of studies have shown that alkali treatment of straw and other low-quality roughages increases fiber digestibility in rabbits. Alkali treatment dissolves lignin, providing greater access to cellulose by bacterial cellulases. Alkali treatment might also promote greater degradation of fibrous feeds to small particles during mastication, increasing their retention in the cecum. Grinding of feeds to reduce the particle size results in an increased cecal retention time (Laplace and Lebas, 1977). Reduction of the fiber particle size by grinding would increase the amount of fiber retained in the cecum and subjected to bacterial digestion. However, this process may interfere with the protective effect of fiber against enteritis.

Other factors associated with fiber that may influence its utilization include bulk density and swelling capacity. Some feedstuffs, such as alfalfa meal and beet pulp, absorb large amounts of water and swell to several times their original volume (Table 6.6). Other feeds, such as cereal grains and rice hulls, have very little swelling capacity (Fig. 10.1). It is plausible that feeds of the same fiber and energy contents, but differing in bulk density and swelling capacity, could have different transit rates through the digestive tract, and differentially affect feed

intake through swelling effects on stomach capacity. Kellems and Church (1981) demonstrated that the consumption of isocaloric diets by cattle was increased when the feed density was increased. This aspect of fibrous feeds warrants investigation in rabbits.

There are pronounced differences in the digestibilities of tropical legumes and grasses in rabbits. Akin (1979) has noted that tropical grasses are of low nutritional value to ruminants, because of their cellular structure. They have a high content of poorly digested components such as vascular tissue, parenchyma bundle sheaths, and epidermis, and a low content of the highly digestible mesophyll cells. Raharjo *et al.* (1986) have reported that the digestibility of the protein, fiber, and energy of some tropical grasses is very low in rabbits. Cheeke *et al.* (1985) found that the degradation in the rabbit of the cellular structure of a temperate grass, orchard grass, was less complete than for legumes, suggesting that grass fiber may be less digestible than legume fiber.

Cecotrophy does not appear to have a major influence on fiber digestion (Table 6.7), as might be expected, since the cecal contents are selectively enriched in the nonfiber components of the digesta.

Uden and Van Soest (1982) compared the utilization of the fiber in timothy hay among a number of herbivorous animals. These data (Table 6.8) confirm the very low digestibility of grass fiber in the rabbit. Since the dry matter digestibility was similar among the various animals, rabbits must have used the nonfiber components of the grass very efficiently.

There appear to be breed differences in ability to utilize high-fiber diets. Grobner *et al.* (1985) compared digestibility of low, medium, and high-fiber diets in breeds varying in size from the Netherland Dwarf to the Flemish Giant (Table 6.9). The ADF digestibility of the high-fiber diet was lowest in the dwarfs, and highest in the Flemish Giants. It is likely that in a large breed the gut

TABLE 6.7

Effect of Cecotrophy (Coprophagy) on Fiber Utilization

Diet	Coprophagy[a]	Digestibility (%)		References
		DM	ADF	
High-alfalfa pellets	+	48.3	13.1	Robinson *et al.* (1985)
High-alfalfa pellets	−	45.3	14.2	
Fresh grass	+	49.8	20.4	Robinson *et al.* (1985)
Fresh grass	−	52.6	8.7	
Laboratory diet	+	60.8	15.7	Stephens (1976)
Laboratory diet	−	58.2	12.1	

[a] +, Coprophagy permitted; −, coprophagy prevented.

TABLE 6.8

Comparison of Fiber Digestibility of Timothy Hay in Several Herbivores[a]

Species	Digestibility[b] (%)				
	NDF	C	HC	L	DM
Cattle	51	53	57	21	52
Goats	44	46	49	19	49
Sheep	44	46	49	15	48
Ponies	37	37	42	21	45
Horses	33	33	40	11	42
Large rabbits (+)[c]	7	4	11	6	52
Large rabbits (−)	9	7	13	6	51
Small rabbits (+)	11	10	12	14	53
Small rabbits (−)	11	9	13	10	52

[a] Adapted from Uden and Van Soest (1982).

[b] NDF, Neutral detergent fiber; C, cellulose; HC, hemicellulose; L, lignin; DM, dry matter.

[c] (+), Coprophagy allowed; (−), coprophagy prevented. Large rabbits, Flemish Giant; small rabbits, Dutch.

capacity and digesta retention time are more favorable for fiber digestion than in a small animal. Uden and Van Soest (1982) did not observe differences in fiber digestibility between Dutch and Flemish Giants (Table 6.8).

C. Effect of Fiber on Growth

Growth rate is reduced when fryer rabbits are fed a low-fiber diet (Champe and Maurice, 1983; Cheeke and Patton, 1978; de Blas *et al.*, 1986; Lebas and

TABLE 6.9

Percentage Digestibility of Acid Detergent Fiber (ADF) in Rabbits of Different Breeds[a]

Breed	Body weight (g)	ADF in diet (%)		
		29	19	15
Netherland Dwarf	1200	13.9	18.0	15.5
Mini Lop	3400	19.5	27.8	16.2
New Zealand White	4900	16.5	18.0	14.3
Flemish Giant	6900	23.1	25.2	15.1

[a] From Grobner *et al.* (1985).

Laplace, 1977; Pote *et al.*, 1980). Typical effects of the addition of a fiber source such as alfalfa meal to a cereal-based diet are shown in Table 6.10. The diet giving the poorest growth rate was a corn–soybean meal diet of the type expected to give the maximum performance when fed to chicks and pigs. Rabbits, in contrast, do not do well on high-energy diets.

DeBlas *et al.* (1986) studied the effects of variable dietary levels of crude fiber and starch on growth and enteritis incidence of fryer rabbits. They determined that the growth rate was optimal in the range of 10–15% dietary crude fiber (corresponding to 13–25% ADF), while a high diarrhea incidence was observed with a crude fiber level below 10% (dietary starch level of 30%). Hypomotility of the hindgut was indicated on the low-fiber diets by an increase in cecal weight, and low cecotrope levels in the stomach (indicative of a reduced clearance of cecal contents via cecotrophy). Digestibility of nutrients was highest with the low-fiber diets, probably because of prolonged cecal retention times.

There are several possible explanations for the low growth rate of rabbits fed a high-energy, low-fiber diet. Laplace and Lebas (1977) observed that finely ground feed increased the retention time of digesta in the cecum, decreasing the dry matter intake. They further reported that highly digestible diets are consumed in lower quantities and retained in the digestive tract longer than high-fiber diets. Laplace (1978) noted that a prolonged retention time of feed in the digestive tract is a precursory sign of diarrhea, which tends to be preceded by cecal-colonic hypomotility. He concluded that attempts to improve the efficiency of feed utilization by lengthening the retention time in the cecum through fine grinding are generally unsuccessful. Any disturbance of the normal rhythms of feed intake and fecal excretion patterns are generally deleterious. Thus a credible explanation for the reduced growth of rabbits fed low-fiber diets is that prolonged cecal

TABLE 6.10

Effect of Dietary Fiber Level on Growth Rate and Feed Intake of Weanling Rabbits[a]

Level of dietary alfalfa (%)	ADF (%)	Average daily gain (g)	Average daily feed intake (g)	Average daily DE intake (kcal)
0	3.8	31.4	84.2	310
10	6.6	44.0	107.5	374
20	9.4	36.6	105.3	350
30	13.7	40.1	110.4	349
40	15.7	36.4	115.8	344
50	19.1	41.1	130.9	365
60	20.1	37.3	134.3	349
74	24.5	38.2	147.6	346

[a] From Pote *et al.* (1980).

retention time occurs, with reduced feed intake and a predisposition to diarrhea. The favorable effects of fiber, termed a "ballast" effect by Colin *et al.* (1976), are apparently due to a stimulation of cecal-colonic motility, probably due to the scabrous effects of the larger particles and the increased bulk of the digesta. This is analogous to the roughage effect of fiber in ruminants, in which normal motility of the rumen is dependent on stimulation by fiber. Another, perhaps less likely explanation of reduced performance on low-fiber diets is that they may be less palatable, reducing feed intake. Low-fiber pelleted diets tend to crumble easily, further reducing acceptability.

A minimum of 10% dietary crude fiber is necessary for maximum growth rate of fryers, while levels in excess of 17% depress growth by restricting energy intake (de Blas *et al.*, 1986).

D. Other Beneficial Effects of Fiber

Dietary fiber has an important role in prevention of enteritis in rabbits. This will be further discussed in Chapter 12. Fiber also has protective effects against hair pulling and trichobezoars (hair balls) in the stomach. On low-fiber diets, rabbits engage in fur pulling, removing the fur from each other. This is unsightly and reduces the value of a fryer. Fur balls are an important problem in does, especially Angoras. Dietary fiber helps to prevent hair accumulation.

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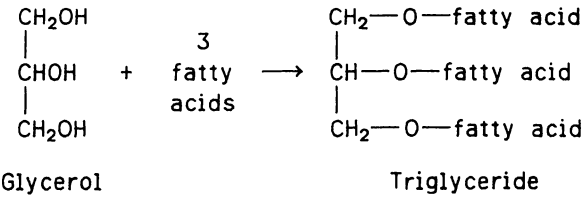
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Fats

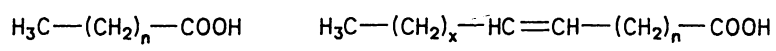
I. CHEMICAL CHARACTERISTICS OF FATS

Fats are a concentrated source of energy, yielding about 2.25 times as much DE as carbohydrate on an equivalent-weight basis. High-energy diets *a priori* contain added fat.

Fats and oils are also known as lipids, which are substances in plant and animal tissue that are soluble in organic solvents like ether. Fat is measured by ether extraction, so the term "ether extract" is often used synonymously with fat. Technically, fats and oils are triglycerides, or substances containing three fatty acids bonded to a glycerol molecule:



The properties of fats and oils are determined by the fatty acids they contain, which can be either saturated or unsaturated:



saturated unsaturated

Saturated fatty acids are fully saturated with hydrogen, while the unsaturated ones have one or more double bonds. The unsaturated fatty acids can become saturated by the addition of hydrogen, a process called hydrogenation. This can be done chemically, and also occurs in the rumen, explaining in part why ruminants tend to have body fat with a fairly high content of saturated fatty acids.

The common fatty acids in feeds and animal tissues generally contain 16, 18, or 20 carbon atoms. Some of the common fatty acids are listed in the accompanying table.

The two saturated fatty acids in this group are palmitic and stearic. The iodine number is a measure of the degree of unsaturation, so with more double bonds,

Fatty acid	Designation[a]	Iodine number	Melting point (°C)
Palmitic	16 : 0	0	62.9
Stearic	18 : 0	0	69.9
Oleic	18 : 1	90	14.0
Linoleic	18 : 2	181	−5.0
Linolenic	18 : 3	274	−14.4
Arachidonic	20 : 4	316	−49.5

[a] 16 : 0 means 16 carbons and 0 double bonds.

the iodine number increases. Iodine reacts with the double bonds and becomes bound to the fatty acid. The iodine number is the grams of iodine taken up by 100 g of fat. Two characteristics of a fatty acid affect the melting point. These are the number of carbons and the number of double bonds (degree of unsaturation). The fewer the number of carbons, the lower the melting point (e.g., compare palmitic and stearic acids). The greater the degree of unsaturation, the lower the melting point. This is important, because it influences the properties of the fats and oils.

Fats are triglycerides that are solid at room temperature. They are often of animal origin (e.g., lard, tallow) and have a significant content of saturated fatty acids (accounting for their high melting point). Oils are liquids at room temperature and usually have a high content of unsaturated fatty acids. The physical and chemical properties of several fats and oils are shown in Table 7.1. It is notable that animal fats, contrary to popular belief, contain appreciable levels of unsaturated fatty acids, as well as having a higher level of saturated fatty acids

TABLE 7.1

Physical and Chemical Properties of Several Fats and Oils

Type of fat	Iodine number	Melting point (°C)	Fatty acids (% of total)				
			16:0	18:0	18:1	18:2	18:3
Vegetable oils							
Coconut oil	8–10	20–35	8.0	2.8	5.6	1.6	—
Corn oil	115–127	<20	12.0	2.7	30.1	54.7	1.4
Olive oil	79–90	20	14.0	2.6	74.0	8.1	—
Safflower oil	145	<20	12.3	1.8	11.2	74.3	—
Soybean oil	130–138	<20	11.5	4.3	27.3	49.7	6.9
Animal fats							
Beef tallow	35–45	36–45	26.2	22.4	45.3	1.6	—
Butter	26–38	28–36	27.0	12.5	35.0	3.0	0.8
Menhaden oil	148–172	31–33	23.2	5.6	15.3	2.7	1.9
Lard	50–65	35–45	25.7	12.1	49.2	9.6	1.1
Poultry fat	80	<30	21.4	5.9	39.5	23.5	1.0

than most vegetable oils. An exception to the general relationship between degree of unsaturation and melting point is coconut oil, which, though highly saturated, has a high content of short-chain fatty acids. Normally, fats and oils contain long-chain fatty acids of 16 and 18 carbon atoms. The major short-chain fatty acids are the VFA, which are rarely found in fats. An exception is butter, which contains about 3% butyric acid (4 carbons).

II. DIGESTION AND ABSORPTION OF FATS

Fats and oils are digested in the small intestine. The digestive process involves splitting fatty acids off the triglyceride molecules, which is accomplished by the lipase enzymes secreted by the pancreas gland. Because fat is not water soluble, it is necessary that fats be emulsified in the digestive tract. Bile, produced in the liver and secreted into the duodenum through the bile duct, contains bile salts, which emulsify fats and also function in fat absorption. Fatty acids, bile salts, and other lipid-soluble materials aggregate into micelles that transport the fats to the villi membranes, where absorption occurs.

Little information is available on specific sites of fat digestion in rabbits, but it probably occurs primarily in the small intestine, where lipase and bile are secreted.

Unsaturated fatty acids consumed by ruminants are hydrogenated in the rumen, converting them to saturated fatty acids, accounting in part for the high saturated fatty acid content of ruminant carcass fat. It is not known if this hydrogenation process occurs in the hindgut of the rabbit, but because fatty acid absorption occurs in the small intestine, it is unlikely that there is much hydrogenation of unsaturated fats in the rabbit.

Parigi-Bini *et al.* (1974) reported the percentage digestibility of the fat in diets containing 5 or 10% beef tallow to be 85–89% in rabbits. They suggested that the presence of saponified fat in the feces that is not detected by ether extraction may give spuriously high apparent digestibilities for fat. Acid hydrolysis (in 5 *N* HCl) of fecal samples prior to ether extraction will avoid possible underestimation of fat because of calcium soap formation. Cook and Thomson (1951) compared the digestibility of the fat in a diet containing 17% olive oil in rats, rabbits, and guinea pigs. The percentage digestibilities of the fat were 94, 92, and 79% in rats, rabbits, and guinea pigs, respectively.

III. USE OF FAT IN RABBIT DIETS

Thacker (1956) fed diets containing 5, 10, 15, 20, and 25% vegetable oil to rabbits, and observed satisfactory performance with all levels of added fat.

Arrington *et al.* (1974) tested 11 and 14% added fat, and found it was well accepted. Pote *et al.* (1980) used 20% vegetable oil in an alfalfa-based diet, and noted a significant improvement in feed conversion efficiency. Feed/gain ratio was 2.70 with a 74% alfalfa diet, and 2.06 when 20% of the alfalfa was replaced with vegetable oil. These workers suggested that use of fat may offer a means of maintaining adequate energy levels in high-forage diets, without causing carbohydrate overload of the hindgut. King (1981) found increased gains and feed efficiency when 5 and 8% vegetable oil were added to a typical commercial-type diet. Partridge *et al.* (1986) examined the effect of the addition of either 6 or 10% fat (both soybean oil and tallow were tested) to diets for growing rabbits, and found a slight improvement in growth rate and an improved feed conversion efficiency.

Added fat may increase feed palatability. Cheeke (1974) noted a pronounced preference for a diet with 5% added fat over a similar diet without fat. A diet with 10% corn oil was preferred over one with 20% corn oil. Fat tends to reduce the dustiness of feeds, which may increase the acceptability of high-roughage diets.

Common sources of fats available for incorporation into feeds include animal fats and vegetable oils. Lard (swine fat), tallow (beef, lamb fat), and poultry fat are common sources of animal fat obtained from slaughter houses and rendering plants. Vegetable oils, such as soybean, cottonseed, and corn oils, are used in the manufacture of cooking and salad oils and margarine, so they are usually too expensive to be used in animal feeding. Hydrolyzed fats are byproducts of processes used in making edible products or soap and contain a high proportion of free fatty acids.

It is well recognized that vegetable oils usually are more digestible and have a higher energy value for swine and poultry than do animal fats. This appears to be true in rabbits also. Maertens *et al.* (1986) compared beef tallow, lard, mixed renderers fat, and soybean oil at the 6 and 12% levels in rabbit diets and measured digestibility and digestible energy content. The digestible energy values (kcal/kg) for the different fat sources were: beef tallow, 6525; lard, 7290; mixed fat, 8460; soybean oil, 8390. The percentage digestibility values ranged from 87 to 90%. However, when saponified fatty acids were removed by acid hydrolysis of the feces prior to ether extraction, the percentage digestibility of the fat ranged from 52% (beef tallow) to 83% (soybean oil). These results indicate that tallow has a lower digestibility and lower energy value than vegetable oils.

Several factors influence the optimal level of added fat. Of major importance is economics, or the cost per kilocalorie of DE from fat versus other available energy sources. Another factor is pellet quality. The maximum level of added fat that can be used without adversely affecting pellet quality ranges from 2 to 10%, depending on the other ingredients and the particular pellet mill involved. Some feed mills have special dies for high-fat rations, and so can successfully incorporate the higher fat levels.

The use of full-fat soybeans or other oilseeds is another means of increasing the fat and energy contents of the diet. Sanchez *et al.* (1984) substituted extruded soybeans for soybean meal and observed equal growth and an improved feed conversion with the extruded product. Johnston and Berrio (1985) found satisfactory growth with various extruded oilseeds, including soybean, cottonseed, safflower, and flax seeds.

Characteristics of Carcass Fat of Rabbits

The fat content of the carcass of an animal depends a great deal on the energy content of the diet. With high-energy diets, fat deposition is higher than when low-energy feeds are used, because the regulation of feed intake does not precisely match caloric intake with metabolic needs, with the result that excess energy is deposited as fat. Rabbits are fed lower energy diets than are other livestock, so not surprisingly, the fat content of rabbit meat is low. An example of the effect of dietary energy level on the fat content of rabbit meat is shown in Table 7.2, showing that the fat content of the meat is increased with high dietary energy levels.

The fatty acid composition of rabbit meat reflects that of the diet, as is generally true for nonruminant animals (Fig. 7.1). Palmitic acid (16 : 0) and oleic acid (18 : 1) tend to be the main fatty acids (Table 7.3), with the unsaturated fatty acids comprising 50–60% of the total. Moore and Williams (1968) compared the effects of feeding 20% corn oil, butterfat, or coconut oil on the fatty acid composition of rabbit carcass fat. Feeding corn oil increased the unsaturated fatty acid level to 83% of the total, while unsaturated fatty acids were 63 and 62% for butter and coconut oil treatments. With a low-fat diet, the percentage unsaturated fatty acids was 66%, with oleic acid (18 : 1) comprising 41% of the total. This would indicate that rabbit body fat would generally tend to be mostly unsaturated, regardless of the level or type of dietary fat.

Cottonseed oil contains the cyclopropenoid fatty acids sterculic and malvalic acids. They induce elevated blood cholesterol levels and atherosclerosis in rabbits (Ferguson *et al.*, 1976).

Subcutaneous fat makes up about 40–50% of total carcass fat. The intermuscular and perirenal fat contents increase with age (Table 7.4).

There has been considerable interest in the cholesterol content of rabbit meat, which has been claimed to be lower than for other meats (Rao *et al.*, 1979). Reported values for cholesterol content of a variety of meat products are shown in Table 7.5. These values would indicate that the cholesterol content of rabbit meat is not substantially different from that of other meats. Beyman (1984) has suggested that because of the interrelationships between cholesterol content, saturated and polyunsaturated fatty acids, and caloric content, the actual choles-

TABLE 7.2

Effect of Dietary Energy Level on the Composition of Rabbit Meat[a]

Item	Dietary energy level (kcal DE/kg)		
	3678	2974	2342
Dressing (%)	48.4	48.1	49.2
Crude protein (%)[b]	73.3	72.0	76.4
Ether extract (fat, %)[b]	17.9	17.9	11.0

[a] From Pote *et al.* (1980).
[b] Dry matter basis.

terolemic effect of rabbit meat in humans may be lower than for red meat sources, and comparable to chicken and turkey.

Saponins are glycosides in legume forages that cause reductions in serum cholesterol levels in animals fed alfalfa (Cheeke and Shull, 1985). Cheeke (1970) reviewed the biological effects of saponins and suggested that they may

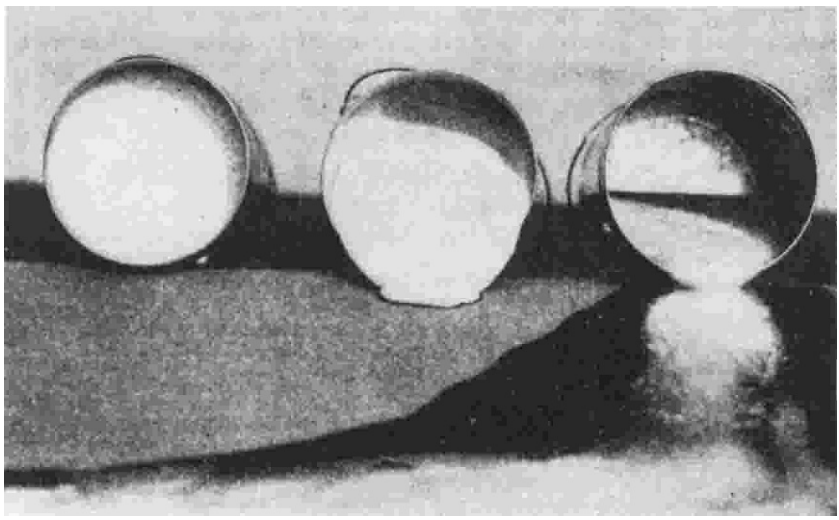


Fig. 7.1 The effect of diet fatty acid composition on carcass fat of nonruminant animals. These are lard samples from pigs fed saturated (left) unsaturated (middle), and polyunsaturated (right) fats in the diet. The more unsaturated a fat, the greater the tendency for it to be liquid at room temperature. Taken from *U.S. Dep. Agric., Bull.* **1492** (1928).

TABLE 7.3

Fatty Acid Composition of Carcass Fat of Different Species

Species	Fatty acids[a]									Reference
	Myristic 14 : 0	Palmitic 16 : 0	Palmitoleic 16 : 1	Stearic 18 : 0	Oleic 18 : 1	Linoleic 18 : 2	Linolenic 18 : 3	Total saturated	Total unsaturated	
Rabbit	3.2	27.4	3.9	6.3	31.2	22.5	5.2	37	63	Rao *et al.* (1979)
	4.4	40.2	6.8	6.7	26.0	10.1	5.0	51	49	Hougham and Cramer (1980)
	1.9	23.6	5.2	6.1	12.7	8.9	39.7	32	68	Hungate (1966)
Horse	4.9	25.9	6.8	4.9	33.7	5.2	16.3	36	64	Hungate (1966)
Beef	4	30	5	25	35	1	—	59	41	Mattson *et al.* (1964)
Sheep	5	27	3	27	35	2	1	59	41	Mattson *et al.* (1964)
Swine	1	28	3	15	42	9	2	44	56	Mattson *et al.* (1964)

[a] All values as percentage of total fatty acids.

TABLE 7.4

Distribution of Carcass Fat in Rabbits of Different Ages[a,b]

Fat depot	Age (days)			
	10	30	52	74
Subcutaneous	54.1	58.1	41.3	41.6
Intermuscular	16.4	16.9	25.2	24.3
Mesenteric	22.2	14.4	20.4	16.5
Perirenal (kidney fat)	7.3	10.6	13.1	17.6
Total fat (as % of carcass)	3.5	3.7	3.7	4.8

[a] From Vezinhet and Prud'hon (1975).
[b] Given as percentage of total.

have potential in lowering the cholesterol content of animal products. Barichello and Fedoroff (1971) observed pronounced serum cholesterol-lowering properties of alfalfa meal when fed to rabbits, suggesting that an effect on lowering tissue cholesterol levels is plausible. However, Holmes *et al.* (1984) found that the meat cholesterol content of rabbits was not reduced when high-alfalfa diets were fed.

TABLE 7.5

Cholesterol Content of Various Meat Products

Meat source	Cholesterol content (mg/100 g)		References
	Fresh weight basis	Dry weight basis	
Raw lean beef	65	218	Reiser (1975)
Chicken breast	79	NA	Reiser (1975)
Chicken drumstick	91	388	Reiser (1975)
Lamb	70	250	Reiser (1975)
Pork	60	194	Reiser (1975)
Veal	70	NA	Reiser (1975)
Smoked ham	NA[a]	257	Reiser (1975)
Smoked bacon	NA	83	Reiser (1975)
Rabbit	75	288	Holmes *et al.* (1984)
Rabbit	39	136	Rao *et al.* (1979)

[a] NA, Not available.

IV. RANCIDITY OF FATS

Fats containing unsaturated fatty acids, such as vegetable and fish oils, are susceptible to the development of rancidity. Rancidity is a process where oxidation of the double bond of unsaturated fatty acids occurs, resulting in the formation of aldehydes and ketones having offensive odors and taste. It is advisable to use a synthetic antioxidant, such as ethoxyquin, in diets to be stored for appreciable periods. Vitamin E has antioxidant activity also. Rancidity can occur in meat as well as in feeds. Because rabbit meat tends to have a fairly high content of unsaturated fatty acids, it is susceptible to development of rancidity while stored as frozen meat. This detracts from its eating quality. Work with other species has indicated that feeding natural or synthetic antioxidants in the diet increases the shelf life of the meat.

V. ESSENTIAL FATTY ACIDS

Linoleic, linolenic, and arachidonic acids are often referred to as the essential fatty acids, because when absent from the diet, deficiency symptoms such as dermatitis and poor growth occur. The essential fatty acids function as constituents of cellular membranes and as precursors of a class of hormones called prostaglandins. Because the others can be synthesized from it, linoleic is the primary essential fatty acid.

Essential fatty acids are found in vegetable oils and the lipid component of forages such as alfalfa. The likelihood of an essential fatty acid deficiency in rabbits is remote. These acids are involved in forming the grease secreted from hair follicles. Addition of vegetable oil to the diet helps in promoting a shiny, lustrous hair coat desirable in show animals. One way of providing this is the addition of a teaspoon of corn oil to a rabbit's feed every few days.

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8

Mineral Nutrition of Rabbits

Animals have dietary requirements for a number of mineral elements, which can be categorized in two groups, the macroelements (macrominerals) and the microelements (trace elements). The macroelements are required in much larger quantities than are the trace elements. Some of the trace elements (so named because they are needed in "trace" amounts) are required in extremely minute quantities. The members of these two groups are listed here:

Macrominerals	Trace minerals
Calcium	Manganese
Phosphorus	Zinc
Magnesium	Iron
Sodium	Copper
Potassium	Molybdenum
Chlorine	Selenium
	Iodine
	Cobalt
	Chromium

Mineral elements have several different types of metabolic roles. Some participate in the structure of the body. These include calcium and phosphorus, which are major constituents of bone. Sodium, chlorine, and potassium are involved in a regulatory role, particularly with respect to the regulation of the pH of body fluids and fluid balance between the different fluid compartments of the body (digestive tract, blood, intercellular spaces, tissue cells). The other elements function primarily as cofactors or activators of enzymes and hormones. For example, iodine is part of the hormone thyroxine, while selenium is a part of the enzyme complex called glutathione peroxidase.

When a particular mineral is deficient in the diet, characteristic deficiency symptoms develop. These symptoms reflect the metabolic role of the element. A calcium deficiency will result in defective, demineralized bones, while an iron deficiency will cause anemia because of the role of iron in hemoglobin formation and oxygen transport in the blood.

In this chapter, each mineral element will be discussed in terms of its metabolic functions, metabolism, and deficiency symptoms.

I. CALCIUM

Calcium is the mineral present in largest quantity in animals, and the one required in greatest amount in the diet. About 99% of the body calcium is in the bones and teeth, so obviously its major role is as a constituent of the skeletal system. Bones consist of an organic (protein–polysaccharide) matrix, which becomes mineralized with calcium and phosphorus in a 2 : 1 ratio. Other functions of calcium include a role in blood clotting, muscle contraction, function of the heart muscle, and the transmission of nerve impulses to muscle tissue (normal neuromuscular excitability).

Calcium is absorbed from the small intestine. In many animal species, calcium absorption is closely regulated to balance metabolic needs. This regulation is accomplished by the interaction of the parathyroid hormone (PTH) and a metabolite of vitamin D, or 1,25-dihydroxycholecalciferol (1,25-OHD_3). An increased need for calcium absorption is indicated by a drop in the blood calcium level. A decrease in blood calcium triggers secretion of PTH from the parathyroid gland into the blood. PTH stimulates the enzymatic conversion of 1-OHD_3 to 1,25-OHD_3 in the kidney. The 1,25-OHD_3 is secreted into the blood and travels to the intestine, where it stimulates increased formation of calcium-binding protein, which functions in the transport of calcium from the intestine into the blood. When adequate calcium has been absorbed, the blood calcium level rises, inhibiting PTH secretion, which in turn shuts down vitamin D activation. Thus in many species, such as the chicken and rat (animals in which vitamin D–calcium interrelations have been studied intensively), calcium absorption is regulated according to metabolic need.

These regulatory controls of calcium absorption do not seem to operate in rabbits—or at least not in a very refined manner. In the rabbit, calcium is absorbed in direct proportion to the amount in the diet. Cheeke and Amberg (1973) fed a very high dietary calcium level (10% calcium carbonate) to rabbits and rats. Comparative apparent digestibility, and fecal and urinary excretion are shown in Table 8.1. The urine of the rabbits was thick and creamy, whereas the rats had a clear yellow urine. These observations on rabbit urine were virtually identical with those of Schmidt-Nielsen (1964) regarding the pack rat:

> The interest in calcium excretion in the pack rat began with the observation that urine samples from recently trapped animals contained such large amounts of white precipitate that the urine looked like heavy cream. Frequently, the urine was also strongly colored orange, or even rust colored or deep red. If pack rats were given cactus and grain to eat in the laboratory their urine contained the white precipitate, but white rats on the same diet had a clear yellow urine.

TABLE 8.1

Comparative Calcium Metabolism in Rats and Rabbits Fed a High-Calcium Diet[a]

Item (%)	Rabbits	Rats
Ingested Ca in feces	19.8	92.7
Ingested Ca in urine	59.0	2.0
Apparent Ca digestibility	80.2	7.3

[a] Data from Cheeke and Amberg (1973).

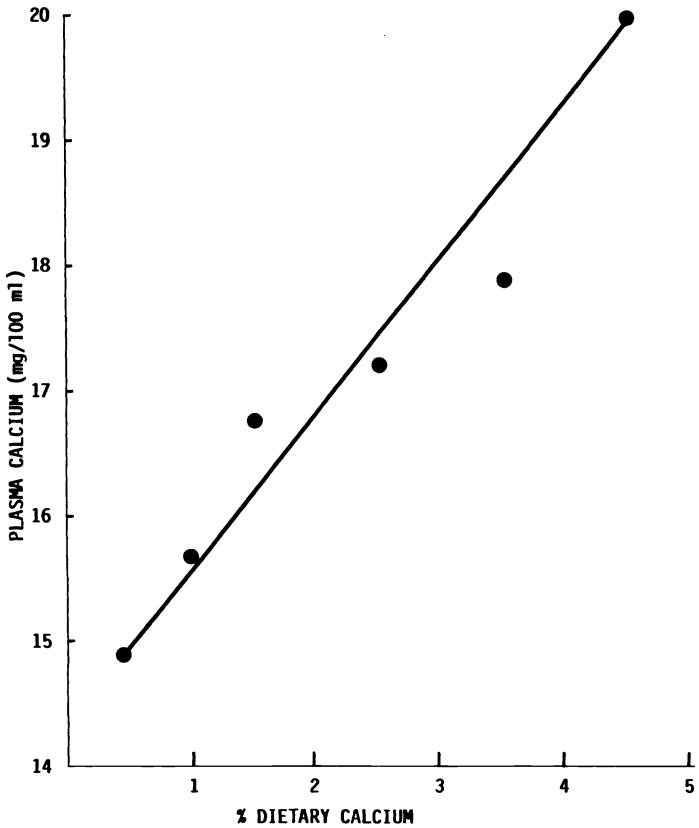


Fig. 8.1 In rabbits, in contrast to most other animals, the serum calcium level rises as the dietary calcium level is increased. (Data from Chapin and Smith, 1967a.)

Rabbits also excrete a highly pigmented urine, reddish or orange. The pigments responsible have not been conclusively identified. The white precipitate in the urine is calcium carbonate.

Chapin and Smith (1967a,b) noted that as the dietary calcium level is increased, the blood calcium level rises (Fig. 8.1). This is unusual, because in most species the serum calcium level is maintained at a nearly constant level by the interactions of vitamin D and the hormones PTH and calcitonin. PTH is secreted in response to a reduction in blood calcium, and stimulates calcium absorption. Calcitonin, produced by the thyroid gland, stimulates removal of calcium from the blood into bone. This type of action is called homeostasis (constancy of the internal environment). Homeostatic mechanisms function in stimulating reactions that compensate for some change in the blood or tissue concentration of nutrients such as calcium or glucose.

The excretion of calcium in the urine of rabbits is related to the lack of homeostatic control of serum calcium levels. When dietary calcium levels in rabbit diets are higher than necessary, the extra calcium is absorbed, the blood calcium level rises and exceeds the kidney threshold, and the excess blood calcium is excreted in the urine. Buss and Bordeau (1984) found that the fraction of blood calcium that can be filtered out of the blood in the kidney (ultrafilterable calcium) is higher in the rabbit than in other animals, being about 2.25 m*M* as compared to about 1.5 m*M* in other species, with the result that the kidney of the rabbit has a high fractional excretion of calcium.

Swick *et al.* (1981) advanced an hypothesis to account for the high urinary calcium levels and the red pigment in the urine. They proposed that when the maximum kidney tubular reabsorption of calcium is reached, calcium filtered from the blood is excreted in the urine. Damage to the kidney due to the high filtration rate when the plasma calcium level is very high could result in appearance of blood pigments in the urine, from irritation caused by physical effects of crystalline calcium salts (Fig. 8.2).

The plasma calcium level in rabbits is not as closely regulated homeostatically as in other species, in which the normal plasma calcium level is about 10 mg/100 ml. Barlet (1980) reported a normal value of 12.4 mg/100 ml, while Cheeke *et al.* (1985) noted values of about 16.8 mg/100 ml for serum and Swick *et al.* (1981) reported an average of about 15 mg/100 ml. Prolonged intake of high calcium diets (4% calcium) may result in calcification of aorta and kidney. Elevated vitamin D intake intensifies the effect (Kamphues *et al.*, 1986).

In many animals, the initial perod of lactation is a critical time for calcium metabolism. The high calcium content of milk coupled with a high milk production necessitates that some calcium be mobilized from bone to meet the heavy demands of lactation. In dairy cattle, the disease milk fever or parturient paresis is common, when the cow cannot mobilize calcium rapidly enough from bone to balance the loss of calcium in the milk. The result is that the blood calcium level



Fig. 8.2 A jar of rabbit urine from rabbits fed a standard commercial diet, showing the calcium carbonate sediment. (Courtesy of D. J. Harris and Oregon State University Rabbit Research Center, Corvallis.)

falls (hypocalcemia), interfering with normal neuromuscular function. The cow goes down in a coma-like condition. Milk fever is not common in rabbits, but sometimes occurs. Barlet (1980) noted that some rabbits exhibit a syndrome similar to parturient paresis, which is characterized by tetany and hypocalcemia. In a study of does of the Fauve de Bourgogne (Bergundy Fawn) breed, Barlet (1980) observed that a drop in plasma calcium from a normal value of about 14 mg/100 ml to about 10 mg/100 ml occurred at parturition, and the level remained low during the first 3 weeks of lactation. In 6 of 14 does, milk fever developed. No particular symptom except loss of appetite was observed before the crisis. On the morning of the crisis, does were found lying on their sides, with jerking of the hindlimbs, muscle tremors, and ear flapping. Plasma calcium (5.8 mg/100 ml) and phosphorus (2.9 mg/100 ml) levels were very low, while magnesium (1.96 mg/100 ml) was normal. Injection of calcium gluconate induced a rapid recovery within 2 hr, with plasma calcium and phosphorus levels returning to normal. No relapses occurred. Thus, according to Barlet (1980), the end of pregnancy and beginning of lactation in rabbits is associated with mild depressions in blood calcium and phosphorus levels, and in some animals the drop is sufficiently pronounced to cause tetany.

Cheeke *et al.* (1985) reported the apparent availability of calcium from various sources. The percentage apparent digestibility ranged from 81% for limestone, 55% for dicalcium phosphate, 53% for alfalfa meal, 61% for red clover, to 49% for calcium oxalate. About 20–30% of the calcium in alfalfa is in the form of calcium oxalate (Ward *et al.*, 1979).

The differences between rabbits and many other animals in calcium metabolism can be summarized as follows:

1. Rabbits have a high rate of net calcium absorption, which is not regulated according to metabolic need for calcium.
2. The blood calcium level is not homeostatically regulated, but is in direct proportion to dietary calcium level.
3. The ultrafilterable fraction of the blood calcium is high, resulting in a high fractional clearance of calcium from the blood in the kidney.
4. The main route of excretion of excess calcium in rabbits is the urine (Besançon and Lebas, 1969; Cheeke and Amberg, 1973; Kennedy, 1965), whereas in other animals the bile is the major route.

Sources of calcium in rabbit feeds include legume forages, such as alfalfa and clovers. Alfalfa contains about 1.3% calcium, so a diet with 40% or more alfalfa should contain an adequate quantity. Common calcium supplements are ground limestone (calcium carbonate) and dicalcium phosphate (dical). Most rabbit diets contain more than sufficient calcium, as evidenced by its excretion in the urine, resulting in chalky-white deposits beneath the cages (see Fig. 18.3)

II. PHOSPHORUS

The phosphorus requirements of rabbits have not been well studied. Most of the available data have been obtained with small breeds such as the Dutch, so the values may not be applicable to the larger commercial breeds.

Along with calcium, phosphorus is a major mineral constituent of bone. About 80% of the total body phosphorus occurs in bones and teeth. Phosphorus is of particular importance in metabolism, having a critical role in energy metabolism as a constituent of ATP (adenosine triphosphate) and phosphorylated carbohydrates and derivatives. Many compounds require the presence of one or more phosphate groups.

Phosphorus absorption, like that of calcium, is in most animals regulated by the vitamin D metabolite, 1,25-OHD_3. The importance of this regulation in rabbits is not known.

A major factor influencing phosphorus absorption is the presence of phytates in plant materials. Phytic acid is an organic material in grains and protein supplements that forms a complex with phosphorus, called phytate. Grains and soybean meal contain a high proportion of their phosphorus in the form of phytates. In swine and poultry, a high percentage of this organic phosphate is unavailable, while in ruminants, microbial phytase activity breaks down phytate in the rumen, making the phosphorus available. Swick *et al.* (1981) studied the availability of phosphorus in a corn–soybean meal diet for rabbits, and found an apparent phosphorus digestibility of about 75%. This would indicate that phytate phos-

TABLE 8.2

Comparative Bioavailability of Minerals in Alfalfa for Rabbits and Ponies

Species	References	Apparent digestibility (%)		
		Calcium	Phosphorus	Magnesium
Rabbits	Cheeke *et al.* (1985)	53.4	16.9	53.4
Ponies	Hintz *et al.* (1984)	46.0	22.9	51.3

phorus is of high bioavailability to rabbits. Cheeke *et al.* (1985) observed apparent digestibility values for phosphorus of 55% for dicalcium phosphate, 35% for red clover meal, and 17% for alfalfa meal. With a corn–soybean meal diet, the phosphorus digestibility was 50%. These data indicate that the availability of phosphorus in grains, soybean meal, and dicalcium phosphate is quite high in rabbits, but alfalfa phosphorus is of low availability.

Because horses have a similar type of digestive tract as rabbits, similarities in mineral absorption might be expected. A comparison of the results of Cheeke *et al.* (1985) for rabbits and Hintz *et al.* (1984) for ponies shows very close agreement for the bioavailability of calcium, phosphorus, and magnesium in alfalfa (Table 8.2).

Barlet (1980) noted a normal plasma phosphorus level of about 6 mg/100 ml in mature does. During lactation, the level dropped to about 4 mg/100 ml. In animals that developed hypocalcemic tetany, the plasma phosphorus dropped to about 2.9 mg/100 ml. Both the plasma calcium and phosphorus levels returned to normal rapidly after calcium gluconate injection. Cheeke *et al.* (1985) reported serum phosphorus levels ranging from 5 to 8 mg/100 ml, while Mathieu and Smith (1961) found levels averaging about 7 mg/100 ml in young rabbits.

Although the National Research Council (NRC) (1977) recommends dietary phosphorus levels of 0.22% for growth and 0.5% for lactation, these values were obtained with Dutch rabbits and seem too low for commercial production. Lebas (1980) recommended 0.8% phosphorus for does and fryers fed the same diet. Lebas and Jouglar (1984) found the optimal level to be about 0.64–0.67%, with reduced litter size with 0.42% or 1.0% phosphorus levels.

Calcium and Phosphorus Interrelationships

The metabolism and dietary requirements of calcium and phosphorus are closely interrelated. It is common in animal nutrition to maintain calcium and phosphorus levels within a 2 : 1–1 : 2 ratio. This ratio range does not seem to be critical in rabbits, as satisfactory results are obtained with much wider ratios than

these. Chapin and Smith (1967b) found that a calcium/phosphorus ratio of 12 : 1 allowed normal growth and bone ash. Diets with high phosphorus levels (>1%) are unpalatable, resulting in feed rejection (Chapin and Smith, 1967c).

Inadequate calcium or phosphorus intakes in young animals cause rickets. In rabbits fed deficient diets, the bones become highly demineralized and very susceptible to fracture. The backbone may break spontaneously. In mature animals, osteoporosis occurs with dietary calcium or phosphorus deficiencies. Osteoporosis results from excessive mobilization of bone salts to maintain normal blood calcium and phosphorus levels. As in rickets, bone fracture readily occurs.

III. MAGNESIUM

About 70% of the body magnesium occurs in the bone. Magnesium is a cofactor for many enzymes, particularly those functioning in energy metabolism.

In livestock, the major magnesium deficiency problem is a condition called grass tetany, associated with low forage magnesium levels and organic acids (*trans*-aconitic acid, tricarballylic acid), which complex magnesium in an unavailable form. Signs of grass tetany, associated with low serum magnesium levels, include excessive nervousness, hyperexcitability, muscle twitching, convulsions, and death. Similar symptoms have been experimentally induced in rabbits by feeding a magnesium-deficient diet. Kunkel and Pearson (1948) characterized magnesium deficiency in rabbits as causing poor growth, hyperexcitability, and convulsions. Woodward and Reed (1969) observed alopecia (loss of hair), blanching of the ears, and alteration of fur texture and luster in rabbits fed a diet containing magnesium at 5.6 mg/kg. Gaman *et al.* (1970) observed fur chewing that was overcome by including more magnesium in the mineral mixture. Magnesium oxide is sometimes added to rabbit feed at 5 lb/ton to control fur chewing, although there is no experimental evidence to support this practice.

The bioavailability (apparent digestibility) of magnesium in rabbit diets is about 50% (Cheeke *et al.*, 1985), and about 75% for magnesium oxide. The normal plasma magnesium level is about 2 mg/100 ml (Barlet, 1980; Cheeke *et al.*, 1985; Swick *et al.*, 1981). The major route for magnesium excretion in rabbits is the urine (Cheeke and Amberg, 1973; Cheeke *et al.*, 1985; Swick *et al.*, 1981).

Evans *et al.* (1983a) examined the magnesium requirement for growth, and observed a higher growth rate (31–36 g/day) with 0.35% magnesium than that (22–23 g/day) with 0.17% magnesium. In a subsequent study (Evans *et al.*, 1983b), they concluded that the magnesium requirement for growth of New Zealand White fryers was between 0.25 and 0.34% of the diet, which is considerably higher than the NRC (1977) recommendation of 0.003%.

IV. POTASSIUM

Potassium functions primarily in a regulatory role in metabolism, in the maintenance of osmotic relationships and of acid–base balance. It is found mainly within cells; for example, the concentration of potassium in the red blood cells is about 25 times higher than in the plasma. Its distribution is opposite to that of sodium, which is primarily extracellular. Potassium is required for heart function, and is a cofactor for several enzymes.

Potassium deficiency causes hypokalemia or low blood potassium, resulting in muscle weakness, cardiac weakness, and respiratory distress. Under conditions of stress, urinary excretion of potassium is increased, and may result in temporary hypokalemia. The value, if any, of supplementation of rabbits during stress periods with potassium has not been examined experimentally. In calves with diarrhea, administration of electrolytes, including potassium salts, aids in preventing dehydration. Its effects on diarrhetic rabbits should be tested.

Licois *et al.* (1978a,b) studied water balance and electrolyte metabolism in the digestive tract of the rabbit, with particular reference to the changes in diarrhea induced by coccidiosis. Animals with diarrhea had a reduced feed and water intake, and the excretion of water in the feces and urine was less than in control animals (Licois *et al.*, 1978a). Water reabsorption from the cecum and proximal

TABLE 8.3

Water and Electrolyte Balance in Rabbits with and without Coccidiosis-Induced Diarrhea[a]

Item[b]	Control animals	Inoculated animals	
		Eimeria intestinalis	*Eimeria pellerdyi*
Sodium intake	9.85	1.30	3.62
Sodium in feces	4.15	1.10	2.88
Sodium in urine	3.81	3.19	2.17
Net sodium balance	1.89	−2.99	−1.43
Postassium intake	28.39	3.59	10.31
Potassium in feces	11.64	3.27	5.79
Potassium in urine	9.50	5.38	7.53
Net potassium balance	7.25	−5.06	−3.01
Water consumed	173.0	73.0	114.0
Water in feces	77.0	50.0	50.0
Water in urine	63.0	57.0	57.0
Water balance	33.0	−34.0	7.0
Plasma sodium (mEq/liter)	137.6	124.7	123.6
Plasma potassium (mEq/liter)	5.6	3.7	2.7

[a] Data from Licois *et al.* (1978a,b).

[b] Sodium and potassium in mEq/24 hr; water in ml/24 hr.

colon was reduced in diarrhea, producing watery feces, but since fecal excretion was less with diarrhea, the actual fecal water loss was lower in animals with diarrhea than in controls. Control animals always had a positive water balance, whereas animals inoculated with coccidia sometimes had a negative water balance. Rabbits with diarrhea did not show tissue dehydration or hemoconcentration. Licois *et al.* (1978b) studied electrolyte metabolism in rabbits inoculated with coccidia (*Eimeria intestinalis* and *Eimeria pellerdyi*), which induce diarrhea. Sodium and potassium balance (Table 8.3) shows that a negative potassium balance occurs in diarrhea. These workers suggest that the pathogenesis of diarrhea (induced by coccidiosis) in the rabbit is a result of a nutritional deficiency of potassium, induced by a lack of potassium intake (low feed intake) and a lack of conservation of potassium by the kidney. They state, "There are also some doubts about kidney function, as it is difficult to understand why, in an animal with a negative water and electrolyte balance, the kidney did not attempt to compensate for the water and mineral losses." An explanation may reside in the low mineralocorticoid secretion in the rabbit. S. I. Helman (University of Illinois, personal communication, 1978), stated, "The rabbit seems to be a weird beast with an unusually low level of spontaneous adrenocortical activity." In subsequent work, Licois and Mongin (1980) found that in the colon, sodium is absorbed against potassium secretion from the blood. This exchange mechanism explains the excessive loss of potassium in rabbit diarrhea as well as the hypokalemia.

These reports suggest that use of supplemental potassium as a preventative for symptoms of diarrhea should be evaluated.

Hove and Herndon (1955) produced classic signs of potassium deficiency, including weakness and paralysis, by feeding diets deficient in potassium to rabbits. They estimated the potassium requirement to be about 0.6% of the diet. Alfalfa and other forages are rich in potassium, so a deficiency under practical conditions seems unlikely. French workers have found that high dietary levels of potassium (0.8–1.0%) may induce nephritis in rabbits (Surdeau *et al.*, 1976). Evans *et al.* (1983a) observed slight growth depression with 1% dietary potassium as compared to 0.6%.

Adrenal hormones such as aldosterone (mineralocorticoids) cause the kidney to conserve sodium and increase potassium excretion. The rabbit has an unusually low activity of these hormones, which may have consequences in sodium and potassium balance.

V. SODIUM AND CHLORINE

Like potassium, sodium is involved in the regulation of body fluids, including pH and osmotic relationships. Sodium occurs outside cells, whereas potassium is concentrated in cells. Thus in blood the sodium is in the plasma while potassium

TABLE 8.4

Effect of Dietary Chlorine Level on Performance of Growing Rabbits[a]

Item	Dietary chlorine level (%)		
	0.17	0.32	0.47
Average daily gain (g)	33.7*[b]	38.7**	37.5**
Average daily feed intake (g)	103.0*	116.0**	117.0**
Feed/gain	3.07	2.99	3.14

[a] Data from Colin (1977).

[b] *Different from ** ($p < 0.05$).

is inside the red blood cells. Specific requirements for sodium have not been examined for rabbits. Sodium is provided by way of salt, for which a dietary level of 0.5% is commonly used. Salt can also be provided free choice, by means of a salt spool hung in the cage. It will cause corrosion of wire cages.

Chlorine functions as an anion to balance sodium, potassium, and other cations, and is involved in acid–base regulation. Chloride is concentrated by gastric cells in the stomach mucosa, and secreted as hydrochloric acid, which functions in protein digestion.

Colin (1977) studied the chlorine requirement of rabbits. A level of 0.17% chlorine was deficient, while 0.32% and 0.47% were adequate as assessed by performance (Table 8.4). Harris *et al.* (1984b) fed various levels of supplementary salt to New Zealand White fryers. Results are shown in Table 8.5. Slightly better gains were obtained with salt levels less than 1.5%. Because salt in the diet stimulates water consumption, there may be some benefit from increasing the

TABLE 8.5

Effect of Supplementary Salt Levels on Performance of Growing Rabbits[a]

Added salt (%)	Average daily gain (g)	Average daily feed intake (g)	Feed/gain
0	37.5	115	3.06
0.5	39.5	111	2.81
1.0	38.1	114	3.02
1.5	34.1	102	3.10
2.0	35.9	111	3.10

[a] Data from Harris *et al.* (1984b).

salt level to 1.0% in hot weather, to aid in prevention of cecal impaction. There is some evidence that impaction may be initiated by inadequate water intake (Lang, 1981), particularly under conditions of heat stress. Withdrawal of water from the cecal contents into the blood to prevent tissue dehydration may be one of the initiating factors in cecal impaction.

French poultry scientists have established that for poultry, an optimal relationship among sodium, potassium, and chlorine exists (Sauveur and Mongin, 1978). The $Na^+ + K^+ - Cl^-$, measured in milliequivalents per kilogram diet, should be about 200 for chickens. This relationship has not been studied in rabbits.

Acid–Base Properties of Feed

The acid–base properties of feeds are a reflection of the acidity or alkalinity of the ash remaining after complete combustion. Foods containing an excess of inorganic cations (sodium, potassium, calcium, magnesium) over inorganic anions (chloride, phosphate, sulfate) have an alkaline ash. An excess of inorganic anions yields an acidic ash. An excess of inorganic cations reflects the presence of organic anions, such as acetate and propionate, which, being organic, are combusted in the ashing process. These organic anions yield bicarbonate when metabolized. Organic cations yield hydrogen ions when metabolized.

Richardson *et al.* (1979) compared the urinary acid excretion in rats and rabbits. Rabbits excreted a more alkaline urine than rats, even when the same diet was fed to both species. Rabbits consuming Purina Rabbit Chow, which contains a high percentage of inorganic cations (calcium, potassium, magnesium), had a very alkaline urine (pH 8.23). These authors suggested that inorganic anions are converted by bacteria in the digestive tract to bicarbonate, which is absorbed and excreted in the urine. The rabbit is particularly vulnerable to acid loads because it has virtually no kidney ammonium ion excretion, and has low hydrogen ion secretion. These authors concluded, "Thus this species [the rabbit] appears to have evolved coordinated renal, metabolic, and gastrointestinal mechanisms which under most physiologic circumstances do not expose the animal to significant acid loads."

VI. MANGANESE

Manganese functions primarily in the formation of the organic mucopolysaccharide matrix of bone. Manganese is a cofactor for a galactotransferase enzyme that participates in the formation of the mucopolysaccharide. It also is involved in amino acid metabolism.

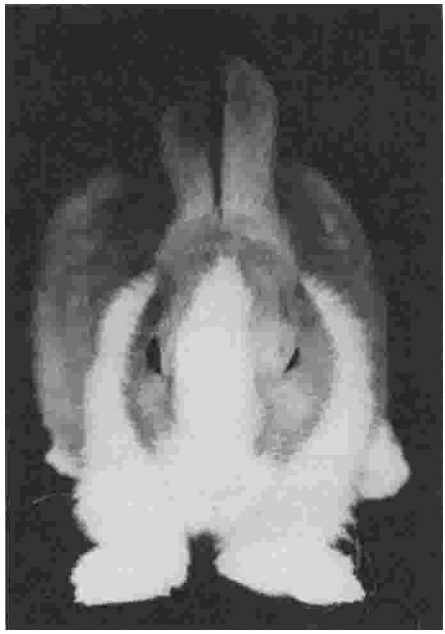


Fig. 8.3 Manganese deficiency, showing crooked front legs resulting from defective bone matrix formation. (Courtesy of S. E. Smith, Cornell University, Ithaca, N.Y.)

Manganese deficiency in rabbits was studied by Smith and Ellis (1947) at Cornell University. They demonstrated that crooked legs, brittle bones, and decreased bone density occurred in rabbits on the deficient diet (Fig. 8.3).

Reproductive failure occurs in ruminants fed a low-manganese diet. Hidiroglou *et al.* (1978) studied the manganese content of tissues of sheep and rabbits fed diets varying in manganese content, to determine if there might be an association of tissue manganese concentrations with reproductive organs. Levels of manganese fed to rabbits were 0.63, 56, and 167 ppm. The major tissues concentrating manganese were kidney, liver, and spleen. On the deficient diet (0.67 ppm), the decreases in liver and kidney manganese concentrations were much greater than in sheep fed similar levels. The concentration in uterine tissue was unaffected by dietary manganese status.

VII. ZINC

Zinc is a component of numerous metalloenzymes (enzymes containing a mineral element). A zinc metalloenzyme, thymidine kinase, functions in the biosynthesis of the activated form of thymidine, a pyrimidine base that is a

component of nucleic acids (DNA and RNA). Thus zinc is essential for fundamental life processes and cell division. Zinc deficiency affects tissues with a rapid growth rate, such as skin. Dermatitis is a classic sign of zinc deficiency in animals. Impaired reproduction and growth inhibition are other effects of zinc deficiency.

Apgar (1971) fed a low-zinc diet to Dutch rabbits during gestation, and noted some impairment of reproductive performance, including a lack of maternal care (poor nest-building, lack of cleaning of kits). When fed a zinc-deficient diet (3 ppm), weanling rabbits ceased growth after about 2 weeks, and had sparse hair, skin scaliness, and lesions around the mouth. Shaw *et al.* (1972, 1974) observed various deficiency signs when young rabbits were fed a low-zinc diet, including reduced feed consumption, lowered hematocrit, loss of weight, graying of dark hair, alopecia (loss of hair), dermatitis, and reproductive failure.

In swine and poultry, a zinc deficiency can be more easily produced by feeding soybean meal as the protein supplement as compared to casein protein. Soybean meal has a high phytate content, which binds zinc in an unavailable complex. Swick *et al.* (1981) compared zinc metabolism in rabbits fed casein versus soybean meal-based diets, and found that soybean meal did not impair zinc absorption. Urinary zinc excretion was very low (about 1% of ingested zinc) with the feces the major route of excretion (about 50% of ingested zinc).

Experiments to quantitate the dietary zinc requirement of rabbits have not yet been conducted.

VIII. IRON

Iron is a constituent of several respiratory pigments, including hemoglobin, myoglobin, cytochromes, and enzymes such as catalase and peroxidase. Iron pigments and enzymes are involved in oxygen transport and metabolism. Hemoglobin is the blood pigment that transports oxygen, while myoglobin is a muscle pigment to which oxygen is transferred. The cytochrome system is a series of reactions in which oxidation occurs, with production of ATP and formation of water from oxygen and hydrogen.

The primary effect of iron deficiency is the development of anemia due to impaired hemoglobin formation. The red blood cells (erythrocytes) are made in the bone marrow, with iron incorporated into the hemoglobin molecule. Iron is recycled when old red blood cells are broken down.

Milk is very low in iron, so in many animals iron deficiency anemia can be induced by feeding a diet of only milk. Because rabbits have a very large iron reserve at birth (Tarvydas *et al.*, 1968), the kits are not dependent on milk for iron.

Smith *et al.* (1944) studied iron deficiency in rabbits, and noted the development of typical iron deficiency anemia.

Iron deficiency in rabbits is unlikely because of the generous distribution of iron in feedstuffs. Products such as alfalfa meal are usually contaminated with soil, an excellent source of iron.

IX. COPPER

Copper is a constituent of several metalloenzymes such as cytochrome oxidase, which functions in cellular respiration, and lysyl oxidase, important in connective tissue formation. Lysyl oxidase is necessary for a reaction in which an hydroxyl group is added to lysine residues in collagen, allowing crosslinking between collagen fibers. In copper deficiency, the bone collagen is defective, and malformations of the skeletal system may occur. Bone abnormalities, including defective cartilage formation, have been noted in copper-deficient rabbits (Hunt *et al.*, 1970). Copper is a constituent of tyrosinase, an enzyme involved in conversion of the amino acid tyrosine to melanin, the black pigment of hair. Smith and Ellis (1947) observed a graying of the black hair in Dutch rabbits fed a copper-deficient diet (Fig. 8.4). Anemia also occurred. Copper, as a component of a metalloprotein called ceruloplasmin, functions in iron absorption, so copper

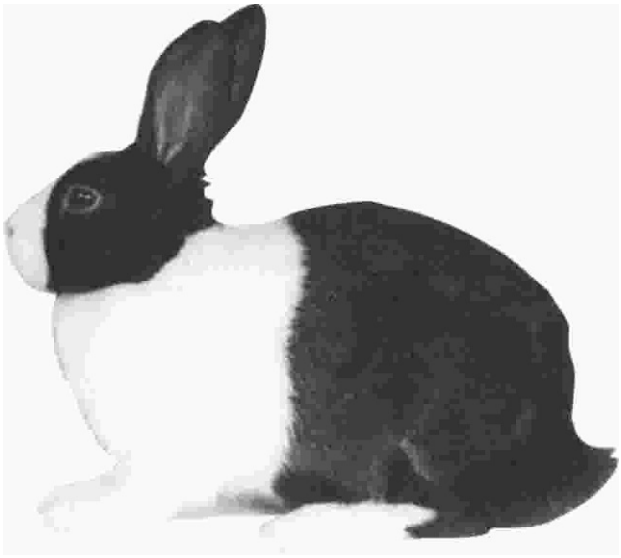


Fig. 8.4 Graying of the black hair of Dutch rabbits caused by a copper deficiency. (Courtesy of S. E. Smith, Cornell University, Ithaca, N.Y.)

TABLE 8.6

Effect of Dietary Copper Status on Rabbit Tissues[a]

Item	Diet	
	Control	Copper deficient
Hematocrit (%)	40.7	26.4
Hemoglobin (g/100 ml)	12.4	7.8
Liver cytochrome oxidase[b]	89.4	41.3
Heart cytochrome oxidase[b]	37.9	29.1
Liver iron (μg/g wet wt.)	143.7	238.0
Liver copper (μg/g wet wt.)	4.5	2.4

[a] Data from Hunt *et al.* (1970).

[b] Reaction rate constant/min/mg nitrogen ($\times 10^3$ for liver, $\times 10^2$ for heart).

deficiency results in an induced iron deficiency anemia. Copper also has a role in iron metabolism at the cellular level, and is necessary in the synthesis of hemoglobin and red blood cell maturation.

Effects of copper deficiency on tissue parameters in rabbits are shown in Table 8.6. Anemia was manifested by low hematocrit and hemoglobin levels. Liver iron was elevated, because of the reduced hemoglobin formation. Cytochrome oxidase activities of liver and heart were depressed.

Swick *et al.* (1981) found no difference in efficiency of copper absorption between casein and soybean meal-based diets, indicating that phytates in soybean meal do not impair copper absorption in rabbits.

Besides its role as an essential nutrient, copper has been used as a feed additive for swine and poultry to increase growth rate and reduce enteric disease. The British researcher R. Braude noticed pigs chewing on copper rings in a pen. This observation led to trials with copper sulfate as a feed additive that showed growth responses similar to those obtained with certain antibiotics. In some European countries, copper sulfate is extensively used as a feed additive for swine, because of its growth-promoting properties. A variety of studies have been conducted with rabbits evaluating copper sulfate as a growth promoter, with conflicting results (Omole, 1980). King (1975) found no increase in growth rate when 200 ppm copper sulfate was fed; average daily gains were 18.36 g for controls and 18.85 g for the copper group. A thinning of the cecal wall was noted with the copper supplementation, which King (1975) suggested could facilitate nutrient absorption. Omole (1977) conducted an experiment using three levels of dietary protein (14, 18, and 22%), each with 0, 100, 150, or 200 ppm copper. A slight increase in average daily gain was noted, with values of 18.1, 19.6, 20.3, and 21.1 for 0, 100, 150, and 200 ppm copper, respectively. There was an indication

that with higher protein levels the amount of supplemental copper required to increase growth was reduced.

Patton *et al.* (1982) reported a highly significant response to 400 ppm dietary copper, in terms of growth, feed efficiency, and reduced mortality from diarrhea. Average daily gain was 40.8 g for the copper-supplemented group versus 31.1 g for the controls. Mortality from enteritis was 25% in the control group and 4% in the copper-supplemented group. This experiment was conducted during a period of considerable heat stress, which may indicate an interaction between copper response and environmental temperature. In further studies, Grobner *et al.* (1986b) determined the effect of copper sulfate on the *in vitro* growth and toxin production of *Clostridium spiroforme*, one of the major microbes implicated in rabbit enterotoxemia (see Chapter 12). With a concentration of 250 ppm copper in the medium, both growth (colonies formed) and toxin production were markedly reduced, suggesting a mechanism of action for copper sulfate in protecting against enterotoxemia.

Grobner *et al.* (1986a) conducted a further evaluation of the effects of copper sulfate, using both high-energy and low-energy diets. No significant positive response to copper was observed (Table 8.7), although gains with the 50, 100, and 250 ppm copper were 11, 15, and 7% higher than for the control diet. The toxic level of copper, in terms of growth depression, was between 500 and 1000 ppm.

TABLE 8.7

Performance and Liver Copper Levels of Weanling Rabbits Fed Various Levels of Copper Sulfate in Diets High or Low in Alfalfa[a]

Diet	Average daily gain (g)	Average daily feed intake (g)	Liver copper (ppm, dry weight basis)
54% Alfalfa			
0 ppm added Cu	31.7	104	12.3
50 ppm added Cu	37.4	124	26.1
100 ppm added Cu	38.3	120	116.4
250 ppm added Cu	34.1	114	195.4
500 ppm added Cu	37.5	124	890.2
1000 ppm added Cu	29.2	107	1743.9
20% Alfalfa			
0 ppm added Cu	31.8	89	23.7
50 ppm added Cu	32.9	94	25.5
100 ppm added Cu	34.5	94	36.9
250 ppm added Cu	33.6	83	84.8
500 ppm added Cu	28.3	89	981.4
1000 ppm added Cu	15.1	68	1390.4

[a] From Grobner *et al.* (1986a).

TABLE 8.8

Effect of Dietary Copper Level on Tissue and Fecal Copper Concentration[a]

Level added copper (ppm)	Copper concentration (ppm, dry matter basis)			
	Muscle	Kidney	Liver	Feces
0	2.6	9.6	12.3	57.6
50	3.0	15.7	26.1	87.5
100	3.0	11.4	116.4	171.2
250	3.6	10.9	195.4	352.2
500	3.4	14.6	890.2	661.4
1000	2.0	37.1	1743.9	1741.3

[a] Data from Grobner *et al.* (1986a).

A high dietary alfalfa level protected against the growth-depressing effects of 1000 ppm copper (Table 8.7), despite the fact that daily copper intake was greater with the high-alfalfa diet. One explanation for this protective activity could be that alfalfa fiber may bind copper, and cause it to be excreted with the fiber in the hard feces. With a low-fiber diet, more of the copper may be returned to the cecum by antiperistaltic movements, and be recycled via the cecotropes. Thus, on low-fiber diets, copper may be retained and result in greater copper accumulation than with high-fiber diets. Eden (1941) noted that in the normal rabbit a single supplement of copper required 4–5 weeks for complete excretion, while excretion was complete in 5 days in animals prevented from reingesting cecotropes.

The effects of copper supplementation on tissue and fecal copper levels are shown in Table 8.8. Copper does not accumulate in the meat, but liver and kidney copper concentrations are increased as dietary copper level rises.

The preceding studies were conducted with weanling rabbits, fed copper for a relatively short period of time. Harris *et al.* (1984a) conducted a longer term study with does, receiving a control diet or the same diet with 250 ppm copper. No differences in performance were seen, with 65 litters from the control group and 51 litters from the copper group, over the 6-month experimental period.

Concern has been expressed in Europe that the use of copper sulfate as a feed additive for swine may cause elevated forage copper levels when the manure is used as a fertilizer. Sheep are quite susceptible to copper toxicity, so it is possible that sheep grazing areas where high-copper manure has been used may develop copper toxicity. It is interesting that there are pronounced breed differences in sheep in susceptibility to copper toxicity. The North Ronaldsay breed inhabits beaches on remote islands in Scotland, and subsists primarily on seaweed, which is low in copper. Apparently this breed has developed efficient mechanisms for

copper retention to aid its survival on a low-copper diet. As a result, it is so sensitive to copper toxicity that it cannot be kept alive on normal sheep pastures, a finding that has complicated plans to raise the animals elsewhere to prevent their extinction in case of oil spills or other environmental catastrophe in their native habitat.

Grobner *et al.* (1985) examined the effect on plant copper levels of fertilizing comfrey with rabbit manure from rabbits fed either a low-copper or high-copper diet. The manure averaged 58 ppm and 352 ppm copper, respectively. Copper content of the comfrey over a growing season was not different between the two treatments (18.6 and 22.0 ppm, respectively). Izquierdo and Baker (1986) and Suttle and Price (1976) noted that the copper in the feces of pigs fed high dietary copper levels and in pasture fertilized with copper-rich swine manure was of low availability to both chicks and sheep. Thus it appears that use of copper sulfate as a feed additive is unlikely to result in copper toxicity when the manure from the copper-fed animals is used as a fertilizer.

Pyrrolizidine alkaloids are toxic compounds in several plant species which cause irreversible liver damage and elevated liver copper levels (Cheeke and Shull, 1985). Comfrey contains pyrrolizidine alkaloids. Grobner *et al.* (1985) fed fresh comfrey free choice to rabbits for 120 days, and observed no significant differences in liver copper levels (456 ppm for controls and 440 ppm for animals fed comfrey). No liver abnormality was observed. Comfrey apparently can be safely fed to rabbits, as they are resistant to the toxic effects of pyrrolizidine alkaloids (Pierson *et al.*, 1977).

Aulerich *et al.* (1982) noted that mink fed 100 or 250 ppm copper had darker fur than controls, suggesting that copper might have beneficial effects in intensifying hair color of dark animals. This might have implications in Rex fur production.

TABLE 8.9

Effect of Dietary Copper on Rabbits Experimentally Infected with *Trypanosoma brucei*[a]

Item	Dietary copper supplementation (ppm)		
	0	125	250
Average initial weight (g)	567	564	563
Average final weight (g)	1594	1705	1918
Average daily gain (g)	16.3*[b]	18.1*,**	21.5**
Feed/gain	3.77*	3.29*,**	2.90**
Parasites (10^3/mm^3)	203	155	62

[a] From Omole and Onawunmi (1979).

[b] *,**Different ($p < 0.05$).

TABLE 8.10

Effect of Coccidiosis Infection on Performance and Liver Copper of Chicks[a]

Treatment	Experiment 1		Experiment 2	
	Weight gain (g)	Liver copper (ppm)[b]	Weight gain (g)	Liver copper (ppm)[b]
Basal	257	18	288	12
Basal + 500 ppm copper	246	324	216	353
Basal + coccidiosis	226	30	250	7
Basal + 500 ppm copper + coccidiosis	210	901	195	927

[a] Data from Southern and Baker (1982).
[b] Dry matter basis.

An interesting observation of Omole and Onawunmi (1979) is that 250 ppm dietary copper may help protect rabbits from the effects of infection with *Trypanosoma brucei,* a protozoal parasite that causes sleeping sickness in tropical countries. Added copper resulted in improved performance and lower parasite infection levels of rabbits experimentally infected with trypanosomes (Table 8.9). It is not known if copper sulfate influences other protozoal infections of rabbits, such as coccidiosis. Southern and Baker (1982) found that coccidiosis infection in chicks resulted in markedly higher liver copper levels when 500 ppm copper was fed (Table 8.10).

The effects of copper sulfate as a feed additive at levels above 100 ppm appear to be that, in general, there is a 5–10% improvement in growth rate and feed efficiency with supplementary copper. There may be a beneficial effect on reduction of enteritis. As is the case with swine, in some studies there may be dramatic responses, in others virtually no response, and overall, a moderate positive response.

X. MOLYBDENUM

Molybdenum is a mineral element of considerable importance in ruminant nutrition, because of its interrelationships with copper. In some parts of the world, copper deficiency symptoms have occurred in cattle grazing pastures that contained normal copper levels. The problem was found to be associated with elevated concentrations of molybdenum in the forage. High intakes of molybdenum induce a copper deficiency. In contrast, low levels of forage molybdenum can be associated with copper toxicity. A further complicating factor is that the

copper—molybdenum interrelationship is influenced by the level of inorganic sulfate present. Under conditions of low copper, high sulfate intensifies the toxic effects of molybdenum, whereas with adequate copper levels, much higher levels of molybdenum are required to induce copper deficiency, and inorganic sulfate intensifies the molybdenum effect.

Arrington and Davis (1953) showed that a high level of molybdenum induced copper deficiency in rabbits, with typical signs such as anemia.

Molybdenum is an essential nutrient, being a constituent of the enzyme xanthine oxidase. This enzyme functions in the metabolism of nucleic acids and the formation of uric acid.

Either deficiency or toxicity of molybdenum in rabbit feeding is extremely unlikely.

XI. SELENIUM

Selenium has been of interest in animal nutrition since the 1930s, when it was discovered to be the toxic factor responsible for "alkali disease" and "blind staggers" in livestock in the Great Plains area of the United States. Interest in the element was exclusively concerned with its toxic properties until 1957, when it was demonstrated to be an essential nutrient. Selenium deficiency was shown to induce liver degeneration in rats. This discovery was soon followed by the demonstration that supplemental selenium prevented "white muscle disease" in calves and lambs. Degeneration of skeletal and heart muscle occurs with this disorder. In the early 1970s the metabolic role of selenium was found to be as a constituent of the enzyme glutathione peroxidase. This enzyme catalyzes the detoxification of hydrogen peroxide and other peroxides formed in metabolism. The action of selenium is closely linked with that of vitamin E. Vitamin E, as a natural antioxidant, prevents the development of peroxides while selenium, as a constituent of glutathione peroxidase, functions in the disposal of any peroxides that are formed. Peroxides cause damage to cell membranes and enzymes, so with a deficiency of vitamin E or selenium, widespread tissue damage occurs. White muscle disease is also called nutritional muscular dystrophy. Other selenium–vitamin E responsive diseases include liver necrosis in rats and swine and exudative diathesis in chickens.

Occurrence of selenium deficiencies and toxicities shows a geographical distribution (Fig. 8.5). Areas of selenium deficiency are usually those with soils of volcanic origin, such as the U.S. Pacific Northwest. This is because selenium is a volatile element, and is released into the atmosphere by volcanic action. The Great Plains area has soils with a high selenium content (Fig. 8.5), because the volatile selenium from the volcanic areas of the west coast was deposited in the plains area.

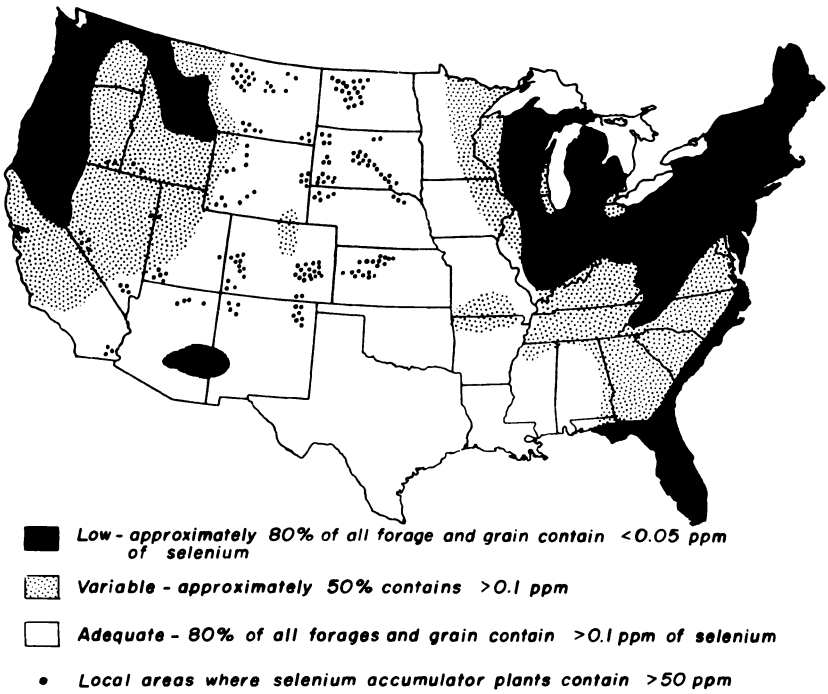


Fig. 8.5 Selenium concentration in plants in various parts of the United States. The Pacific Northwest, the Northeast, and Florida are characterized by selenium deficiency, while areas of toxic selenium concentrations are found in the Great Plains states. (Courtesy of J. Kubota, U.S. Plant, Soil, and Nutrition Laboratory, Ithaca, N.Y.)

In many animals, selenium and vitamin E have a mutual "sparing effect," and some deficiency symptoms of one of these nutrients can be prevented by adequate levels of the other. For example, if rats are fed a low-selenium, low-vitamin E diet based on torula yeast (which, coincidentally, has very low levels of both vitamin E and selenium), they will develop liver necrosis and die. If either vitamin E or selenium is added, growth is normal and liver necrosis does not occur. In contrast, if rabbits are fed a torula yeast-based diet, they develop nutritional muscular dystrophy, which is only prevented by the addition of vitamin E. Selenium has no effect (Draper, 1957; Hove *et al.*, 1958). This work suggests that rabbit tissues depend on vitamin E for their protection against peroxide damage.

Because of the apparent lack of response to selenium by the rabbit, Cheeke and Whanger (1976) examined rabbit tissues for their activity of the selenium-containing enzyme glutathione peroxidase. Normal levels, comparable to those in rats, were found. Lee *et al.* (1979) reported that rabbit tissues such as kidney and liver have a high content of non-selenium-dependent glutathione peroxidase

activity. This may help to explain in part the lack of response by rabbits to dietary selenium deficiency.

Jenkins *et al.* (1970) fed low-selenium hay to sheep, cattle, and rabbits. The ruminant animals developed typical signs of selenium deficiency (white muscle disease). The rabbits were not adversely affected by the low-selenium hay. When linoleic acid was fed along with the hay, to increase the requirement for protection against peroxides, rabbits developed severe muscular dystrophy. Added selenium gave no protection. These authors concluded that the rabbit depends on vitamin E rather than on selenium for its protection against peroxide damage, and that the vitamin E requirement of rabbits is higher than for ruminants.

The available literature suggests that selenium is not a dietary requirement for rabbits. However, before this conclusion can be reached, long-term multi-generational experiments with rabbits fed a low-selenium diet supplemented with adequate vitamin E must be conducted. In rats, for example, a selenium deficiency in the presence of adequate vitamin E can only be demonstrated in second-generation animals, derived from parents fed the selenium-deficient diet. In practical terms, it is unlikely that selenium supplementation of rabbit diets, even in low-selenium areas, is needed.

XII. IODINE

Iodine functions as a component of the thyroid hormones, which are thyroxine (tetraiodothyronine) and triiodothyronine. In the thyroid gland, the amino acid tyrosine reacts with iodine, and two iodinated tyrosines react together to produce thyroxine. Thyroxine contains four iodines (tetraiodo), while triiodothyronine contains three.

The thyroid hormones function in regulating energy metabolism. The exact mode of action at the cellular level is unknown, but the net effect is that the metabolic rate is largely controlled by the thyroid hormones.

Lack of dietary iodine results in goiter, an enlargement of the thyroid gland. This is often most evident in the offspring of females fed an iodine-deficient diet. A common cause of goiter in livestock is the presence of goitrogens in feedstuffs. Goitrogens are substances that interfere with iodine metabolism and the synthesis of thyroid hormones. Goitrogens are most common in *Brassica* species, such as cabbage, kale, rape, turnips, and mustard. Goitrogens are discussed in more detail in Chapter 15.

No minimum requirement of rabbits for iodine has been established. The question of a minimum requirement is a bit academic, since the routine use of iodized salt in the diet will ensure that no deficiency occurs. The NRC (1977) recommends at least 0.2 mg of iodine per kilogram of diet.

Iodine toxicity, resulting in a high mortality of newborn rabbits, has been reported by Arrington *et al.* (1965). Excess iodine, as with a deficiency, may cause goiter.

XIII. COBALT

Many areas of the world have soils that are deficient in cobalt. Cattle and sheep grazing pastures in cobalt-deficient areas may "starve in the midst of plenty." In spite of abundant pasture, they waste away and become extremely emaciated. Australian scientists discovered that lack of cobalt was the cause of "wasting disease." In 1948, vitamin B_{12} was isolated, and its structure elucidated in 1955. A feature of the structure of vitamin B_{12} is that it contains cobalt. The only known metabolic role of cobalt is as a component of this vitamin. Cobalt deficiency is a metabolic deficiency of vitamin B_{12}. In ruminants, rumen microorganisms synthesize vitamin B_{12}, so cobalt is required in the diet for the bacteria to incorporate it into the vitamin molecule. Vitamin B_{12} functions in the metabolism of one of the volatile fatty acids (VFA), propionic acid. In ruminants on a cobalt-deficient diet, the metabolic deficiency of vitamin B_{12} prevents the metabolism of propionic acid, causing a metabolic shortage of ATP. In addition, the accumulation of propionic acid in the blood depresses feed intake, with the result that the animal wastes away in the presence of abundant feed.

Ruminants have a higher cobalt requirement than horses or rabbits (Underwood, 1977). Horses thrive on cobalt-deficient pastures on which cattle and sheep cannot survive. Reasons for this include the use of cobalt by rumen microorganisms to synthesize nonactive cobalt-containing compounds other than vitamin B_{12}, and the greater metabolic requirement for the vitamin because of their dependence on VFA metabolism. Rabbits can survive on diets providing only 0.1 μg/day of cobalt (Thompson and Ellis, 1947).

Utilization of cobalt by bacteria in the rabbit hindgut is much more efficient than in the rumen (Simnett and Spray, 1965a). After 51 weeks on a diet containing less than 0.03 ppm cobalt, no deficiency signs were observed in rabbits. Absorption of vitamin B_{12} is more efficient in the rabbit than in humans, rats, or sheep (Simnett and Spray, 1965b), because of coprophagy. These authors found that rabbits had very high serum vitamin B_{12} levels, up to 150 times higher than the highest values reported in humans or rats. Rabbits probably have a lower metabolic requirement for vitamin B_{12} than do ruminants, because propionic acid is the VFA produced in lowest concentration in the cecum. Acetate and butyrate, the two major VFA in rabbits, do not require vitamin B_{12} for their metabolism.

Cobalt deficiency in rabbits would thus appear to be extremely unlikely.

XIV. CHROMIUM

Chromium has been shown to be an essential nutrient, involved in the functioning of insulin in the regulation of carbohydrate metabolism. Chromium-deficient animals have impaired glucose tolerance, meaning that the ability to remove glucose from the blood and metabolize it in the tissues is impaired. Chromium deficiency symptoms are similar to those of insulin insufficiency, or diabetes.

Chromium deficiency in rabbits has not been reported.

XV. SOME CONCLUDING COMMENTS

The preceding discussion may have given the impression that if rabbit diets are not carefully formulated, mineral deficiencies or imbalances can easily occur. In fact, it is fair to say that under most circumstances the mineral needs of rabbits are very easy to meet. In most parts of the world, particularly in North America and Europe, alfalfa meal is a major constituent of rabbit diets. Alfalfa is an excellent source of calcium, magnesium, and trace elements. Cereal grains, and particularly grain milling by-products such as wheat bran, wheat mill run, wheat middlings, and rice bran, etc. are excellent sources of phosphorus. Phytate phosphorus is of high bioavailability in rabbits. Thus, a simple mixture of alfalfa and grain or grain by-products will generally meet the calcium and phosphorus requirements. The trace element needs can be met by using 0.5% trace mineralized salt, a standard practice. A salt–trace mineral mixture that is formulated for swine or poultry will be adequate for rabbits. Therefore, in most cases, the mineral needs of rabbits are readily met just from the ingredients normally used. The recycling of ingesta via coprophagy further aids in mineral absorption and conservation. Rabbits are usually fed low-energy diets, which result in a high relative feed intake, further providing abundant opportunity for adequate minerals to be consumed. While these comments should not be interpreted to mean that minerals should be ignored, it should be recognized that nutritional problems relating to minerals are not commonly seen in rabbits.

The suggested dietary mineral requirements for rabbits are listed in Tables 16.1 and 16.2. Fortification of diets to meet mineral requirements is best left to professional nutritionists associated with feed manufacturing plants, rather than being attempted by rabbit raisers. Many factors influence the optimal composition of mineral mixtures, including the bioavailability of minerals from individual chemical compounds (e.g., the copper in copper sulfate is much more available to animals than the copper in copper oxide), the amount of water in the mineral source (water of hydration), the tendency of some mineral sources to

absorb water and become hard (cake) and so on. In general, limestone (calcium carbonate) is a good source of calcium, and dicalcium phosphate is a good source of calcium and phosphorus. Trace elements can be obtained from a commercially formulated trace mineral mixture prepared for swine or poultry feeds.

Requirements for trace elements are often expressed in parts per million (ppm). A feed with 250 ppm copper has 250 parts of copper for every 1 million parts of feed. That is, 1 lb of copper per million pounds, 1 g per million grams, and so on. Another common way of expressing requirements is in milligrams per kilogram of feed. It is helpful to remember that ppm and mg/kg are synonymous. As an example, suppose that a feed sample contains iron at 15 mg/kg. To convert this to ppm iron, the following apply:

1 kg feed contains 15 mg iron.

Therefore, 1000 g feed contain 15 mg iron (1 kg = 1000 g).

1 million mg of feed contain 15 mg iron (1 g = 1000 mg) = 15 mg iron per 1 million parts of feed = 15 ppm.

This figure can also be converted to a percentage:

1000 g of feed contain 15 mg iron = 0.015 g iron.

Therefore, 100 g of feed contain 0.0015 g iron = 0.0015% iron.

TABLE 8.11

Composition of a Salt–Mineral Premix[a,b]

Ingredient	Amount per kilogram of mix
$CoSO_4 \cdot 7H_2O$	40 mg
$CuSO_4 \cdot 5H_2O$	350 mg
$MnSO_4 \cdot H_2O$	810 mg
$(NH_4)_6Mo_7O_{24} \cdot 7H_2O$	230 mg
$Ca(IO_3)_2 \cdot H_2O$	120 mg
$ZnSO_4 \cdot 7H_2O$	3 g
$FeHOCH_2(CHOH)_4CO_2 \cdot 2H_2O$	7.5 g
NaCl	50 g
$CaCO_3$	110 g
$CaHPO_4 \cdot 2H_2O$	134 g
$MgSO_4 \cdot 7H_2O$	205 g
$NaHCO_3$	80 g
$KHPO_4$	100 g
$KHCO_3$	100 g
Corn starch	210 g

[a] From Partridge and Allan (1982).

[b] Added at a level of 5% to the diet.

A common point of confusion is to regard mineral elements and mineral salts as being synonymous. One pound of copper sulfate (a salt) is not the same as 1 lb of copper (an element). The amount of copper in copper sulfate is determined by adding up the atomic weights of copper, sulfur, and oxygen (times four, because there are four oxygens in copper sulfate) and calculating the percentage of copper in the total. In feed-grade copper sulfate, the copper content is 25.5%. Thus, 1 lb of copper sulfate provides only 0.25 lb of copper. Feed-grade copper sulfate contains water of hydration, so the copper content is different than for anhydrous copper sulfate. Hopefully, these complications are sufficient evidence that preparation of a mineral supplement should not be attempted by the average rabbit raiser.

A mineral premix which has been successfully used in commercial-type rabbit diets is that of Partridge and Allan (1982), shown in Table 8.11.

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9

Vitamins

Over the last several hundred years, the existence of substances later to be called vitamins was suspected. Early explorers, such as Captain Cook, recognized that scurvy could be prevented by consuming green plants and citrus fruit. Cook grew a plant called "scurvy grass" on board his ship, and forced the sailors to eat it. Another disease, beri-beri, was recognized to be of nutritional origin. The Dutch scientist, Eijkman, in what is now Indonesia, noted that rice polishings contained a factor that prevented or cured beri-beri. The active component was found to be an amine. In 1912, the Polish scientist Casimir Funk referred to this compound as a "vital amine," which was later shortened to vitamine, and finally to vitamin. Although most vitamins are not amines, the term came into general use.

Vitamins are defined in the following manner:

1. They are organic compounds, distinct from carbohydrates, proteins, and fats.
2. They are present in foods in very small amounts compared to amounts of carbohydrates, proteins, and fats. Even a huge dose of a vitamin is a very small quantity of substance by weight.
3. Vitamins are essential for some metabolic process, so when they are deficient in the diet, specific deficiency signs develop.
4. With some exceptions, vitamins cannot be synthesized by animals and so must be present in the diet. Exceptions include vitamin D, which can be synthesized in the skin upon exposure to ultraviolet light; niacin, which can be synthesized from the amino acid tryptophan; and vitamin C, which most animals can make from glucose.

Vitamins can be classified into two groups: the fat-soluble and water-soluble vitamins. The fat-soluble group, which includes vitamins A, D, E, and K, tend to be stored for long periods of time by animals, particularly in the liver. With the exception of vitamin K, they are not synthesized by microbes in the digestive tract. The water-soluble vitamins, which include the vitamin B complex (thiamin, riboflavin, niacin, pyridoxine, pantothenic acid, folacin, biotin, choline, vitamin B_{12}) and vitamin C (ascorbic acid), are synthesized by intestinal micro-

bes, which is particularly important in rabbits because of the cecal microbes and coprophagy.

In this chapter, the properties, metabolism, deficiencies, toxicities, and occurrence in feeds will be described for each vitamin.

I. VITAMIN A

Vitamin A is actually a mixture of compounds that have vitamin A activity. Plants do not contain vitamin A as such, but rather contain carotenoid pigments, of which β-carotene is the most important. β-Carotene is converted to vitamin A within animals, primarily in the intestinal mucosa. Xanthophylls are carotenoid pigments that do not contain vitamin A activity but are responsible for the yellow pigmentation of egg yolks and the fat and skin of broiler chickens. Rabbits do not normally deposit xanthophylls in their fatty tissues. Some rabbits have a genetic lack of an enzyme that hydrolyzes xanthophylls, and therefore may develop yellow body fat. The yellow fat condition is caused by a homozygous condition for a recessive gene.

The β-carotene molecule can be split apart to yield two molecules of vitamin A. The efficiency of this conversion varies among animals (Table 9.1). The conversion of β-carotene occurs primarily in the cells of the intestinal mucosa. A copper-containing enzyme cleaves the β-carotene molecule in half, to yield two molecules of vitamin A.

TABLE 9.1

Efficiency of Conversion of β-Carotene to Vitamin A in Different Animal Species[a]

Species	Conversion efficiency (%)	IU Vitamin A equivalent to 1 mg β-carotene
Rat	100	1667
Chicken	100	1667
Rabbit	100	1667
Swine	30	500
Cow	24	400
Sheep	30	500
Horse	33	555
Human	33	555
Dog	67	1111

[a] Adapted from Bondi and Sklan (1984).

Three compounds with vitamin A activity are vitamin A alcohol (retinol), vitamin A aldehyde (retinal), and vitamin A acid (retinoic acid). Retinol is the most potent form. In its metabolism, retinol may form an ester linkage with fatty acids, producing retinyl esters. Synthetic vitamin A is usually sold in the form of retinol esters, such as retinol acetate and retinol palmitate. The ester forms are more stable than free retinol, which is very readily oxidized in the presence of light.

A. Vitamin A Units

Vitamin A activity is expressed in international units (IU). One IU of vitamin A is equivalent to 0.3 μg of retinol (0.344 μg retinyl acetate and 0.55 μg for retinyl palmitate) and 0.6 μg β-carotene.

B. Metabolism of Vitamin A

Vitamin A activity in plants is associated with β-carotene, which is converted to retinol in the intestinal mucosa. Dietary vitamin A, usually from synthetic sources, is generally in the form of retinyl esters such as retinyl palmitate. The esters are hydrolyzed in the intestine, and retinol is absorbed into the mucosal cells. Both carotene and retinol are emulsified with fatty acids and bile salts in the intestine, forming temporary micelles that facilitate absorption. In the mucosal cells, retinol is esterified with palmitic acid, producing retinyl palmitate. Retinyl esters enter the blood via the lymphatic tissue, are removed from the blood by the liver, and are stored in the liver cells as retinyl ester. As it is needed, liver vitamin A enters the blood, bound to a retinol-binding plasma protein, and is transported to the cells in this form. Retinol is transferred from the blood retinol-binding protein to intracellular retinol-binding protein. Within the cells, it participates in a number of metabolic activities.

C. Regulation of Vitamin A Metabolism

Vitamin A is stored in the liver. It is poorly excreted, although some is excreted via the bile as retinyl glucuronide. The blood plasma level of retinol is homeostatically regulated to a more or less constant level, while the liver level reflects the dietary vitamin A level (Fig. 9.1). Plasma vitamin A levels do not reflect an animal's vitamin A status except in severe deficiencies or toxicities. For this reason, if it is desired to assess vitamin A status, liver rather than blood should be analyzed.

The normal level of vitamin A in the blood plasma of most animals is about 30 μg/100 ml (100 IU/100 ml), with a range of about 20–60 mg/100 ml. The normal level in the rabbit may be somewhat higher. Lorente and Miller (1977)

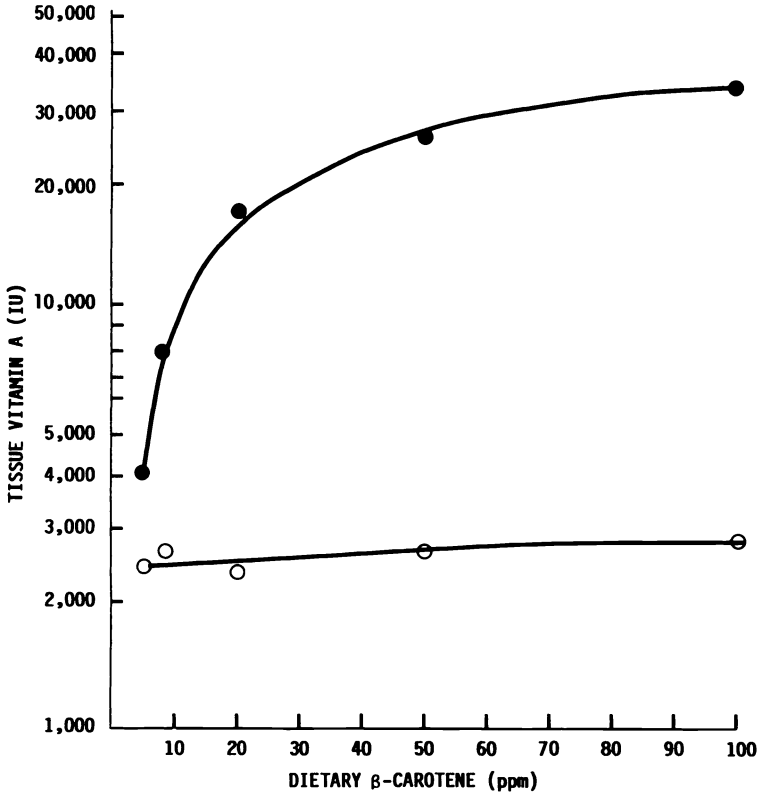


Fig. 9.1 The blood vitamin A level (○) shows little change over a wide range of carotene or vitamin A intakes, while the liver (●) shows pronounced changes. Note the logarithmic scale for tissue vitamin A concentrations. (Data from Kormann and Schlachter, 1984.)

reported a value of 80 μg (266 IU) of retinol per 100 ml, and a total vitamin A concentration of 143 μg/100 ml of serum in rabbits fed a standard laboratory rabbit diet. Deviations from the normal level occur only when the liver is severely depleted in vitamin A (levels below 10 μg/g liver) or with very high dietary vitamin A levels. Normally the level of retinyl ester in the blood is very low; with vitamin A toxicity, increases in retinyl ester occur. Thus the presence of retinyl ester in blood is suggestive of vitamin A toxicity.

D. Metabolic Functions of Vitamin A

1. Vitamin A and Vision

Retinol functions in the eye as part of a visual pigment, rhodopsin. Rhodopsin reacts with light to send a signal to the brain via the optic nerve, allowing vision.

It is particularly involved in vision in dim light, so a symptom of vitamin A deficiency is night blindness. Prolonged vitamin A deficiency may produce permanent blindness.

2. Maintenance of Epithelial Tissue

Vitamin A is necessary for the maintenance of normal epithelial tissue of the skin and mucous membranes. One of the functions of vitamin A is in the reaction of sugars with proteins to form glycoproteins or mucopolysaccharides which are the main constituents of collagen, elastin, cartilage, and other connective tissue. In vitamin A deficiency, the glycoproteins of epithelial cells and mucous membranes are defective. The epithelial cells become keratinized and less functional. Keratinization of mucous membranes of the eye may cause permanent blindness (xerophthalmia). The epithelial tissues, including those of the digestive tract, are susceptible to bacterial infection with vitamin A deficiency. A high incidence of enteritis is seen in vitamin A-deficient rabbits as a result.

3. Vitamin A and Bone Growth

The organic matrix of bone consists of mucopolysaccharides, which require vitamin A for their proper synthesis. In vitamin A deficiency, bone growth is defective. The changes in bone structure may cause elevated cerebrospinal fluid pressure, which in turn may affect nerve function, producing incoordination, staggering, and convulsions in advanced vitamin A deficiency. Neural lesions, ataxia (incoordination), and spastic paralysis occur in vitamin A-deficient rabbits (Mellanby, 1935; Phillips and Bohstedt, 1938).

4. Vitamin A and Reproduction

Vitamin A deficiency impairs fertility in both sexes. In males, testicular degeneration and cessation of sperm production occur (Payne *et al.*, 1972). Vitamin A is required for maintenance of pregnancy. Vitamin A-deficient rabbits may abort or resorb their fetuses. Lamming *et al.* (1954a,b,c) demonstrated that hydrocephalus (fluid accumulation in the head) occurs in kits from vitamin A-deficient does. Besides fetal hydrocephalus, other typical reproductive effects of vitamin A deficiency in rabbits include low conception rates, fetal resorption, abortion, and small, weak litters. The does show poor maternal abilities and lack of milk production.

There have been suggestions that β-carotene may improve reproductive performance in animals. Kormann and Schlachter (1984) obtained preliminary evidence that it may have some beneficial effects on rabbit reproduction, although it was not clear that this was differentiated from a vitamin A response.

5. Vitamin A and Growth

One of the first signs of vitamin A deficiency in growing animals is the cessation of growth. The metabolic role of vitamin A in cellular growth is not

conclusively known, but it appears to be involved in protein synthesis and nucleic acid metabolism (Bondi and Sklan, 1984).

6. Vitamin A and Health

Vitamin A-deficient animals are susceptible to disease and infection, in part because of its role in the maintenance of epithelial tissues and mucous membranes. Vitamin A-deficient animals are susceptible to respiratory disease. Vitamin A seems to increase immunity responses. Washington State University researchers have noted a correlation between vitamin A status and resistance to mastitis in dairy cattle (Chew *et al.*, 1982).

Vitamin A and synthetic retinoid derivatives have been shown to be effective in suppression of cancer (Bondi and Sklan, 1984). Vitamin A-deficient rats have an increased tumor incidence over controls when exposed to carcinogens.

E. Vitamin A Toxicity

The liver can store large quantities of vitamin A, but when it becomes saturated, retinyl ester is released into the blood and toxicity signs develop. Many of the

TABLE 9.2

Effect of a High Dietary Level of Vitamin A on Reproductive Performance of Rabbits[a]

Item	Diet	
	191,180 IU/kg	11,440 IU/kg
Does (*N*)	25	25
Abortions (*N*)	11	0
Kits born alive (*N*)	38	135
Kits born dead (*N*)	63	22
Average total litter birthweight (g)	242	408
Average litter size born alive (*N*)	2.5	6.8
Kits dying 1–7 days (*N*)	22	10
Kits dying 1–7 days (%)	58	11
Total litter weight at 28 days (g)	1483	3356
Kits alive at 28 days (*N*)	7	111
Kits alive at 28 days (%)	18	80
Serum vitamin A of does (μg/100 ml)		
Retinyl palmitate	90.5	10.9
Retinol	87.8	76.5
Total vitamin A	178.3	87.4
Liver vitamin A (μg/g)		
Retinyl palmitate	8,884	35
Retinol	1,257	21
Total vitamin A	10,141	56

[a] From Cheeke *et al.* (1985).

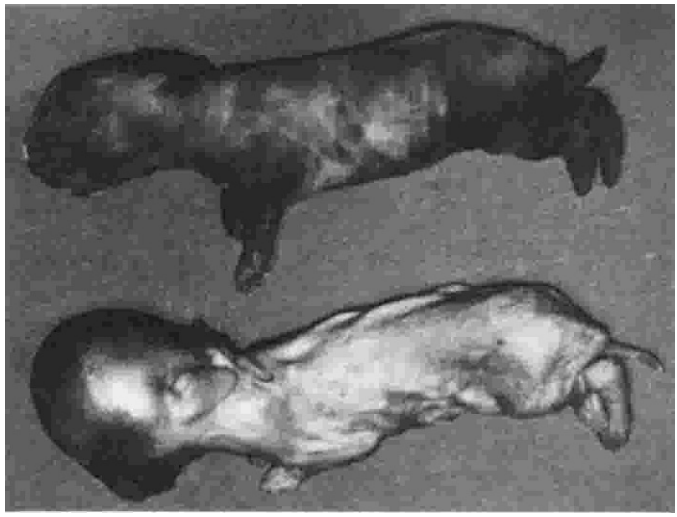


Fig. 9.2 Hydrocephalus in a kit born to a dam fed a high level of vitamin A (bottom). Normal kit at top.

signs of vitamin A toxicity are similar to those of a deficiency, including reduced growth, bone abnormalities, and reproductive failure. According to Scott *et al.* (1982), retinol and its esters are nontoxic to animals at levels up to about 1–1.5 million IU/kg of diet, a level about 500 times the minimum requirement. However, reproduction in the rabbit is adversely affected by much lower levels than this. Cheeke *et al.* (1984) fed a diet with 191,180 IU/kg to does, and observed severe reproductive problems (Table 9.2). In the treatment with high-dose vitamin A, there were abortions, fetal resorptions, small litters, kits with hydrocephalus (Fig. 9.2), and low neonatal viability. Breeding for a second litter per doe was attempted, but all litters were resorbed or aborted. Further studies are needed to determine the minimum level of vitamin A that is toxic for fetal development. It is interesting that these adverse effects of hypervitaminosis A are similar to those of vitamin A deficiency.

Lorente and Miller (1977) found that the pregnant rat and rabbit differ in their responses to high-dose vitamin A. In the rat, high levels of vitamin A given to the dam cause increased fetal liver vitamin A levels capable of causing malformations like cleft palate. The rabbit fetus is protected against such malformations by a low fetal vitamin A uptake, but at a high enough vitamin A level, this protection breaks down suddenly and embryonic mortality occurs.

F. Vitamin A Requirements of Rabbits

Precise vitamin A requirements for growth and reproduction have not been determined. Payne *et al.* (1972) found that 1160 IU/kg diet was not adequate for

does in production. In view of the important effects of vitamin A on reproduction in rabbits, it is important that accurate estimates of the minimum requirement and the maximum tolerated levels be determined. Lebas (1980) set a provisional requirement at 10,000 IU/kg of diet.

G. Sources of Vitamin A in Feeds

Vitamin A activity in plant materials is associated with β-carotene, whereas in products of animal origin it is vitamin A per se. Alfalfa is the richest plant source of vitamin A activity, while fish or marine mammal liver oils are extremely rich in vitamin A. Yellow corn is the only grain with vitamin A activity. Oil meals like soybean meal, canola meal, and cottonseed meal are devoid of vitamin A because the carotene is removed when the oil is extracted. Representative values for vitamin A activity of feedstuffs are given in Table 9.3.

Carotene is susceptible to destruction when plants are harvested. Green alfalfa has a very high carotene content, but as much as 80–95% of it can be destroyed after harvest. Exposure to sunlight during curing of hay results in a bleaching of much of the carotene. Plants contain lipoxidase enzymes that oxidize carotene after the plant is cut. Vitamin A activity is also lost during storage of feeds. Addition of an antioxidant such as ethoxyquin or butylated hydroxytoluene (BHT) will help reduce loss of vitamin A activity. Rancidity promotes destruction of vitamin A. Good-quality alfalfa meal or other forage meals are excellent sources of vitamin A activity, but if they have been stored for extensive periods or are not bright green in color, they may have little or no vitamin A activity.

TABLE 9.3

Vitamin A Activity of Natural Sources

Item	Vitamin A activity (IU/g)
Whale liver oil	400,000
Tuna liver oil	210,000
Cod liver oil	10,000
Butter	35
Eggs	10
Alfalfa meal, dehydrated	150–330
Alfalfa meal, sun-cured	50–150
Carrots	120
Yellow corn	8
Red clover	17

II. VITAMIN D

Vitamin D refers to activated sterols that can prevent rickets. Plants contain a sterol called ergosterol. After plants are harvested and the living tissue killed (as in the curing of hay), the ergosterol is activated by exposure to ultraviolet light (in sunlight) to produce ergocalciferol, also called vitamin D_2. Animals have a sterol called 7-dehydrocholesterol in their skin. With exposure to sunlight, cholecalciferol or vitamin D_3 is formed. Vitamins D_2 and D_3 are also manufactured synthetically and are available as feed additives.

In the metabolism of vitamin D, vitamin D_2, if present, is converted to vitamin D_3 in mammals (but not in poultry). Vitamin D_3 must be activated before it can function in calcium and phosphorus metabolism. Its activation involves the addition of two hydroxyl groups. In the liver, a hydroxyl group is put on C-25, to form 25-hydroxycholecalciferol. This compound then travels via the blood to the kidney, where another hydroxyl group is added to form 1,25-dihydroxycholecalciferol (1,25-OHD_3), which is the metabolically active form of vitamin D. The 1,25-OHD_3 is released into the blood, and acts in the cells of the intestinal mucosa to regulate the synthesis of a calcium-binding protein. This protein transports calcium from the intestine into the blood, and thus controls calcium absorption. As previously described (Chapter 8), the formation of 1,25-OHD_3 is regulated, according to the need for calcium absorption, by the serum calcium level, which in turn regulates release of the parathyroid hormone (PTH). A low serum calcium level triggers release of PTH, which increases the formation of 1,25-OHD_3, increasing the formation of calcium-binding protein, stimulating calcium absorption.

As previously discussed (Chapter 8), calcium is absorbed very efficiently in rabbits, and absorption remains high even after the metabolic need for calcium has been met. This raises the question about the role of vitamin D in rabbit nutrition. It seems likely that any requirement for vitamin D is much lower than for other species.

One international unit (IU) of vitamin D is defined as 0.025 μg of vitamin D_3. Alfalfa meal contains vitamin D activity of 650–2200 IU/kg, so rabbit rations containing alfalfa have adequate vitamin D levels. The only practical problem encountered with vitamin D in rabbit nutrition is vitamin D toxicity. Stevenson *et al.* (1976) reported a case in which a commercial feed contained toxic levels of vitamin D. Symptoms included progressive emaciation and weakness, loss of appetite, diarrhea, intense thirst, ataxia (incoordination), and paralysis leading to death. The soft tissues (liver, kidney, artery walls, muscle) were extensively calcified. Thus vitamin D toxicity causes resorption of bone salts and deposition of calcium in soft tissues. Ringler and Abrams (1970, 1971) observed probable vitamin D toxicity in rabbits fed a diet containing 2300 IU of vitamin D per kilogram.

Another case of suspected vitamin D toxicity was reported by Besch-Williford *et al.* (1985). In this outbreak, rabbits from several commercial rabbitries died a few days after an episode of diarrhea, anorexia (lack of feed intake), and weight loss. The onset of clinical signs occurred 3–7 days after a new batch of feed was used. The tissues showed extensive mineralization suggesting possible vitamin D toxicity. Analysis of the feed showed a value of 8.8 million IU of 1.25-OHD_3 per kilogram of feed, an extremely high level.

Bourdeau *et al.* (1986) studied calcium and phosphorus metabolism in rabbits that were fed a vitamin D-deficient diet. Chronically vitamin D-deficient rabbits had low blood calcium and phosphorus levels, and showed evidence of hyperparathyroidism (serum PTH levels were elevated). The intestinal absorption of calcium and phosphorus in the vitamin D-deficient rabbits was not impaired, but urinary excretion of both minerals was reduced. When the rabbits were fed the deficient diet, it took about 5 months for the complete disappearance of calcitrol (1,25-dihydroxyvitamin D_3) from the blood, whereas the corresponding period in the chick is only 2 weeks.

Kubota *et al.* (1982), in studies of vitamin D metabolism in the pregnant rabbit, noted that administration of large amounts (10,000 IU D_3 per day for 3 days) of vitamin D to does in late gestation (26–28 days) resulted in an increase in maternal but not in fetal plasma calcium. Elevated fetal mortality (18% versus 3% in controls) occurred.

It is interesting that several plants, such as *Solanum malacoxylon, Cestrum diurnum,* and *Trisetum flavescens,* contain 1,25-OHD_3 and cause vitamin D toxicity in grazing animals (Cheeke and Shull, 1985). It is unlikely that these plants would be used in rabbit feeding.

III. VITAMIN E

Vitamin E was discovered in 1922 as a fat-soluble substance in vegetable oils necessary for the maintenance of pregnancy in rats. It was named tocopherol, from the Greek words *tokos* meaning "offspring" and *pherein* meaning "to bear," plus *ol* for the hydroxyl group in its structure. From this beginning, it acquired the unfortunate reputation of being associated with sexual function. It has many other effects of equal or greater importance than its role in reproduction.

As previously discussed (Chapter 8), the metabolic role of vitamin E is closely linked to that of the mineral element selenium. Both nutrients function in the prevention of peroxide damage to tissues. Peroxides are reactive compounds formed during normal metabolic processes. Symptoms of vitamin E deficiency are reflective of damage to and breakdown of cellular membranes, resulting in tissue degeneration. Vitamin E is an antioxidant, combining with peroxides and

TABLE 9.4

Vitamin E Content of Feedstuffs[a]

Feedstuff	Vitamin E (mg/kg, dry matter basis)
Alfalfa, dehydrated	204
Alfalfa hay, sun-cured	60–180
Alfalfa meal, sun-cured	90–280
Barley, grain	26
Carrots, roots	60
Clover, white, hay	130
Corn, grain	7–24
Cottonseed meal, solvent-extracted	10–16
Flax seed (linseed meal)	8
Oats, grain	7–22
Rice, bran	66
Rice, hulls	8
Sorghum (milo), grain	14
Soybean meal, solvent-extracted	3
Wheat, grain	17
Wheat, bran	16–25
Yeast, brewers	2

[a] Adapted from International Feedstuffs Institute, Tables of Feedstuff Composition, Logan, Utah.

free radicals and inactivating them. Selenium, as a component of glutathione peroxidase, functions in the detoxification of peroxides.

One international unit (IU) of vitamin E is equal to 1 mg of *dl*-α-tocopherol acetate. The vitamin E content of common feedstuffs is shown in Table 9.4.

Good sources of vitamin E are green forages such as alfalfa meal, vegetable oils and cereal grains. Synthetic sources of vitamin E are used in the feed industry.

Selenium does not seem to have a sparing effect on vitamin E requirements in rabbits, in contrast to its effects in other species. Synthetic antioxidants can replace vitamin E. The requirement is increased by the feeding of unsaturated fatty acids or vegetable oils.

The principal sign of vitamin E deficiency in rabbits is muscular dystrophy. Rabbits fed a deficient diet develop signs of muscular damage in about 4 weeks, such as the inability to right themselves when placed on their backs. This is followed by paralysis of the hindlegs with death occurring 1–2 days thereafter (Hidiroglou and Jenkins, 1972). Ringler and Abrams (1970) observed muscular dystrophy in young rabbits in a commercial rabbit herd. The young rabbits, usually the entire litter, died at 3–10 days of age with no clinical signs prior to death. The skeletal muscles showed marked degeneration. The does were un-

affected except that fertility declined. Red blood cells from the does were highly susceptible to *in vitro* hemolysis, a sign of vitamin E deficiency. The diet contained 16.7 mg α-tocopherol per kilogram. The National Research Council (NRC) (1977) recommends a vitamin E level of 40 mg/kg, based on work with other species.

IV. VITAMIN K

Vitamin K was discovered by a Danish scientist, Henrik Dam, who named it vitamin K because it was necessary for blood coagulation (*Koagulation* in Danish). Vitamin K functions in the activation of prothrombin, a plasma protein with a role in blood clotting. In vitamin K deficiency, blood clotting is impaired, so that with a severe deficiency, an animal may bleed to death from a slight injury.

Natural sources of vitamin K are plants and bacteria. Good plant sources are leafy materials such as alfalfa meal. Many bacteria synthesize vitamin K, so the gut microflora are a good source. Bacteria in the rabbit cecum synthesize vitamin K, which the rabbit obtains when it engages in cecotrophy. A synthetic form of vitamin K called menadione is available, and has the advantage of being water soluble.

Early work has indicated that placental hemorrhage and abortion may occur in does fed a vitamin K-deficient diet (Moore *et al.*, 1942). A level of 2 ppm vitamin K in a purified diet is adequate to prevent reproductive problems (NRC, 1977).

Because of the cecal microbial synthesis of vitamin K, and the abundance of the vitamin in plant material such as alfalfa and grass meals, vitamin K is probably not of practical concern in rabbit nutrition.

V. B-COMPLEX VITAMINS

The B-complex vitamins are synthesized in the cecum by bacteria, and are obtained by the rabbit when it consumes cecal contents (cecotrophy, coprophagy). Kulwich *et al.* (1953) analyzed soft feces for their contents of some of the B vitamins. The comparative composition of hard and soft feces (cecotropes) for four vitamins is shown in Table 9.5. The cecotropes were three to six times higher in vitamins than the hard feces. On the basis of fecal excretion of the vitamins while the rabbits were collared (to prevent cecotrophy) or uncollared (cecotrophy allowed), it was shown that cecotrophy provided the animals with 83% more niacin, 100% more riboflavin, 165% more pantothenic acid, and 42% more vitamin B_{12} than if the soft feces were not consumed. A balance trial with

TABLE 9.5

Vitamin Content of Hard Feces and Cecotropes[a]

Vitamin	Hard feces	Cecotropes	Content in cecotropes (% of hard feces)
Niacin (μg/g)	39.7	139.1	350
Riboflavin (μg/g)	9.4	30.2	321
Pantothenic acid (μg/g)	8.4	51.6	610
Vitamin B_{12} (ng/g)	892	2922	330

[a] From Kulwich *et al.* (1953).

vitamin B_{12} was conducted with rabbits allowed to engage in cecotrophy. The average daily excretion of vitamin B_{12} was 221-fold greater than the daily intake of the vitamin, demonstrating that large amounts of vitamin B_{12} are synthesized by the gut microflora. Simnett and Spray (1961, 1965a,b) have shown that cobalt is efficiently used for vitamin B_{12} synthesis in the rabbit cecum and the vitamin is absorbed much more efficiently in rabbits than in rats or humans. The levels of vitamin B_{12} in rabbit serum were up to 150 times higher than the highest values found in humans or rats when rabbits were fed a low-vitamin B_{12} diet. They were unable to produce signs of vitamin deficiency when a low-cobalt, low-vitamin B_{12} diet was fed to rabbits for 1 year.

TABLE 9.6

B-Complex Vitamin Content of Common Ingredients Used in Rabbit Diets

Ingredient	Vitamin content (mg/kg, as-fed basis)					
	Thiamin	Riboflavin	Pyridoxine	Pantothenic acid	Niacin	Biotin
Alfalfa, dehydrated	4	12	8	18	23	0.3
Corn, yellow	2	1	5	7	30	0.06
Barley	4	1	6	7	75	0.14
Oats	6	2	3	7	14	0.24
Wheat	5	1	4	11	35	0.11
Wheat mill run (middlings)	19	2	9	13	53	0.10
Rice bran	23	3	14	23	293	4.2
Soybean meal	2	3	8	13	60	0.32
Cottonseed meal	6	5	6	14	41	0.6

Harris *et al.* (1983) showed that the addition of a vitamin mixture had no effect on the performance of weanling rabbits fed a diet containing 54% alfalfa, indicating that microbial synthesis of B vitamins adequately met the requirements for growth.

Under practical conditions, the B vitamins are not dietary essentials for rabbits. They obtain sufficient quantities of all B vitamins from consumption of the soft feces and from the dietary ingredients used in rabbit diets. Alfalfa meal, other forages, grains, and grain by-products are excellent sources of B vitamins (Table 9-6). Keeping rabbits on wire does not influence the amount of vitamins obtained by cecotrophy, since the cecotropes are consumed directly from the vent.

With purified diets, deficiencies of B vitamins have been demonstrated, using purified ingredients low in the vitamins in question. Besides being low in vitamins, these purified diets usually result in a low feed intake and low growth rate, so cecal vitamin synthesis is probably less than normal. The results of these studies will be briefly summarized. It should be emphasized that these results are not applicable under practical conditions.

Reid *et al.* (1963) found that rabbits fed a thiamin-deficient diet developed a mild ataxia (incoordination) after prolonged feeding of a low-thiamin diet. Hove and Herndon (1957) fed weanling rabbits a pyridoxine-deficient diet and produced typical signs of pyridoxine deficiency similar to those seen in other animals. These included dermatitis of the ears; loss of hair from the nose, around the eyes, and forepaws; convulsions; paralysis of the hindquarters; and death. Olcese *et al.* (1948) found that rabbits grew normally when fed pantothenic acid-defi-

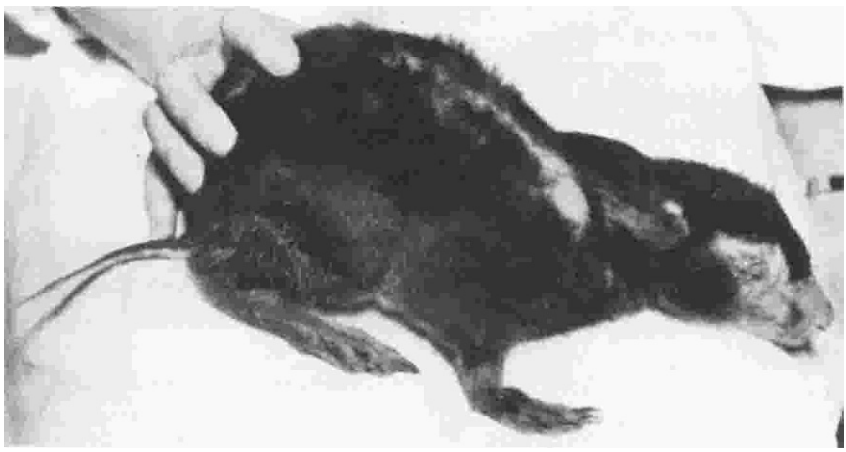


Fig. 9.3 Biotin deficiency induced in a rabbit by administration of raw egg white. (From Lease *et al.*, 1937.)

cient and riboflavin-deficient diets, and that the urinary excretion of these vitamins greatly exceeded dietary intake, indicating adequate microbial synthesis in the cecum. Biotin deficiency was induced by Lease *et al.* (1937) when rabbits were fed raw egg white (Fig. 9.3). Egg whites contain avidin, a glycoprotein that binds with biotin and induces a biotin deficiency (Cheeke and Shull, 1985). Symptoms of biotin deficiency were dermatitis and loss of hair. Choline deficiency has been produced (Hove *et al.*, 1954, 1957), with signs of reduced growth, fatty liver, kidney necrosis, and muscular dystrophy (Hove and Copeland, 1954). Niacin deficiency signs in rabbits include reduced growth, loss of appetite, emaciation, and diarrhea (Wooley and Sebrell, 1945). Niacin can be synthesized from the amino acid tryptophan in rabbits (Wooley, 1947).

Again, it is emphasized that these symptoms occur only when purified diets deliberately made deficient in vitamins are fed.

VI. VITAMIN C

Vitamin C or ascorbic acid is a simple compound synthesized from glucose. A few species, such as primates (humans, monkeys), guinea pigs, fish, and a number of exotic species (red-vented bulbul bird, fruit-eating bat, pale-billed flowerpecker) are unable to synthesize vitamin C. This is no doubt a result of evolutionary processes. Animals that consumed a diet high in fruit, with an adequate intake of vitamin C, lost their ability to synthesize it because they had no need to. Numerous studies have shown that because it is energetically expensive to maintain enzyme systems, they tend to be lost if they are not needed.

Harris *et al.* (1956) fed young rabbits for 25 weeks on an ascorbic acid-free diet with no evidence of deficiency, and with normal excretion of vitamin C in the urine. Animals that cannot synthesize vitamin C lack the enzyme L-gulonolactone oxidase in their livers. Jenness *et al.* (1978) determined the activity of this enzyme in the livers of domestic rabbits and several species of wild lagomorphs. Domestic rabbits had L-gulonolactone oxidase activity, indicating an ability to synthesize vitamin C. The activity was considerably higher in New Zealand White than in Dutch rabbits, indicating genetic differences in ascorbic acid-synthesizing ability. The liver activity of L-gulonolactone oxidase (μmol/g/hr) and the ascorbic acid content of liver (mg/100 g) were 6.2 and 18.4 for New Zealand Whites, and 2.4 and 10.6 for Dutch rabbits. It is apparent that vitamin C is not a dietary essential of the rabbit.

A possible beneficial effect of vitamin C in preventing diarrhea in rabbits has been suggested by Grobner *et al.* (1986), who noted that vitamin C when added to the medium *in vitro* inhibited toxin production by *Clostridium spiroforme*, a major organism implicated in rabbit enterotoxemia (see Chapter 12). It would be

useful to assess further the effect of dietary vitamin C on enteritis incidence, particularly when animals are exposed to stressful conditions. Verde and Piquer (1986) noted that in rabbits exposed to stress (loud noise and high environmental temperature), the plasma ascorbic acid concentration was significantly reduced. In other species, supplementary ascorbic acid has been shown to be beneficial in reducing the effects of stress.

VII. SOME CONCLUDING COMMENTS

The popular perception of vitamins as "wonder drugs" tends to make people skeptical of advice that supplementary vitamins for rabbits are often unnecessary. However, under normal circumstances, using normal dietary ingredients, vitamin supplementation of rabbit diets is usually unnecessary. Alfalfa meal is the richest plant source of vitamin A activity. Any diet with 20% or more of good-quality alfalfa meal should have adequate vitamin A activity. (Good quality in this context means that it should be a bright-green color; poor-quality alfalfa may be brown and devoid of carotene.) Vitamin D is required at very low levels, and again, alfalfa meal is an excellent source of vitamin D activity. The B vitamins are provided by cecotrophy, and in addition the commonly used ingredients such as alfalfa meal, grains, and grain milling by-products are excellent sources.

It is advisable to add a vitamin mixture that provides at least vitamins A and E, at moderate levels, to ensure that no deficiency occurs. Both of these vitamins are necessary for reproduction. With vitamin A, it is important to recognize that abortions, fetal resorptions, and small, weak litters can occur with excess vitamin A as well as with a deficiency. A vitamin mixture formulated for swine or poultry will be satisfactory for rabbits, even though it will contain the B vitamins, which are not normally dietary essentials for rabbits. The volume of feed used is such that for most feed mills, having a separate vitamin premix for use only in rabbit diets is not practical. Alternatively, the following supplement may be used: vitamin A, 9 million IU; vitamin D, 800,000 IU; and vitamin E, 45 g, for each ton (2000 lb) of feed.

Estimates of the dietary vitamin requirements of rabbits are given in Tables 16.1 and 16.2.

It is commonly claimed, particularly by vitamin dealers, that stress increases vitamin requirements. There seems to be little evidence in the scientific literature to support this view, although it is intuitively reasonable. High levels of vitamin supplements, including their addition to the water, is sometimes used when rabbits are exposed to stress, and may be linked to reproductive problems in rabbits from excessive vitamin A intake (Cheeke, 1985).

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10

Water: Functions and Requirements

Water is normally considered a nutrient, although its properties and functions are quite different from those of the other nutrients found in feeds. Water is the major constituent of the animal body, making up about 70% of the lean body mass. Rabbit meat is about 70% water. The water content of the body is highest in newborn animals, and decreases as a percentage of the body weight as deposition of fat occurs during growth.

I. PROPERTIES AND FUNCTIONS OF WATER

Water has remarkable properties for living organisms. Water is the closest thing to a "universal solvent." This high solvent power permits the formation of a large number of true and colloidal solutions in which animal metabolism occurs. Water has a high dielectric constant, favoring the ionization of compounds and thus facilitating metabolic reactions. Water participates in many of the chemical reactions that take place in metabolism. Of great significance is the thermal properties of water. It has a low thermal conductivity, which reduces heat uptake from the environment, and a high specific heat, which reduces the amplitude of variation in body temperature due to environmental influences. Water has a very high heat of vaporization, so the evaporation of water on the skin (sweating) and the expiration of water vapor from the lungs aids in the removal of excess heat. Normal metabolic processes produce enough heat in a few minutes to coagulate body proteins (like cooking an egg), so it is essential that this heat be dissipated rapidly and efficiently. Water has lubricating properties that are important in swallowing food and lubricating joints. As cerebrospinal fluid, it provides a water cushion for the nervous system. It transports sound in the ear and functions in vision. Water can be considered the most important nutrient because it is the largest component of the body, and animals will die more rapidly from water deprivation than from food deprivation.

II. WATER COMPARTMENTS OF THE BODY

The total body water is distributed primarily between intracellular and extracellular fluid. Intracellular fluid is that within the tissue cells, while the extracellular fluid is that in the blood, lymph, and interstitial spaces (space between cells and tissues). The plasma is the extracellular fluid of the blood. Blood plasma is prepared by collecting a blood sample in a tube containing an anticoagulant, and then centrifuging it to spin down the cells. Blood serum is prepared in the absence of an anticoagulant, so the blood clots. The difference between serum and plasma is that plasma contains all the blood proteins, while in serum, the fibrinogen protein has come out in the clot. There is a fundamental difference in the composition of intracellular and extracellular fluids. The intracellular fluid is high in potassium and low in sodium, while the extracellular fluid (e.g., blood plasma) is high in sodium and low in potassium. In certain pathological states, such as diarrhea, potassium exits the cells. It must be replaced, using electrolyte therapy, or severe alterations in cellular metabolism occur.

The balance between the water compartments is very important, and is controlled largely by the phenomenon of osmosis (movements of water controlled by concentrations of dissolved molecules). The blood proteins, particularly the albumin, play a central role in regulating fluid balance. With dietary protein deficiency, or with liver damage (blood proteins are made in the liver), the blood albumin level may decrease, resulting in a movement of water from the blood to the interstitial spaces. This causes edema (accumulation of fluid in tissues) and ascites (accumulation of fluid in body cavities). The swollen abdomen of protein-deficient children is an example of this. Another is the ascites that develops in animals suffering from liver damage caused by consumption of pyrrolizidine alkaloids.

III. WATER REQUIREMENTS

Sources of water include drinking water, water in feed, and metabolic water. Under some circumstances, such as with rabbits fed a diet of green forage, drinking water may be unnecessary. It is a common practice in developing countries to raise rabbits entirely on greens, and not to provide other sources of water. Metabolic water is produced as a result of metabolism. A good example is during the metabolism of glucose:

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O$$

The oxidation of fat and carbohydrate in animal tissues yields metabolic water. This is particularly important in desert animals, adapted to conditions of low

water availability. In their natural habitats, animals like gerbils and kangaroo rats never drink; they satisfy their water needs by using metabolic water and minimizing water loss by excreting a concentrated urine. Camels can go many days without drinking, by using metabolic water.

The amount of water required is influenced by level of feed intake, by feed composition, and by environmental temperature. Rabbits consuming a high-fiber feed will consume more water than those fed a high-energy diet. The extra water is needed to moisten the feed and maintain a fluid mixture in the digestive tract. Feed ingredients such as alfalfa meal absorb a great deal of water (Fig. 10.1). High-protein diets increase water needs. The nitrogen from the excess protein is excreted in the urine as urea. The kidney has a limited capacity to concentrate excretory products in the urine, so the more urea excreted, the more water in the urine is required. The 24-hr urine volume of rabbits ranges from 20 to 350 ml/kg of body weight, with an average of about 130 ml/kg. Rabbit urine is normally alkaline (pH about 8) and is pigmented and turbid in appearance. The reddish-to-yellowish pigmentation is caused either by plant pigments or the animal's own bile pigments, while the turbidity is due to the high content of calcium carbonate typical of rabbit urine.

Environmental temperature has a great influence on water consumption (Table 10.1). Body temperature regulation by rabbits under hot conditions is largely

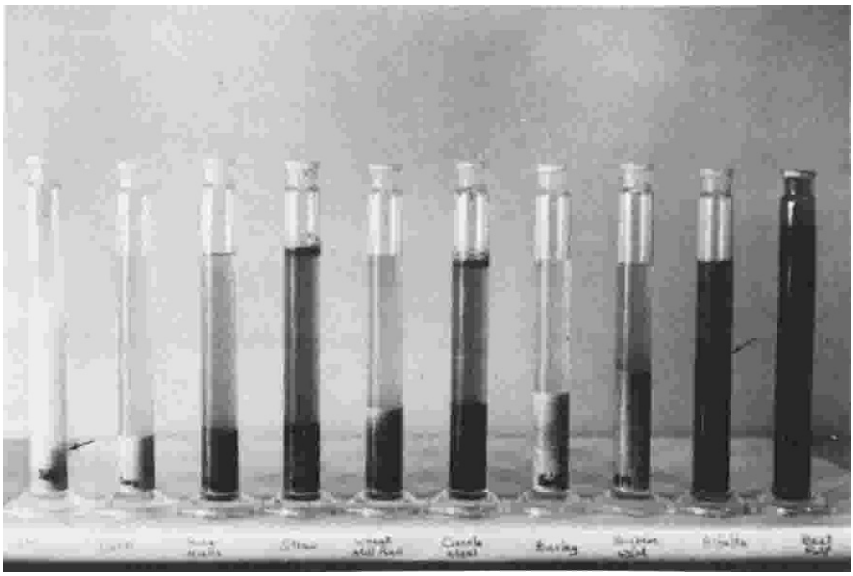


Fig. 10.1 Feed ingredients differ markedly in their water-absorbing and swelling capacities. The dry volume of all feeds shown here was the same. Oats and corn (left) absorbed very little water, while alfalfa and beet pulp (right) increased in volume severalfold as they absorbed water.

TABLE 10.1

Effect of Environmental Conditions on Feed and Water Intake of New Zealand White Rabbits[a]

Air temperature (°C)	Relative humidity (%)	Feed intake (g/week)	Feed/gain	Water intake (ml/week)
5	80	1286	5.02	2350
18	70	1077	4.41	1876
30	60	882	5.22	3138

[a] From Stephan (1980).

controlled by water losses in the expired air. Because of the high heat of vaporization of water, evaporation of water via the lungs removes heat. Under conditions of high environmental temperatures, it is essential that rabbits have free access to fresh water, preferably cool water. There is some evidence that water intake may be inadequate if the water is warm or hot. Under normal circumstances in commercial rabbitries, a doe and her litter will consume about a gallon of water a day. Water intake is about 120 ml/kg of body weight per day. A good rule to use in estimating the water consumption of rabbits is that water intake is about twice the feed intake, on a weight basis.

Stephan (1980) studied the effect of environmental temperature on feed and water intake of rabbits (Table 10.1). Under hot conditions, feed intake is reduced and water intake is increased. The increased water is used to dissipate heat by respiration from the lungs. Under cold conditions, feed intake is increased, to maintain body temperature. Interestingly, water consumption also rises at cold temperatures. This is probably because of the higher feed intake; more water is needed to keep the gut contents in their normal fluid state.

Compared to other animals, rabbits have a high water intake (Cizek, 1961). For example, a 2-kg rabbit consumes about as much water per day as a 10-kg beagle dog. When deprived of food, rabbits develop polydypsia (excessive water intake), resulting in a loss of sodium and induced sodium deficiency (Cizek, 1961).

IV. NUTRIENTS AND TOXIC ELEMENTS IN WATER

Normally, the concentration of mineral elements in water is not of sufficient magnitude to have a significant effect on mineral requirements. Occasionally, highly saline water may cause some problems. Calcium, magnesium, sodium, bicarbonate, chloride, and sulfate are the ions most likely to exert toxic effects.

Sulfates are more injurious than chlorides. Hydroxides are more harmful than carbonates, which in turn are more harmful than bicarbonates. The National Research Council (NRC) (1974) makes the following recommendations concerning the use of saline water for livestock:

1. Total soluble salts of less than 1000 mg/liter. This level presents no problem.
2. 1000–2999 mg/liter. These waters are satisfactory, but may cause transient diarrhea.
3. 3000–4999 mg/liter. These waters are satisfactory for livestock (cattle, horses, sheep, swine), although they may cause transient diarrhea. They are poor for poultry, causing watery feces, reduced growth, and higher mortality. (Suitability for rabbits was not stated, but may be assumed to be similar to suitability for livestock).
4. 5000–6999 mg/liter. These waters are of borderline safety for livestock, and definitely should not be used for poultry.
5. 7000–10,000 mg/liter. These waters are unfit for poultry and probably swine (and rabbits).
6. More than 10,000 mg/liter. Highly saline water unfit under any circumstances.

The recommended upper limits for some toxic substances found in drinking water, as compiled by the NRC, are as follows:

Substance	Safe upper limit (mg/liter or ppm)
Arsenic	0.2
Cadmium	0.05
Chromium	1.0
Cobalt	1.0
Copper	0.5
Fluoride	2.0
Lead	0.1
Mercury	0.01
Nickel	1.0
Nitrate	100
Nitrite	10
Vanadium	0.1
Zinc	25.0

A number of elements, including iron, aluminum, boron, chromium, copper, iodide, manganese, molybdenum, and zinc, are unlikely to ever occur at toxic levels.

Nitrate and nitrite contamination of water is sometimes of concern. These

contaminants enter water supplies from sewage, animal waste, and fertilizer use. Groundwater in the vicinity of feedlots or confinement livestock operations often is contaminated with nitrates–nitrites. Levels of 200 ppm nitrate in water are potentially hazardous; 1500 ppm causes acute toxicity.

Lakes and ponds may contain toxic blue-green algae. The toxins produced by these algae are extremely poisonous. Water with heavy algae growth should be avoided. Algae in farm ponds can be controlled by dragging a porous bag containing copper sulfate through the pond.

Pesticides enter water supplies from agricultural runoff, accidental spills, or faulty waste disposal techniques. The organophosphates, such as malathion, are the most toxic. Insecticides of plant origin, such as pyrethrins and rotenones, are not of concern.

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11

Feeding Behavior and Regulation of Feed Intake

I. INGESTIVE BEHAVIOR OF THE RABBIT

Rabbits have evolved various adaptations to a herbivorous diet, including the enlarged hindgut for fermentation, selective excretion of fiber and retention of small particles for fermentation, cecotrophy, and adaptations involving the teeth. Rabbits masticate their feed thoroughly, so it is finely ground when it enters the stomach. Cheeke *et al.* (1985) found that the cellular structure of forages was completely disintegrated as a result of mastication and passage through the rabbit gut. When forage is fed, the number of jaw movements may be as many as 120 per minute, thoroughly masticating the material. Feeding behavior is very selective, and if given the opportunity, as in the wild, rabbits select tender, succulent leafy material rather than stems, and young plant material rather than the more fibrous mature tissues. Rabbits are fastidious and will readily go off feed or reject a diet for no apparent reason.

The primary feeding periods are early morning and at night (Fig. 11.1). Cecotrophy begins 3–8 hr after feeding (Hornicke and Bjornhag, 1980).

II. FACTORS AFFECTING FEED INTAKE

A. Palatability

Rabbits exhibit distinct preferences for some dietary characteristics. They have a preference for sweet materials, and prefer diets containing sucrose or molasses over similar diets without added sugar (Cheeke, 1974). Rabbits are quite tolerant of bitterness, and may even prefer a certain degree of bitter taste to their diet. Saponins are bitter glycosides in alfalfa. Rabbits were much more tolerant of high-saponin alfalfa in the diet than were rats (Fig. 11.2) in feed preference trials (Cheeke *et al.*, 1977). They did not show a pronounced rejection of the high-saponin alfalfa-containing diet until a level of 40% alfalfa,

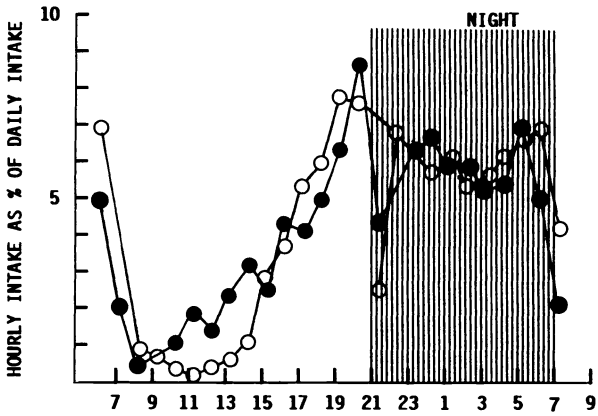


Fig. 11.1 Normal diurnal pattern of feed (●) and water (○) intake of rabbits. (Adapted from Lebas *et al.*, 1984.)

whereas rats showed a pronounced rejection at much lower levels. Rabbits are also much more tolerant of quinine sulfate, a bitter compound, than are rats (Cheeke, 1980), poultry (Cheeke *et al.*, 1983), and swine (LeaMaster and Cheeke, 1979). Another small herbivore, the meadow vole, also has a high tolerance to quinine sulfate (Kendall and Leath, 1976).

Interestingly, the preference for alfalfa-containing diets by rabbits is not markedly different from that for swine, poultry, or rats (Fig. 11.3). When the intakes of an alfalfa-containing or alfalfa-free diet were compared in two-choice preference tests, the intake of the alfalfa-containing diet as a percentage of total feed intake declined with increasing alfalfa levels in all animals tested (Fig. 11.3).

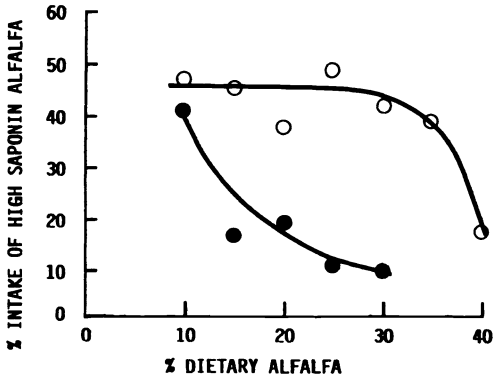


Fig. 11.2 Comparison of tolerance of rats (●) and rabbits (○) to alfalfa meal high in saponin content. At each level of dietary alfalfa, animals were offered a choice of diets containing either high-saponin or low-saponin alfalfa meal. (Data from Cheeke *et al.*, 1977.)

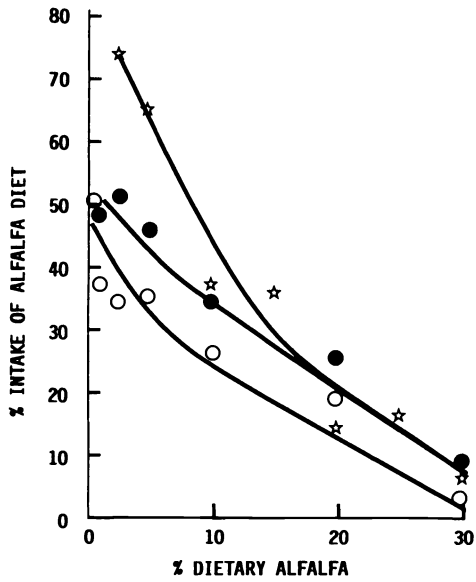


Fig. 11.3 Feed preference responses of rabbits (☆), chickens (●), and swine (○) for diets containing various levels of alfalfa meal. At each dietary alfalfa level, animals were offered a choice of the diet with alfalfa or a control, alfalfa-free diet. (Data for rabbits from Cheeke *et al.*, 1977; for chickens, Cheeke *et al.*, 1983; for swine, LeaMaster and Cheeke, 1979.)

Rabbits were the most tolerant of alfalfa-containing diets, but at all levels above 10% alfalfa, the alfalfa-free diet was preferred. However, when the growth of these different animals fed various dietary alfalfa levels is compared, rabbits perform remarkably better (Fig. 11.4). The growth rate of swine and poultry declines markedly with increasing alfalfa levels, whereas the growth rate of rabbits remains high at alfalfa levels as high as 60% of the diet. This difference is probably mainly due to the rapid excretion of fiber by the rabbit, allowing a high feed intake, and their willingness to consume a high-alfalfa diet. They are able to eat sufficient feed to meet their energy requirements as the dietary alfalfa level increases, whereas swine and poultry cannot.

Sanchez *et al.* (1981) offered fryer rabbits free choice of rolled grains and chopped alfalfa hay. The grain was selected by the animals to make up 60–70% of the total feed intake (Table 11.1). Reyne and Salcedo-Miliani (1981) evaluated the ability of fryers fed high- or low-fiber diets to consume wheat straw selectively as a source of fiber (Table 11.2). The rabbits did consume more straw when fed the low-fiber diet. Straw made up 7% of the total intake with the high-fiber pellet, and 16% of the intake when straw was offered along with the low-fiber pellet. This indicates some ability of the rabbit to select a diet that will meet its fiber needs.

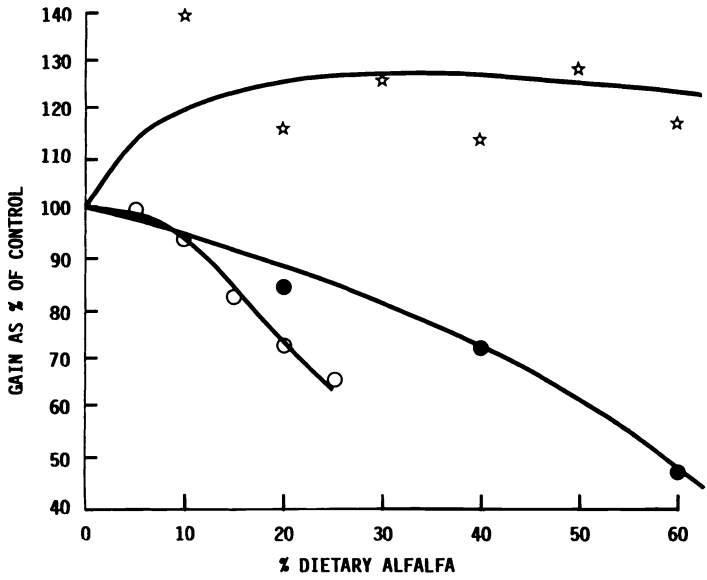


Fig. 11.4 Comparative performance of rabbits (☆), swine (●), and chickens (○) fed various dietary levels of alfalfa. (Data for rabbits from Cheeke *et al.*, 1977; for swine, Powley *et al.*, 1981; for chickens, Cooney *et al.*, 1948.)

B. Environmental Temperature

As discussed earlier (Chapter 5), the environmental temperature affects energy requirements and feed intake. At low environmental temperatures, feed intake is increased, so the animal can obtain sufficient energy to meet productive functions and maintain its body temperature. At high temperatures, feed intake declines. Stephan (1980) reported that feed intake was 19% higher at an environmental temperature of 5°C than at 18°C, and 18% lower at 30°C than at 18°C.

TABLE 11.1

Free-Choice Intake of Grains and Alfalfa Meal When Offered Separately[a]

Grain	Average daily gain (g)	Average daily consumption (g)			Percentage of total	
		Grain	Alfalfa	Total	Grain	Alfalfa
Barley	27.5	65	29	94	69	31
Barley–corn	26.9	86	36	122	70	30
Oats	32.1	75	53	128	59	41
Corn	27.9	56	36	92	61	39

[a] From Sanchez *et al.* (1981).

TABLE 11.2

Self-Selection of Pellets and Straw by Rabbit Fryers When Fed High- and Low-Fiber Pelleted Diets[a,b]

Results	High-fiber (11.7%) pellet (20% straw)		Low-fiber (4.1%) pellet (0% straw)	
	Pellets only	Pellets plus straw	Pellets only	Pellets plus straw
Pellet intake (g/day)	95	88	63	63
Straw intake (g/day)	—	7	—	12
Pellet intake (% of total)	100	93	100	84
Straw intake (% of total)	—	7	—	16
Average daily gain (g)	31.7	31.0	22.4	26.6

[a] From Reyne and Salcedo-Miliani (1981).

[b] Rabbits were offered free choice either a high- or low-fiber pelleted diet, with or without wheat straw as a supplement to the pellets.

C. Dietary Energy Level

One of the most important factors controlling feed intake is the dietary energy level. As is true for other animals, the feed consumption of rabbits increases with decreasing energy concentration of the diet (Fig. 11.5), so that sufficient feed is consumed to meet caloric requirements. Grobner *et al.* (1985) found that small breeds such as the Netherland Dwarf are unable to increase feed intake adequately when fed a low-energy diet (Fig. 11.6), and thus are unable to meet their energy needs. It may be desirable for small or dwarf breeds to be fed a higher energy diet. The variation of feed intake according to dietary energy level is regulated by several factors. As discussed in Chapter 6, the retention time of low-fiber, high soluble carbohydrate diets in the cecum is prolonged, thus limiting feed intake. With high-fiber, low-energy diets, the time of passage of fiber is very rapid, allowing a high level of feed intake. Appetite is controlled primarily by levels of metabolites in the blood. In ruminants, the blood levels of volatile fatty acids (VFA), the major absorbed energy sources of ruminants, regulate feed intake at energy levels where gut fill is not limiting. In nonruminants, the blood glucose level is the primary regulator. Blood glucose levels are homeostatically maintained by mobilization of liver glycogen. When glycogen is depleted, the blood glucose level falls. This is detected by chemoreceptor cells in the appetite center (hypothalamus), which through neural stimulation initiates feed intake. It is assumed that blood glucose operates in this manner in rabbits, as it does in other nonrumiants.

Rabbits can adjust their feed intake patterns rapidly when dietary energy levels are switched. Grobner *et al.* (1983) evaluated a feeding system in which fryers

were fed either a high-energy (20% alfalfa) or low-energy (54% alfalfa) diet at weaning. Two other groups were fed either the high- or low-energy diet and then switched to the other diet after 2 weeks. Feed intake was accommodated rapidly. Putting the fryers on a high-fiber, low-energy diet at weaning, and then switching to the high-energy diet after 2 weeks reduced the mortality from enteritis and improved feed conversion efficiency (Table 11.3). Lebas *et al.* (1982), in a similar study, switched fryers between high-, medium-, and low-energy diets. They noted that the daily energy intake was similar for all groups, and that the rabbit can regulate its energy intake in the long term even when it receives a succession of diets differing in their digestible energy content. Growth rate was not affected by the feed switching. These authors concluded that it is not possible to increase the growth rate of rabbits by modifying the energy content of the diet and the diet feeding sequence, because of the rapid readjustment of voluntary feed intake to accommodate the change in energy level. This is similar to what has been observed with swine. If pigs are presented with diets of different energy content in an alternating feeding scheme, they will adjust their feed intake to maintain a fairly constant total energy intake (Cheeke and Kennick, 1970).

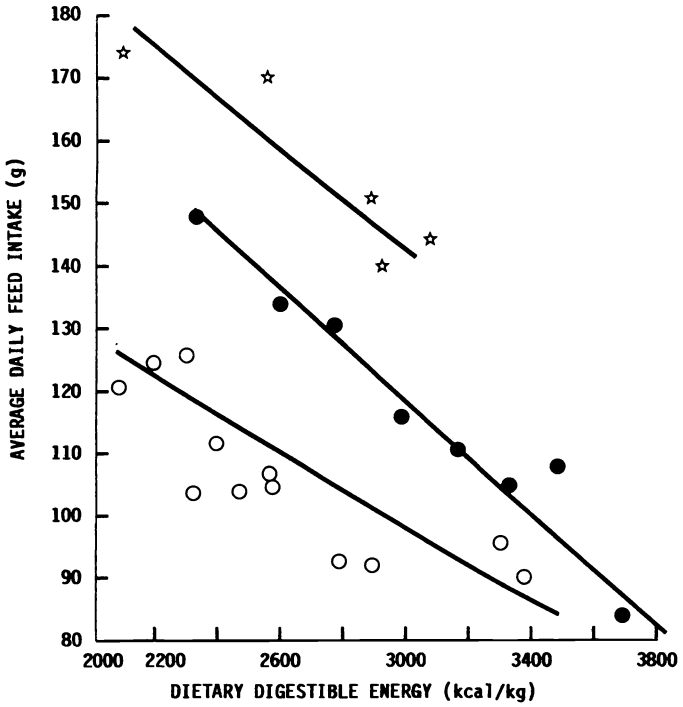


Fig. 11.5 Relationship between feed intake and dietary energy level. (☆ Data from Lebas, 1975; ● data from Pote *et al.*, 1980; ○ data from Spreadbury and Davidson, 1978.)

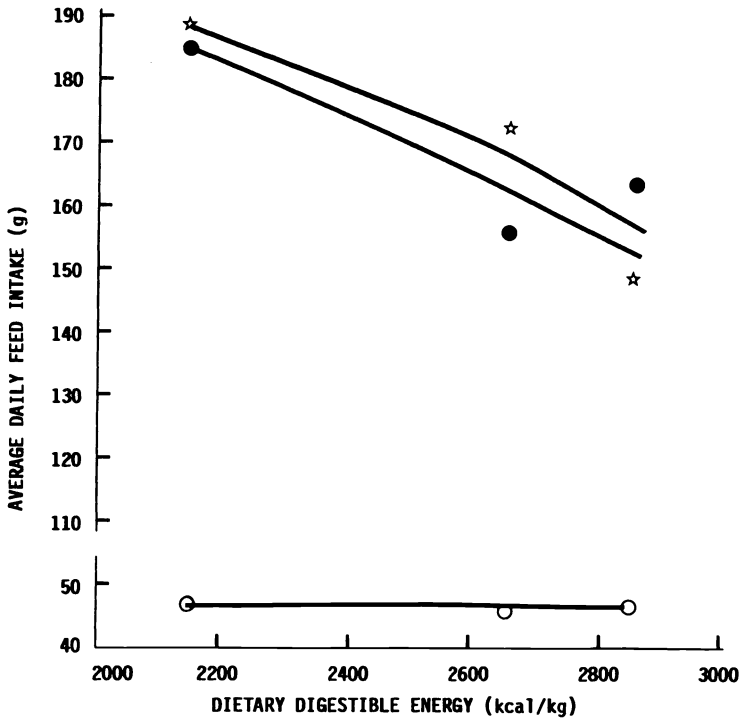


Fig. 11.6 The feed intake of dwarf breeds such as the Netherland Dwarf (○) does not increase with low-energy diets, because gut capacity is limiting. New Zealand White (☆); Flemish Giant (●). (Data from Grobner *et al.*, 1985.)

TABLE 11.3

Effect of Diet Switching between High- and Low-Energy Diets on Performance and Enteritis Mortality[a]

Diet	Average daily gain (g)	Average daily feed intake (g)	Feed/gain	Mortality (%)
20% Alfalfa	39.9	102	2.54	27.8
54% Alfalfa	36.5	124	3.41	16.7
20% Alfalfa, 54% alfalfa[b]	38.0	109	2.86	27.8
54% Alfalfa, 20% alfalfa[b]	38.6	117	3.02	5.6

[a] From Grobner *et al.* (1983).

[b] Two weeks on the first diet, and then switched to 2 weeks on the second diet.

TABLE 11.4

Effect of Form of Diet on Performance of Growing Rabbits

Reference	Type of diet	Average daily gain (g)	Average daily feed intake (g)
Lebas (1973)	Meal	29.7	82
	Pellet	36.0	94
King (1974)	Meal	20.7	79
	Pellet	22.9	85
Machin *et al.* (1980)	Meal	26.5	102
	Pellet	33.1	104
	Mash (40% water)	27.9	78
Harris *et al.* (1983)	Meal	29.3	180[a]
	Pellet	43.0	136
Sanchez *et al.* (1984)	Meal	21.7	177[a]
	Pellet	33.7	92

[a] High intake reflects feed spillage.

D. Physical Form of the Diet

Rabbits prefer a pelleted diet to the same diet in a meal form (Harris *et al.*, 1983). When offered a choice between the two forms, 97% of total feed intake was of the pelleted diet.

Growth is significantly improved when a pelleted diet rather than meal is fed (Table 11.4). Lebas *et al.* (1984) found that daily feed intake and feed conversion ratio were higher when a large-diameter pellet was used (Table 11.5); thus a smaller pellet size is desirable. Harris *et al.* (1984b) observed the best feed conversion with a short, medium-diameter pellet, while gain was reduced with a

TABLE 11.5

Effect of Pellet Diameter on Growth of Weanling Californian Rabbits[a]

	Pellet diameter (mm)		
Results	2.5	5	7
Daily feed intake (g)	117*[b]	122*	131**
Average daily gain (g)	32.4	33.7	32.0
Feed/gain	3.7*	3.7*	4.1**

[a] From Lebas *et al.* (1984).

[b] *Different from ** ($p < 0.05$).

TABLE 11.6

Effect of Pellet Length and Diameter on Performance of Weanling New Zealand White Rabbits[a]

Pellet size (mm)[b]		Average daily gain (g)	Average daily feed intake (g)	Feed/gain
Diameter	Length			
4 ($\frac{5}{32}$)	6.4 ($\frac{1}{4}$)	33.7	111	3.30
4 ($\frac{5}{32}$)	12.7 ($\frac{1}{2}$)	38.5	127	3.32
4.8 ($\frac{3}{16}$)	6.4 ($\frac{1}{4}$)	40.2	127	3.17
4.8 ($\frac{3}{16}$)	12.7 ($\frac{1}{2}$)	37.5	127	3.41

[a] From Harris *et al.* (1984a).

[b] Conversion to inches given in parentheses.

small-diameter pellet (Table 11.6). When these diets were compared in a feed preference test, the intakes as a percentage of total feed intake were highest for the long, small-diameter pellet, and lowest for the short, medium-diameter pellet. It is desirable that pellet length be short, to reduce feed wastage. Young rabbits have a tendency with long pellets to take one bite and let the rest fall through the cage.

E. Particle Size of the Feed

The particle size of ingredients in a pelleted diet can influence feed intake and performance. Finely ground ingredients can increase the proportions of fines and dust, which inhibit feed intake because of their effects on the respiratory tract. Laplace and Lebas (1977) compared three feeds, classified as coarse grind, intermediate grind, and fine grind. The ranges in particle sizes were 0.25–2.0, 0.08–2.0, and 0.08–0.25 mm, respectively. The growth rate and feed intakes of fryers were not significantly influenced by particle size, but there was an improvement in feed conversion ratio with the diet containing finely ground ingredients. Dry matter digestibility was highest with this diet, and the retention time of feed in the cecum was longest. An increased incidence of diarrhea and weight loss was noted in animals receiving the finely ground diets. Lang (1981) suggested that the optimal feeding strategy might be the use of finely ground feed ingredients, to promote prolonged cecal retention and maximum digestibility, along with a source of indigestible fiber in the form of large particles, to promote gut function and hard feces formation.

TABLE 11.7

Feed and Water Intake of New Zealand White Male Rabbits from 6 to 18 Weeks of Age Maintained at 20 ± 1°C[a]

Intake data	Age (weeks)		
	6	12	18
Feed			
Grams per day	98	194	160
Number of feedings per day	39	40	34
Amount consumed per feeding (g)	2.6	4.9	4.9
Water			
Total consumed (g/day)	153	320	297

[a] From Prud'hon *et al.* (1975).

F. Productive Function and Age

The pattern of feed and water intake with increasing age of New Zealand White rabbits is shown in Table 11.7. The actual quantity of feed consumed will vary with the energy level of the diet, environmental temperature, and breed, but the pattern is that the amount of feed consumed increases throughout the growing–finishing period, and then levels off.

The voluntary feed intake during gestation decreases about a week before kindling (Fig. 11.7). Feed intake increases rapidly after kindling (Fig. 11.7) to meet the demands of heavy lactation. During peak lactation (11–21 days), maximal feed intake is not adequate to meet the high energy requirements, so mobili-

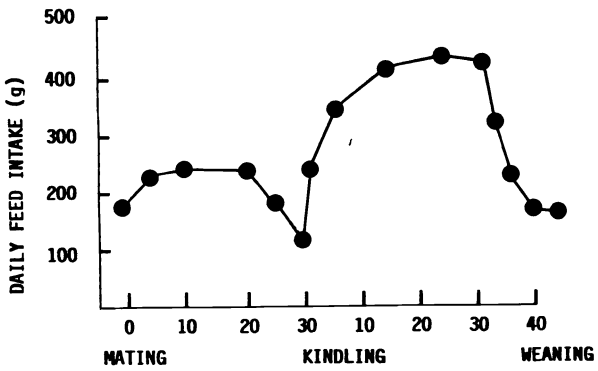


Fig. 11.7 Pattern of feed intake of commercial meat rabbits over a reproductive cycle. (Data modified from Lebas *et al.*, 1984.)

zation of energy from body tissues occurs (Partridge *et al.*, 1983). These workers suggested the use of high-energy lactation diets to meet the demands of peak lactation.

III. FACTORS AFFECTING FEED CONVERSION EFFICIENCY

Feed efficiency (feed conversion, feed/grain ratio) is the amount of feed consumed per unit of gain (e.g., pounds feed/per pound gain, kilograms feed per kilogram gain, etc.) A number of factors influence feed efficiency, with one of the most important being the energy content of the diet. As the energy density increases, less feed is required to satisfy the animal's energy requirements, and feed efficiency is improved (Fig. 11.8).

Feed conversion efficiency declines with age. It is highest (most efficient) at 3

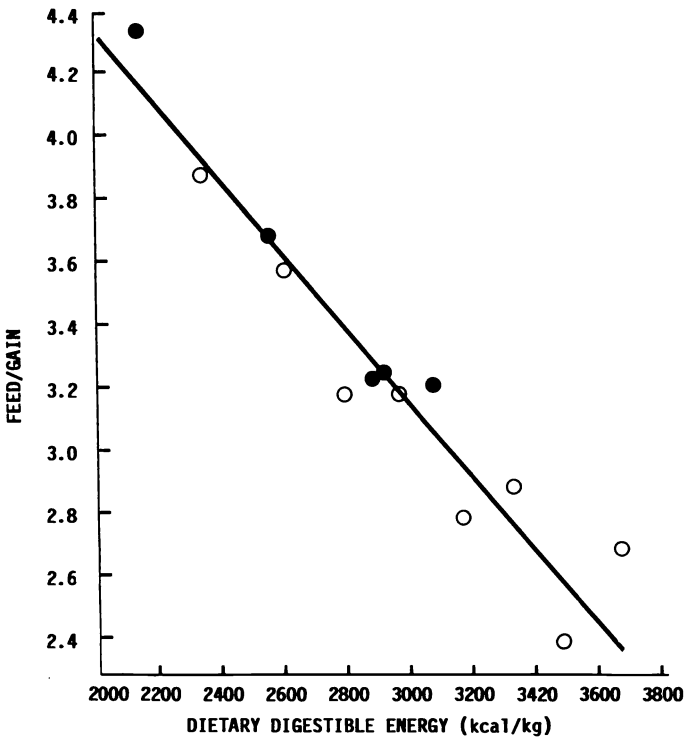


Fig. 11.8 Feed conversion efficiency is improved with increasing dietary energy level. (● Data from Lebas, 1975; ○ data from Pote *et al.*, 1980.)

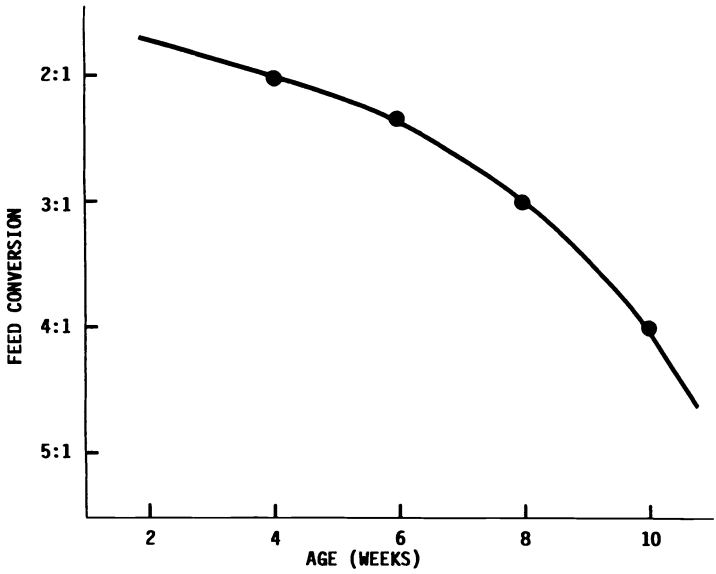


Fig. 11.9 Change in feed conversion efficiency (feed/gain) with age for fryer rabbits.

weeks of age, and declines with increasing age (Fig. 11.9). The period of maximum daily gain (Fig. 11.10) coincides with the period of highest feed efficiency. Thus the least expensive gains are made with the 4- to 6-week-old fryers, so it is important to make maximum use of their full growth potential during that period.



Fig. 11.10 Changes in growth rate with age for fryer rabbits.

IV. FEED RESTRICTION

Restricted feeding of nonlactating does is a common practice, to reduce feed costs and prevent obesity. Animals on restricted feed should be closely monitored to ensure that body condition is maintained. No set quantity of feed that is satisfactory can be stated, because the amount necessary for maintenance will depend on the energy content of the diet and the size and breed of the animals.

In general, feed restriction of growing animals should decrease their growth rate, since feed intake is usually balanced to meet energy needs. However, there is some evidence that moderate feed restriction of rabbit fryers may improve feed efficiency without sacrificing rate of gain. On a practical basis, it is difficult to restrict feed of fryers in a rational manner because of the effects of age, number per cage, and environmental temperature on *ad libitum* feed intake. Harris *et al.* (1984a) restricted feed so that the feeders of the restricted animals were empty at feeding time, and the rabbits were congregated at the feeder with a pronounced eagerness to be fed. A second group was fed the same diet *ad libitum*. The results (Table 11.8) indicate that, in spite of the evident restriction as suggested by the rabbits' behavior, the actual degree of restriction was quite small. There did tend to be a slight improvement in feed efficiency without any effect on rate of gain.

Feed restriction of pelter Rex rabbits is beneficial in improving pelt quality (Taylor and Johnston, 1984). Animals fed *ad libitum* had large abdominal fat deposits, which can make the animals more difficult to pelt, and if the fat is not removed entirely from the skin, it can cause the fur to fall out. Full feeding also resulted in a lower percentage of the pelts in a fully prime condition. Restriction of feed to a level of 75% *ad libitum* feed intake did not significantly reduce pelt size, and increased the percentage of fully prime pelts. The speed of the hair growth cycle is reduced by feed restriction, resulting in the animal remaining in prime condition for a longer period before the next prime cycle begins.

Coudert and Lebas (1985) studied the effect of feed restriction of first-litter does (31 per treatment) on their subsequent reproductive performance over three parities (Table 11.9). Reproductive performance was reduced by the restriction

TABLE 11.8

Effect of Moderate Restriction on Performance of Fryer Rabbits[a]

Treatment	Average daily gain (g)	Average daily feed intake (g)	Feed/gain	Mortality (%)
54% Alfalfa, restricted	39.8	124	3.13	12.5
54% Alfalfa, *ad libitum*	40.8	131	3.23	0
54% Alfalfa + 250 ppm copper, restricted	41.7	136	3.25	6.3
54% Alfalfa + 250 ppm copper, *ad libitum*	42.9	141	3.29	0

[a] From Harris *et al.* (1984a).

TABLE 11.9

Effect of Feed Restriction on Reproductive Performance of Does[a]

Item	Treatment[b]			
	RR	RA	AR	AA
Does at start (*N*)	31	31	31	31
Kindlings (*N*)	71	70	69	76
Live born (*N*)	624	674	664	760
Live born per litter (*N*)	8.79	9.63	9.62	10.0
Weaned (*N*)	529	539	530	636
Weaned per litter (*N*)	7.45	7.70	7.68	8.37
Litter weight at weaning (g)	5141	5004	5199	4918

[a] From Coudert and Lebas (1985).

[b] RR, Restricted to 150 g feed per day during first pregnancy; RA, restricted feed (150 g/day) until positive palpation, then fed *ad libitum*; AR, fed *ad libitum* until positive palpation, then restricted to 150 g/day; AA, fed *ad libitum* throughout entire pregnancy.

at any time during the first pregnancy; the total number of fryers weaned was about 100 more in the *ad libitum*-fed group than for any of the restricted groups. This would indicate that restriction of young does in their first gestation period is not desirable. This study conflicts with an earlier report of Lebas (1975) involving first-parity Californian does. One group was fed *ad libitum*, while another was restricted to 140 g of feed per day during gestation, and then fed *ad libitum* after kindling. The feed intake of the *ad libitum*-fed does averaged 200–240 g/day during the first two-thirds of pregnancy and then declined to about 100–120 g for the last third of gestation. There was no difference in the performance of the litters from the two groups.

Severe nutrient restriction during gestation should be avoided. Does under nutritional stress may abort at about 20–25 days of gestation, or may resorb the fetuses at 15–20 days. Hammond (1965) observed that does severely restricted in nutrient intake during pregnancy essentially ceased reproduction.

Feed restriction of replacement does is often desirable to prevent obesity and reduce feed costs between weaning and the first mating. Prud'hon *et al.* (1975) found that restricting water resulted in decreased feed intake, without adversely affecting weight gains. The practicality of this technique is questionable, and its application is unlikely because of animal welfare considerations.

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12

Nutrition–Disease Interrelationships

Several important diseases of rabbits have a nutrition component in their etiology. In fact, nearly all of the economically significant pathological states can be influenced to some extent by diet. Enteric diseases are closely linked with diet and feeding practices. Respiratory diseases, such as pasteurellosis, are influenced by environmental conditions, particularly the ammonia concentrations in the air. Ammonia production in the rabbitry is in part a function of the diet the animals are fed. Fur chewing and trichobezoars (hair balls) are largely due to feeding inadequacies. Other disease conditions, including hydrocephalus and ketosis, can be associated with nutritional status.

I. ENTERITIS

Enteric diseases, along with respiratory disease, are a major problem in commercial rabbit production. Loss from enteritis of 10–20% of all animals born is routine, on a worldwide basis. Additionally, outbreaks of enteritis sometimes occur, causing devastating losses of 20–60% of all young animals. While there is not yet a full understanding of the causes of enteritis, and more importantly, measures for prevention and treatment are not always effective, great progress has been made in elucidating the disruptions of physiological processes that underlie the condition. The rabbit digestive tract performs very complex functions, particularly in the hindgut where selective retention of fermentable substrate in the cecum occurs, followed by cecotrophy. It is not surprising that disruptions of these mechanisms can occur, with disastrous results for the animal.

The causes of enteritis can be considered in terms of the microbes responsible, and the factors that allow these microbes to become a problem. These factors include diet, stress, and genetic predisposition to gut dysfunction. These factors will be considered separately, and then integrated into a unifying concept of diarrhea in the rabbit.

A. Terminology

There are a number of types of enteric diseases in rabbits, often referred to as enteritis complex. Enterotoxemia is a major problem, caused by the proliferation of pathogens (mainly *Clostridium* species) in the cecum, with the elaboration of toxins that are absorbed and exert toxicological effects. The term "mucoid enteritis" is sometimes used to describe a condition characterized by cecal impaction, mucus accumulation in the hindgut and excretion of mucus in the feces, and apparent diarrhea.

Diarrhea in the rabbit is somewhat unusual in that it is associated with constipation, or lack of gut motility. It would normally be considered that diarrhea and constipation are mutually exclusive terms.

B. Microbiology of Enteritis

For many years, the understanding of enteritis was limited by a lack of knowledge of specific microorganisms involved, and an inability to induce enteritis by administration of microbes. Since the late 1970s, much progress has been made in identifying the causative organisms.

Enterotoxemia in rabbits was first described in 1936 by French scientists (Lesbouyries and Berthelon, 1936). Patton *et al.* (1978) identified *Clostridium*

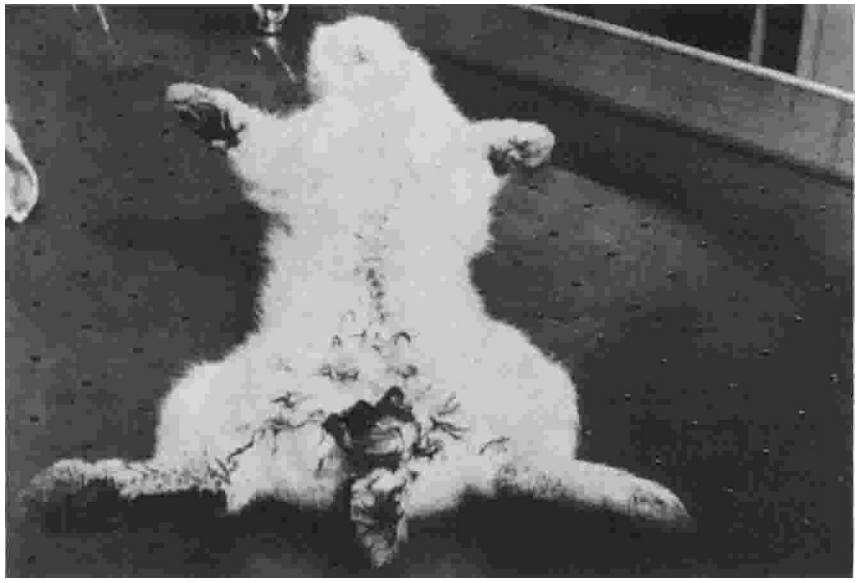


Fig. 12.1 A typical case of enterotoxemia, with soiling of the perianal area.

perfringens type E iota toxin as the probable causative agent in enterotoxemia in Oregon rabbits. The toxicity of diarrheal rabbits' cecal contents injected into mice and rabbits was neutralized by *C. perfringens* type E antitoxin, implicating the involvement of iota toxin. However, *C. perfringens* type E could not be isolated from rabbits with diarrhea. Baskerville *et al.* (1980) and Eaton and Fernie (1980) confirmed the involvement of iota toxin, but, like Patton *et al.* (1978), they were unable to isolate the causative organism. This enigma was solved by Carman and Borriello (1982), who identified a new species, *Clostridium spiroforme,* as the source of the iota toxin. In a series of reports (Carman and Borriello, 1982; Carman and Borriello, 1983, 1984; Borriello and Carman, 1983, 1985; Carman and Evans, 1984), these authors defined the nature of the infection. *Clostridium spiroforme* (Fig. 12.2) is an anaerobic, gram-positive, helically coiled, spore-forming bacillus (Borriello *et al.*, 1986) that produces iota toxin that is neutralized by *C. perfringens* type E antitoxin. Rabbit diarrhea caused by *C. spiroforme* has been demonstrated in Great Britain, western Europe, the United States (Borriello and Carman, 1983; Peeters *et al.*, 1986b), and

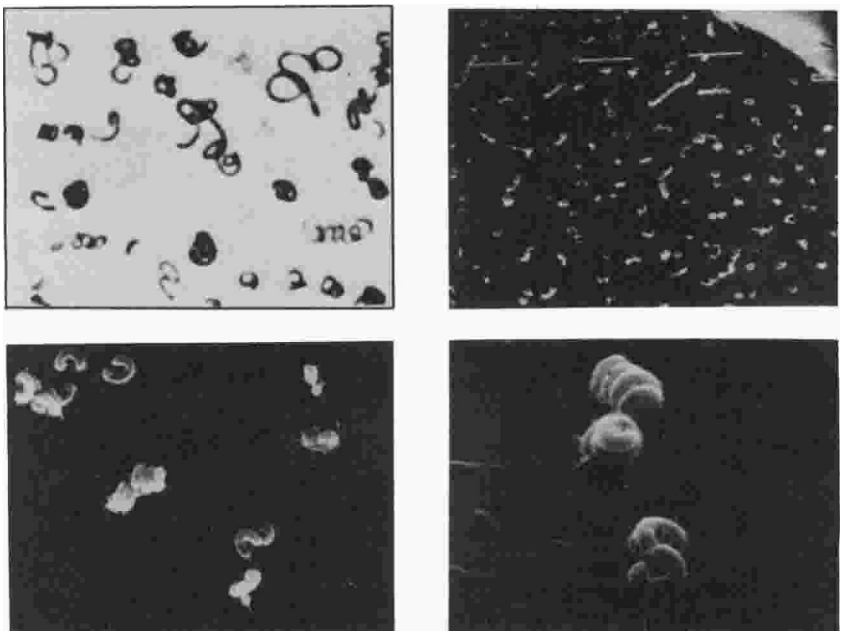


Fig. 12.2 Cellular morphology of *Clostridium spiroforme* as shown by Gram stain and scanning electron microscopy. Gram stain (top left) shows a range of cellular morphologies from helical, figure-of-eight, and semi-circular. The scanning electron microscope figures are of 912× (top right), 3650× (bottom left) and 7300× (bottom right) magnification. Courtesy of S. P. Borriello, Clinical Research Centre, Harrow, England.

Australia (Harris and Portas, 1985), so it appears to be involved in rabbit enteritis on a global basis.

Carman and Borriello (1983) have shown that newly weaned rabbits may develop iota enterotoxemia upon exposure to *C. spiroforme,* while adult animals generally require some environmental stress to induce modifications of the normal gut microflora for enterotoxemia to develop. Administration of antibiotics, such as clindamycin, may disturb the gut microflora and result in *C. spiroforme*-induced enteritis (Katz *et al.,* 1978; LaMont *et al.,* 1979; Rehg and Pakes, 1982).

Clostridium spiroforme may be present as a normal gut inhabitant without inducing enteritis. One factor involved in enteritis is whether or not toxin production occurs. Toxin production by *C. spiroforme* requires the presence of glucose (Carman and Evans, 1984), an observation consistent with the carbohydrate overload theory of enteritis (Cheeke and Patton, 1980). It is grown on a medium with chopped meat, suggesting that high dietary protein levels may favor its growth. This is often the case with *Clostridium* species.

While it seems clear that *C. spiroforme* is an important cause of rabbit diarrhea, it is not the only cause. The other major organism that has been implicated is *Escherichia coli.* Although *E. coli* is not a significant normal inhabitant of the rabbit gut, it may be found in large numbers in the cecum of rabbits with diarrhea. Prescott (1978) reported an outbreak of diarrhea in weanling rabbits associated with *E. coli,* and suggested that death may be caused by hypoglycemia or electrolyte imbalance, arising from cecal lesions and absorption of bacterial endotoxin. Peeters *et al.* (1984a,b, 1985a, 1986a), in Belgium, have observed field outbreaks of enteritis apparently caused by various strains of *E. coli.* The strains of *E. coli* implicated in rabbit diarrhea are known as attaching organisms, because they attach to the intestinal mucosa. They attach first to the Peyer's patch epithelium (Cantey and Inman, 1981) and later to the enterocytes of the small intestine, cecum, and colon. Peyer's patches are lymph nodules visible as irregular raised plaques on the intestinal mucosa. The Peyer's patches are involved in immune systems of the intestine, producing T lymphocytes which function in resistance to bacterial toxins. Majumder and Ali (1986) observed that in rabbits fed low protein diets, the number and size of Peyer's patches were reduced, suggesting that inadequate dietary protein may increase the susceptibility to enteric pathogens. Peeters *et al.* (1985a) found that enteropathogenic *E. coli* caused extensive destruction of the mucosa of the small intestine, cecum, and colon (Fig. 12.3). The lesions probably interfere with normal intestinal and cecal function.

Peeters *et al.* (1984a) surveyed a number of rabbitries in Belgium for the presence of infectious agents, and examined diarrheal rabbits from these rabbitries (Table 12.1). *Escherichia coli* and *Clostridium* species were the major pathogenic bacteria. Rotavirus was also very common. Rotaviruses seem to be

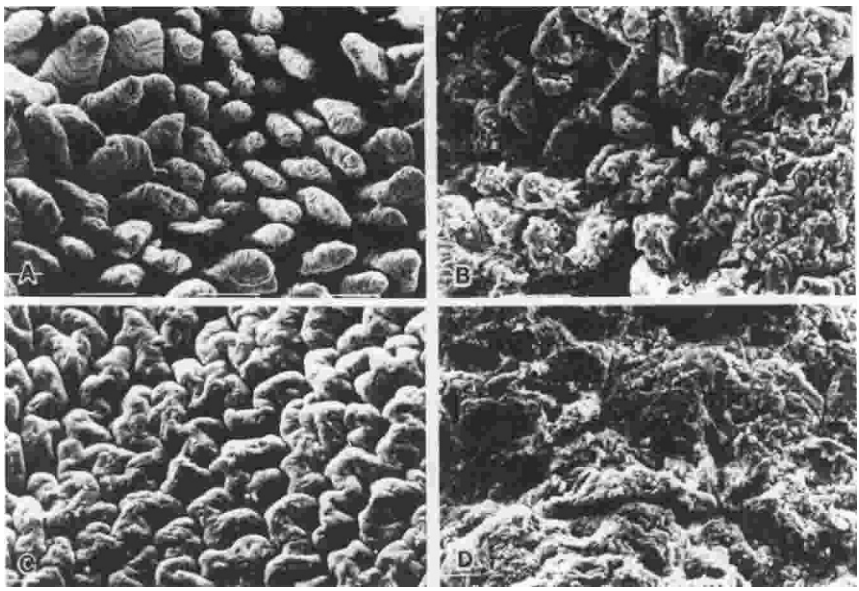


Fig. 12.3 The effects of *Escherichia coli* infection on intestinal and cecal mucosa of rabbits. (A) Normal ileal mucosa. (B) Ileal mucosa 8 days after infection with *E. coli*, showing pronounced destruction of normal morphology. (C) Normal cecal mucosa, with irregularly arranged folds that run over and into each other. (D) Cecal mucosa 8 days after *E. coli* infection, with severe destruction of mucosal integrity. (Courtesy of J. E. Peeters, National Institute of Veterinary Research, Brussels, Belgium.)

TABLE 12.1

Percentage Occurrence of Infectious Agents in Diarrhea-Affected Rabbits and the Rabbitries Involved[a]

Agent	Rabbitry	Rabbits
Coronavirus	4.8	0.8
Rotavirus	81.0	35.4
Escherichia coli	100.0	72.3
Attaching *E. coli*	71.4	40.0
Clostridium spp.	85.7	33.8
Clostridium perfringens	71.4	16.2
Eimeria spp.	42.9	18.5

[a]From Peeters *et al.* (1984a).

endemic in commercial rabbitries but are only mildly pathogenic. They destroy cells that synthesize disaccharidases (Peeters *et al.*, 1984a). Inadequate digestion of disaccharides (e.g., sucrose) could aggravate enteritis caused by other pathogens, and could contribute to carbohydrate overload of the hindgut.

Suckling rabbits with *E. coli* infection die within 48 hr after showing a yellowish diarrhea (Peeters *et al.*, 1984a). Yellow diarrhea in kits 5–15 days of age can be a major problem. For example, a large Brazilian rabbitry has routinely observed a death loss of 15% of suckling kits from yellow diarrhea (Cheeke, 1985).

Coccidiosis has been implicated in rabbit diarrhea. Various species of *Eimeria*, the protozoan responsible for coccidiosis, are common inhabitants of the rabbit gut, and contribute to damage to mucosal surfaces. Coccidiosis can be viewed as a contributor to enteritis but is not generally the primary cause (Meshorer, 1976).

To summarize, the major bacteria involved in enterotoxemia are *Clostridium* species, particularly *C. spiroforme*, and *E. coli*. Rotaviruses and coccidiosis may aggravate enteric disease but are not normally the primary agents involved.

C. Dietary Factors Involved in Enteritis

Numerous investigators (Colin *et al.*, 1976; Cheeke and Patton, 1978; Laplace, 1978; Pote *et al.*, 1980; Spreadbury and Davidson, 1978) have noted that dietary fiber has a protective effect against diarrhea. The beneficial effects of fiber are associated with lignocellulose, the more indigestible components of plant fiber. Highly digestible fiber sources, such as beet pulp, do not have enteritis-preventing properties. Acid detergent fiber (ADF) measures cellulose and lignin, so it is probably the best analytical technique for estimating indigestible fiber. European workers (e.g., Colin *et al.*, 1976) use the term "ballast" to describe indigestible fiber. One favorable effect of "ballast" or indigestible fiber is to provide bulk and a source of large particles in the hindgut. Fiber stimulates cecal-colonic motility (Laplace, 1978), either by a direct stimulatory effect on the mucosa, or a distention effect of the bulk. Low-fiber diets cause cecal-colonic hypomotility (Laplace, 1978), which predisposes the animal to abnormal cecal fermentation and diarrhea. The hypomotility results in prolonged retention times of digesta in the cecum, allowing changes in cecal pH, VFA production, and substrate concentrations, ultimately causing changes in the cecal microflora populations.

Another possible effect of fiber is an indirect one. When high-fiber diets are formulated, the levels of ingredients providing readily available carbohydrate (e.g., starch) are usually reduced. The apparently favorable effects of the increased fiber may in fact be from the lower content of readily fermented carbohydrate. Cheeke and Patton (1980) proposed that enterotoxemia arises from carbohydrate overload of the hindgut. High levels of dietary starch may result in

undigested starch passing through the small intestine and serving as a substrate for bacterial growth in the hindgut. This may provide an environment in which pathogens such as *E. coli* and *Clostridium* species may proliferate. The presence of glucose, which would arise from starch digestion, is necessary for toxin production by *C. spiroforme* (Borriello and Carman, 1983). Thus, a low-fiber, high-starch diet establishes gut conditions of hypomotility and prolonged availability of substrate (starch) to cecal bacteria, allowing pathogens to proliferate and produce toxins that kill the rabbit.

Morisse *et al.* (1979) and Morisse *et al.* (1985) have suggested that a predisposing factor to diarrhea is reduced acidity (a more alkaline pH) of the cecal contents. The pH is determined mainly by the metabolism of VFA, including their rate of production and rate of absorption. Morisse and co-workers believe that suboptimal VFA production leads to an increased cecal pH, resulting in a change in the microflora, with increases in *E. coli* and *Clostridium* species. Morisse *et al.* (1979) reported that administering sources of acid in the drinking water increased the acidity of the cecum, and reduced enteritis incidence. They administered acetic acid, lactic acid, and lactulose (a synthetic disaccharide not hydrolyzed in the small intestine), and noted a lower cecal pH and a reduced incidence of enteritis. In another experiment, they induced enteritis by administration of ampicillin. The control group had 55% mortality, while those receiving acetic acid and lactulose had mortality rates of 19% and 8.7%, respectively.

Lelkes (1986) suggested that the critical event leading to enteritis is a drop in the cecal pH as a result of vigorous fermentation of carbohydrate. He hypothesized that hyperacidity of the cecum destabilizes the microbial population, and is the "smoking gun" responsible for the proliferation of pathogens. He maintains that the subsequent alkalinity of the cecum is due to compensatory mechanisms such as secretion of alkaline fluids into the intestine and secretion of mucus, which has buffering capacity. He noted that mucus was very alkaline and that probably hypersecretion of mucus (in mucoid enteritis) is a physiological mechanism to neutralize the hyperacidity occurring in the early stages of the disease. Part of the beneficial effect of fiber in preventing enteritis may relate to its buffering capacity.

Morisse *et al.* (1985) studied the effect of diet composition on gut function and microbiology. They fed a control diet, similar to normal commercial diets, a high-fiber diet, and a diet high in soluble carbohydrates. The high-fiber diet resulted in a reduction in cecal VFA levels, and a reduction in butyrate and an increase in propionate as proportions of total VFA, and increases in cecal pH and ammonia (Table 12.2). The cecal microflora differed between diets, with the high fermentable carbohydrate diet causing a marked reduction in the normal *Bacteroides*, and increases in *E. coli* and *Clostridium* species (Fig. 12.4). Morisse *et al.* (1985) interpreted the results to indicate that a diet high in fermentable carbohydrate results in high cecal VFA production, keeping the cecum acidic,

TABLE 12.2

Effect of Type of Dietary Carbohydrate on Cecal VFA Production, pH, and Ammonia[a]

Item	Treatment		
	Control	High fiber	High soluble carbohydrate
Diet composition (%)			
Crude protein	15.5	15.2	17.7
Crude fiber	13.5	17.0	10.0
Neutral detergent fiber	29.0	37.2	22.4
Acid detergent fiber	15.8	22.9	11.7
Soluble carbohydrates	26.6	23.4	41.0
Starch	20.1	18.5	35.0
Cecal VFA			
Total VFA (mmol/kg)	83.7*[b]	34.2**	74.9*
Acetic acid (%)	73.2	72.2	69.9
Propionic acid (%)	6.9	18.1	6.9
Butyric acid (%)	19.8	9.6	23.0
Cecal pH	5.7*	6.5**	5.8*
Cecal NH_3 (mmol/kg)	12.9*	28.8**	16.4*

[a]From Morisse *et al.* (1985).
[b]*Different from ** ($p < 0.001$).

and preventing changes in microflora, aiding in the prevention of enteritis. However, the changes in cecal bacteria (Fig. 12.4) suggest that a diet high in soluble carbohydrates promotes the development of a microflora dominated by *E. coli* and *Clostridium* species, supporting the carbohydrate overload concept.

As discussed previously (Chapter 6), the rabbit is unusual in that butyric acid is a more important VFA than propionic acid as an end product of cecal fermentation. This may be important in preventing enteritis. Rolfe (1984), in studies with hamsters, noted that cecal VFA, and particularly butyric acid, are inhibitory to the growth of *Clostridium difficile*. The more acid the cecum, the more inhibitory were the VFA. The greater effectiveness of butyric acid than of acetic acid may be explained by the greater proportion of butyric acid in the undissociated state at the normal pH of the cecum; it is the undissociated acid molecules that are inhibitory to bacterial growth (Rolfe, 1984). In rabbits with diarrhea, the proportion of butyric acid was reduced to 17% of total VFA as compared to a value of 27% in controls (Morisse *et al.*, 1985).

Morisse *et al.* (1985) found that with a high-fiber diet, the cecal ammonia concentration was elevated (Table 12.2). They suggest that a high ammonia level allows greater dissociation of VFA, with a drop in their effectiveness in inhibit-

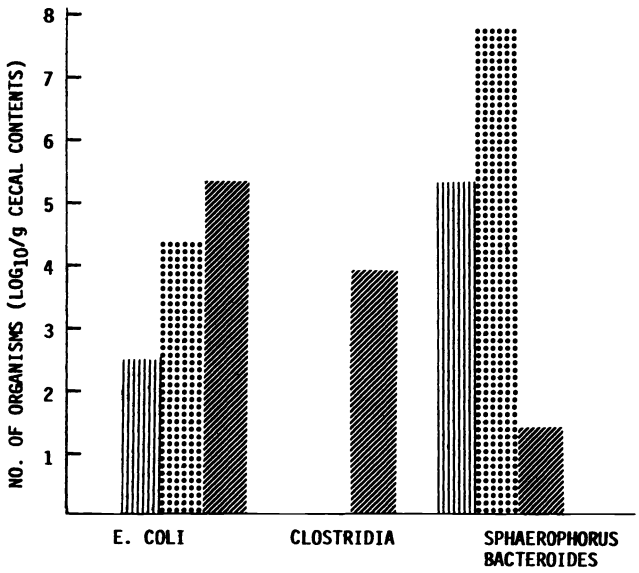


Fig. 12.4 Effects of diet on cecal microflora. With a low-fiber diet high in fermentable carbohydrate (diagonal hatching), *Clostridium* spp. and *Escherichia coli* are dominant. No *Clostridium* spp. were found in animals fed the control diet (vertical hatching) or the high-fiber diet (dotted area). (Data from Morisse *et al.*, 1985.)

ing growth of *E. coli* and *Clostridium* species. A high dietary protein level could have an aggravating effect on enteritis, by increasing the cecal ammonia level. Sanchez *et al.* (1985) noted a tendency for enteritis mortality to increase as the dietary protein level was increased from 17.5% to 20.5%.

The preceding discussion suggests that a diet with sufficient indigestible fiber to maintain cecal motility as well as an abundance but not an excess of fermentable substrate to maintain acidic conditions in the hindgut might be the optimal dietary state for maximum performance and minimum enteritis. A minimum dietary crude fiber level of 10% is suggested for minimizing enteritis incidence (de Blas *et al.*, 1986).

D. Physiological Changes in Enteritis

Hungarian workers (Vetesi and Kutas, 1973, 1974) studied physiological parameters in rabbits with *E. coli*-induced enteritis. This is the most important disease of rabbits in Hungary, with losses exceeding those from all other diseases combined. Two peaks of incidence are in the postweaning period (4–11 weeks) and in suckling kits (2–8 days of age). Changes in physiological parameters with enteritis (Table 12.3) indicate dehydration (increase in hematocrit and serum protein), a marked rise in serum urea, metabolic acidosis (reduced blood pH),

TABLE 12.3

Comparison of Blood and Urine Constituents of Normal Rabbits and Those with Enteritis[a]

Group	Hematocrit (%)	Blood HCO_3 (mEq/liter)	Blood pH	Urine pH	Plasma			
					Total protein (g/100 ml)	Na^+ (mEq/liter)	Cl^- (mEq/liter)	Urea (mg/100 ml)
Normal	37.8	20.5	7.298	6.62	5.38	166	100	36
Enteritis	44.6	10.3	7.056	4.94	7.94	152	88	308

[a]From Vetesi and Kutas (1973).

severe blood base deficit (reduced plasma bicarbonate), and acid urine. Vetesi and Kutas (1973) explain the sequence of events as follows. *Escherichia coli,* for some reason, proliferates in the hindgut. Toxins produced by the bacteria damage the gut mucosa, resulting in hypersecretion of mucus, water, and electrolytes into the gut. Reabsorption of the alkaline digestive secretions is impaired. The contents of the hindgut become watery and alkaline. The loss from the blood of water, electrolytes, and bases causes severe disturbances in body fluids. The cessation of cecotrophy during diarrhea further increases the losses of water and electrolytes. Dehydration characterized by decreased plasma volume and decreased serum sodium occurs. These alterations cause decreased cardiac function, a decline in blood pressure, and symptoms of shock. Absorbed bacterial toxins cause toxic reactions including impaired liver function, as evidenced by the marked rise in plasma urea. Depletion of liver and heart glycogen is observed (Vetesi and Kutas, 1974), further aggravating the shock condition.

Similar effects may be produced by *Clostridium* toxins. Stringer (1985) reviewed the mode of action of *Clostridium* enterotoxins. The enterotoxins cause increased capillary permeability and vasodilation (thus reducing blood pressure). The intestine shows increased secretion of fluid and sodium, inhibition of chloride and glucose uptake, and sloughing of epithelial cells. Liver function, as assessed by oxygen consumption of liver mitochondria, is impaired. Other evidence of impaired liver function includes elevated blood ammonia and liver lesions. A hyperlipemia occurs, with elevated plasma triglycerides. This is probably due to mobilization of body fat for energy, after the cessation of feed intake. The effects on capillary permeability would explain the hemorrhage and edema of the cecal wall seen in enterotoxemia (Patton *et al.*, 1978).

Licois *et al.* (1978a,b) studied fluid and electrolyte metabolism in rabbits with diarrhea induced by infection with coccidiosis. While coccidiosis-induced diarrhea may not exactly duplicate changes in enterotoxemia, it may be a model for general effects of diarrhea on rabbit physiology. Changes in fluid balance and electrolyte metabolism were shown earlier (Table 8.3). In diarrhea, there was a net loss of sodium and potassium and decreased plasma sodium. The hematocrit was 41.7% in control animals, and 35.1% in infected animals, quite similar to values reported by Vetesi and Kutas (1973) (Table 12.3). Other changes noted with diarrhea were decreases in plasma sodium, potassium, and chloride, and elevated plasma urea. These authors suggested that the high blood urea nitrogen level was a reflection of the breakdown of body tissue, since the rabbits may lose 10% of their body weight in 3 days after diarrhea begins, and this loss was not due to dehydration and increased water excretion. Lipemia, with elevated plasma triglycerides and ketone bodies, occurs and is a symptom of fasting ketosis in diarrhetic rabbits (Coudert *et al.*, 1978). This may also explain the elevated serum cholesterol levels seen in rabbits with diarrhea (Ekpenyong, 1986; Gascon and Verde, 1985).

E. Other Factors Involved in Enteritis

Enteritis can be induced by antibiotic administration. This is due to a suppression of other organisms, allowing *Clostridium* species to proliferate. Clindamycin has been used to induce enterotoxemia in rabbits for experimental purposes (Katz *et al.*, 1978), and results in growth of *C. spiroforme* and production of iota toxin (LaMont *et al.*, 1979; Rehg and Pakes, 1982). Other antibiotics may cause enteritis, including lincomycin, penicillin, ampicillin, and erythromycin (Thilsted *et al.*, 1981). These antibiotics selectively kill gram-positive aerobes and certain gram-negative anaerobes, allowing proliferation of nonsensitive organisms, including *E. coli* and *Clostridium* species. Outbreaks of enteritis may occur when rabbit feed is contaminated with antibiotic-containing feed intended to be used for another animal species.

Susceptibility to enteritis may have a genetic component. A strain of nonalbino white rabbits with pigmented eyes was observed to be susceptible to diarrhea (M. A. Grobner, P. R. Cheeke, and N. M. Patton, unpublished observations). Evidence of insufficient nerve ganglia in the intestine was seen, suggesting that inadequate neural supply to the gut in this strain could cause hypomotility. A similar defect has been noted in white progeny of overo spotted horses (Hultgren, 1982). Hultgren states that during embryonic development, both melanocytes (pigment cells) and myenteric ganglia cells (intestinal nerve cells) arise from the neural crest. Retinal pigment cells originate from neural ectoderm and not from neural crest. Thus a white rabbit with pigmented eyes could have a deficiency of innervation to the gut, leading to hypomotility and susceptibility to enteritis. Another mechanism by which genetic susceptibility to enteritis could occur is from activity of gastrointestinal hormones. Bishop *et al.* (1984) described a condition known as grass sickness in horses, in which gut motility ceases, and the colon becomes impacted with hard feces and mucus. A deficiency of a class of gastrointestinal hormones known as regulatory peptides in affected horses was found. These peptides include substance P and vasointestinal polypeptide (VIP). These hormones are released from nerve cells, and stimulate intestinal motility. Bishop *et al.* (1984) suggested that a neurotoxin could be involved in grass sickness, causing damage to the enteric nerves, leading to bowel stasis. It is possible that bacterial toxins in the rabbit gut could likewise inhibit secretion of regulatory peptides, leading to hypomotility and enteritis.

Stress seems to increase enteritis incidence. Stress can inhibit intestinal motility, by direct neural effects and epinephrine-mediated action. Sudden changes in environmental temperature can affect feed intake, and may influence gut motility. A sudden cold spell is often followed by an enteritis outbreak. This can be rationalized on the basis of a sudden increase in feed intake, leading to carbohydrate overload of the hindgut. Monnier and Desbals (1985) studied the

relationship of stress to diarrhea. They measured plasma ACTH (adrenocorticotropic hormone), a hormone regulating secretion of adrenal hormones in response to stress, in rabbits with diarrhea and in rabbits stressed by transport by car. In rabbits with diarrhea, plasma ACTH and total corticosteroids were 293 pg and 111 ng/ml, respectively, while corresponding control values were 130 pg and 66 ng/ml. Moving animals by car resulted in a 2.5-fold increase in ACTH levels. These workers believe that stress, documented by changes in adrenal hormones in the plasma, is a causal factor in rabbit diarrhea. Vitamin C may reduce the effects of stress in rabbits (Verde and Piquer, 1986) and may also inhibit toxin production by *Clostridium spiroforme* (Grobner *et al.*, 1986). Further studies on the effects of vitamin C are required before its potential as a feed or water additive to reduce enteritis can be assessed.

II. MILK ENTEROTOXEMIA

This term has been suggested for a situation in which young kits, 3–6 days of age, die in the nest box with full stomachs, indicating that they did not die from lack of milk intake. It is postulated that bacterial toxins are absorbed from the gut by the doe, and passed in the milk. If the kits are more sensitive to the toxins than the doe, they may be killed at a concentration of toxins that has no observable effect on the mother. While this is a rational explanation for one of the major causes of nest box mortality, it has not been proven experimentally. If milk enterotoxemia is suspected, a reduction of feed given to the doe for the first week after kindling is indicated. It is important that the body condition of the doe and the presence of large amounts of milk curd in the stomachs of the kits be assessed, because another cause of neonatal mortality is inadequate nutrient intake of the does. Feed restriction would aggravate this situation (Fig. 12.5).

III. CECAL IMPACTION (MUCOID ENTERITIS)

Another disorder commonly afflicting rabbits is cecal impaction (mucoid enteritis). A thorough description of the symptoms has been provided by Van Kruingen and Williams (1972). As in enterotoxemia, this is a paradoxical situation in which signs of diarrhea are evident in animals that are constipated. Cecal impaction seems to be a result of similar circumstances that induce enterotoxemia, but insufficient bacterial toxins are produced to kill the animal. Cecal motility is impaired, and a hard mass of fine particulate matter accumulates in the cecum. Impaction is often noted under conditions of high environmental temperature. The cecum is a large reservoir of body water, and if tissue water needs are not met by direct water consumption, fluid can be drawn into the blood from the cecum. Conditions that might reduce water intake below requirements are

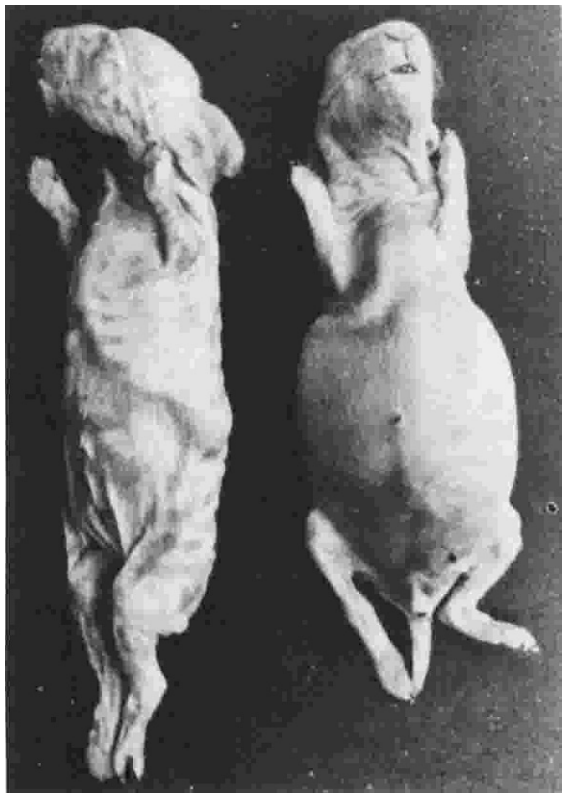


Fig. 12.5 Comparison of a "starve-out" (left) and a kit with a milk curd in the stomach (right). Kits that develop milk enterotoxemia have the appearance of the animal on the right. The "starve-out" condition may be caused by inadequate feed or energy intake of does. (Courtesy of Dr. H. C. Loliger, Institute for Small Animal Sciences, Celle, Federal Republic of Germany.)

high environmental temperature (Prud'hon, 1976) and a high water temperature. Thus, a low-fiber diet, causing cecal-colonic hypomotility, along with conditions resulting in excessive water uptake from the cecum, could cause cecal impaction. Procedures to increase water intake, such as increasing the salt content of the diet, may aid in preventing impaction.

The possible involvement of the water-absorbing properties of dietary fiber in impaction is suggested by the observation that highly hydrophilic (water-absorbing) materials, such as guar gum and psyllium hydrophilic mucilloid (psyllium is a plant grown in India from which a highly water-absorbing fiber is obtained for manufacture of laxatives), cause severe intestinal dehydration in laboratory animals (Struthers, 1986). The psyllium colloid absorbs over 40 g of water per gram of dry weight, whereas wheat bran absorbs 2–3 g water per gram of dry weight.

Feeding a highly water-absorbant material causes intestinal blockage and damage to the intestinal mucosa. Struthers (1986) cites research that feeding 10% psyllium husk to rabbits caused damage to the intestinal mucosa, by dehydrating the tissues of the intestinal wall. Based on these effects of an extreme situation, it is reasonable to speculate that diets high in water-absorbing capacity may induce impaction in rabbits. One mechanism by which cecal impaction could be induced is that dehydration of the cecum could occur to replenish water in the blood that has been secreted into the stomach to hydrate the ingested feed. In other words, when the feed has a high water-absorbing capacity, it must absorb a lot of water in the stomach to produce the normal fluid gut contents. This water comes primarily from the blood. A sudden demand for water in the stomach following eating could result in withdrawal of water from the cecum, which serves as a reservoir of body water. Thus the impaction could occur in the cecum even though the actual water uptake by feed occurs in the stomach and upper small intestine (Fig. 12.6).

Toofanian and Targowski (1986) demonstrated that a substance produced in the cecum of rabbits with mucoid enteritis stimulates the production and secretion of mucus by goblet cells in the colon. Various factors, including mechanical and chemical irritation and bacterial toxins, cause increased goblet cell secretion. Lelkes and Chang (1987) observed that an organism that is or is similar to *Clostridium cocleatum* is invariably present in the cecum when mucoid enteritis occurs. They postulated that this organism may secrete an enterotoxin that stimulates mucus secretion. *Clostridium cocleatum* is quite similar in appearance to *C. spiroforme* (Kaneuchi *et al.*, 1979).

Toofanian and Hamar (1985, 1986) reported evidence of abnormal cecal fermentation in rabbits with mucoid enteritis. The proportions of acetate and butyrate in the cecal contents were reduced in comparison to normal cecal contents, while proportions of propionate, isobutyrate, valerate, and isovalerate were increased. These indicate abnormal fermentation, which is probably a consequence of, rather than a cause of, the cecal dysfunction. Similarly, Lelkes (1986) noted that the cecal contents taken from rabbits with mucoid enteritis had a much lower rate of glucose fermentation *in vitro* than those obtained from healthy animals. Microbial changes, with proliferation of opportunistic species, often occur after the onset of mucoid enteritis (McLeod and Katz, 1986).

Morisse *et al.* (1985) coined the term "cecal paresis–pulmonary edema" to describe the condition seen when lung damage accompanies cecal impaction. Principal factors in the etiology of this condition are cecal impaction and environmental conditions such as cold and drafts. Bacterial toxins may cause lung damage, so perhaps absorbed toxin (e.g., clostridial iota toxin) may be responsible for the lung edema, especially as the iota toxin is known to increase capillary permeability.

For experimental purposes, mucoid enteritis can be induced by ligating the

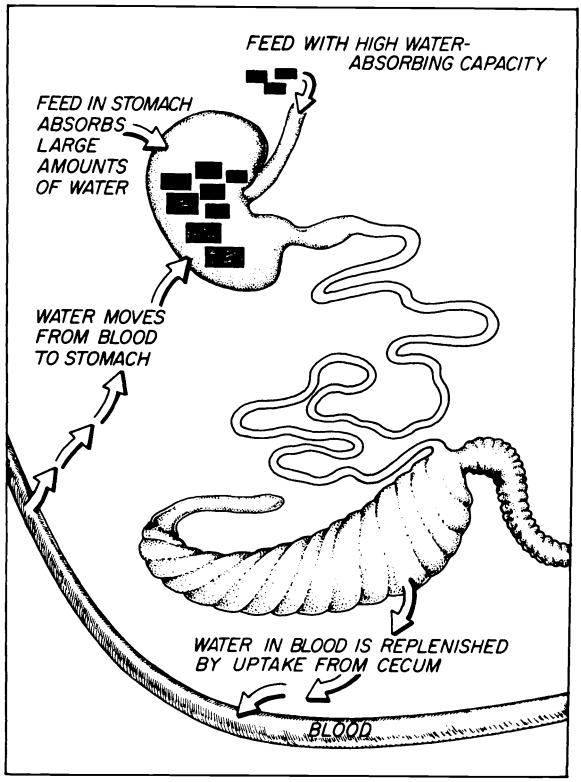


Fig. 12.6 A possible mechanism to explain cecal impaction. When feed with a high water-absorbing capacity is consumed, large amounts of water may be secreted into the stomach. Replenishment of this water lost from the blood may be by uptake of water from the cecum, causing impaction of cecal contents.

cecum (Sinkovics, 1986; Targowski and Toofanian, 1982; Toofanian and Targowski, 1983).

IV. TYZZER'S DISEASE

Tyzzer's disease is an infectious disease of rabbits that causes diarrhea, and may sometimes be implicated with outbreaks of enteritis in commercial rabbitries (Peeters *et al.*, 1985b). It is caused by a rod-shaped, motile organism, *Bacillus piliformis*, which can be identified microscopically with appropriate staining techniques. Because diagnosis of Tyzzer's disease is somewhat difficult, it is possible that it is more widespread in commercial rabbitries than generally believed (Peeters *et al.*, 1985b). The organism is resistant to many antibiotics;

oxytetracycline is active against it (Peeters *et al.*, 1985b). Borriello and Carman (1985) have proposed that the organism is not a *Bacillus* but rather is a *Clostridium* spp., which they have named *Clostridium piliformis* (Carmen and Evans, 1984).

V. COCCIDIOSIS

Two forms of coccidiosis, an intestinal and a liver form, occur in rabbits. Both types may cause diarrhea, so should be considered as possible causative agents when enteritis occurs. Coccidiosis is caused by various species of *Eimeria*, a protozoan parasite. At least nine *Eimeria* species occur in rabbits (Peeters *et al.*, 1981). A number of species can cause intestinal coccidiosis. *Eimeria steidae* causes liver coccidiosis, which may have effects on digestion because of the impairment of bile secretion with liver damage.

Coccidiosis can be treated with coccidiostats such as sulfaquinoxaline, which is given in the water (0.04%) or in the feed (0.025%). The coccidiostat should be given for at least 3 weeks to clear up an outbreak. Coccidiosis can be controlled with good sanitation. The protozoa produce oocytes (eggs), which are excreted in the rabbit feces. The oocytes cannot reinfect the rabbit until they have sporulated, which requires a period of incubation of at least 24 hr outside the rabbit. If the fecal pellets are knocked from the cage *every* day, there will be little opportunity for the rabbit to become reinfected, and the disease will gradually disappear from the rabbitry. On the other hand, Sinkovics (1984) presents evidence that ingestion of just one oocyte could give rise to 26 million protozoans, so the likelihood of complete control with sanitation alone is questionable.

Sinkovics (1984) believes that coccidiosis is a component of most enteritis outbreaks in rabbits. The role of coccidia could be a direct pathological effect on the intestinal mucosa, allowing invastion by other agents such as viruses and bacteria. Also, according to Sinkovics (1984), coccidiosis causes a pronounced inhibition of intestinal motility, which, as described earlier, is a feature of enteritis. It is likely that coccidiosis is a contributing factor to many outbreaks of rabbit diarrhea. Different species of *Eimeria* may occupy different locations in the gut. For example, *E. intestinalis* infects the epithelial cells of the ileum, whereas *E. pellerdyi* colonizes the crypts of Lieberkuhn of the cecum and colon (Licois *et al.*, 1978a). In spite of their different habitats, their effects on enteritis are similar.

Coccidiosis can affect nutrient digestion and metabolism. Diel (1960) found that liver coccidiosis adversely affects the metabolism of fat-soluble vitamins. The liver levels of vitamin A and vitamin E were depressed in *E. stiedae*-infected rabbits (Table 12.4). This may mean that coccidiosis infection increases the requirements for these vitamins in rabbits.

In chickens, coccidiosis affects mineral metabolism. Infection increases liver

TABLE 12.4

Effect of Liver Coccidiosis on Liver Vitamin A and E Concentrations[a]

Treatment	Vitamin E		Vitamin A	
	μg/g Liver	μg in liver/100 g BW[b]	IU/g Liver	IU in Liver/100 g BW
Eimeria-infected rabbits with liver lesions	4.0	19.9	62	305
Eimeria-infected rabbits without liver lesions	4.8	18.4	105	389
Noninfected rabbits	14.6	56.7	195	582

[a]From Diehl (1960).
[b]BW, Body weight.

copper levels and intensifies copper toxicity (Southern and Baker, 1982, 1983; Czarnecki and Baker, 1984), and intensifies zinc deficiency (Southern and Baker, 1983). These relationships have not been investigated in rabbits, but could be of significance. For example, since coccidiosis infection causes increased liver copper levels and enhanced copper toxicity (in chicks), it might have an effect on the response to copper as a feed additive in rabbit diets.

Yvore and Guillaume (1976) studied the effects of hepatic coccidiosis on the digestibility of fat and energy. They hypothesized that since *E. stiedai* grows in the biliary canals and adversely affects hepatic function, it might have an effect on digestive processes through inhibition of bile secretion. Animals free of *E. stiedai* were used as controls, and a similar group was infected with 10,000 oocysts per animal. The results (Table 12.5) show that infection with liver

TABLE 12.5

Effect of Hepatic Coccidiosis on Growth Performance and Digestion[a]

Item	Treatment	
	Noninfected	Infected with *Eimeria stiedai*
Weight gain (g/20 days)	659	222
Dry matter digestibility (%)	60	36
Lipid digestibility (%)	58	19
Digestible energy (kcal/kg)	2451	2131
Liver weight (g on day 46)	98	294

[a]From Yvore and Guillaume (1976).

coccidiosis markedly impaired fat digestion, and reduced the digestible energy content accordingly. Reduction in digestibility of other components is indicated by the decreased digestibility of dry matter. Gain was markedly depressed, and pronounced enlargement of the liver occurred.

It is apparent that infection with coccidiosis can have pronounced effects on diet utilization by rabbits, as well as having a role in enteric disease.

VI. PREGNANCY TOXEMIA

Pregnancy toxemia (ketosis) is a disease that can affect many different animals. It is a major problem in livestock, particularly with dairy cattle and sheep. As the name implies, it occurs with pregnant animals, or in the case of dairy cows, in the period immediately following parturition when heavy lactation begins. It is associated with a combination of a high nutritional demand and conditions that limit intake, so that the animal cannot consume enough feed to meet its energy needs. To make up for the energy deficit, body fat is mobilized. Ketosis results when the carbohydrate-metabolizing metabolic pathway (citric acid cycle) is not able to metabolize all of the acetic acid produced from the metabolism of fatty acids arising from body fat. The acetic acid that cannot be further metabolized is converted to compounds called ketone bodies, which are

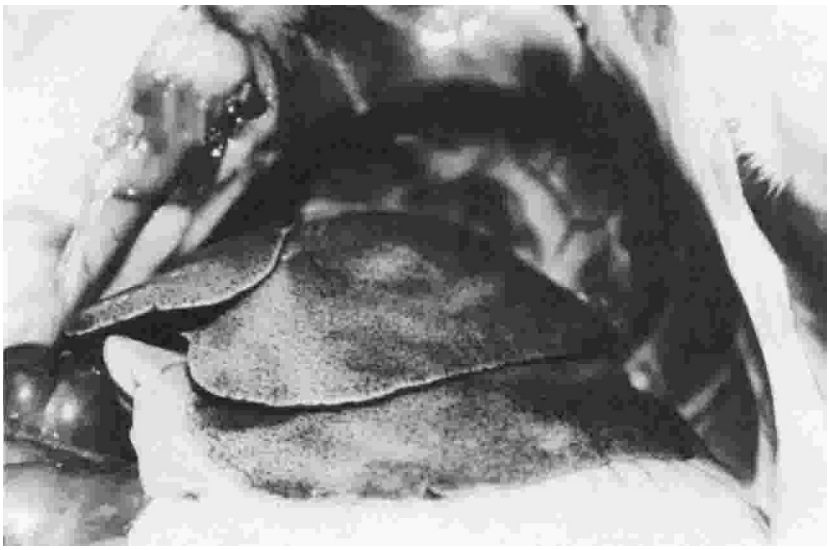


Fig. 12.7 Fatty liver, resulting from mobilization of body fat following inhibition of feed intake by a hair ball in the stomach.

excreted in the urine, and in the case of acetone, in the expired air from the lungs. The smell of acetone can be detected in the breath of animals with ketosis. As a result of the inability to utilize the fat reserves in normal metabolism, fat accumulates in the liver, causing a fatty liver condition (Fig. 12.7). The ketone bodies may cause metabolic problems such as acidosis. The affected animal suffers an insufficiency of cellular energy. The brain is particularly affected because of its high metabolic rate. The animal goes into a coma, and dies unless treated. Because of the inadequate energy supply, the blood glucose level is depleted, so hypoglycemia is characteristic of pregnancy toxemia. Injeciion of glucose is an effective treatment.

Pregnancy toxemia may develop in rabbits after kindling, if their feed intake is inadequate, the diet is too low in energy, or if they go off feed. Often, pregnancy toxemia is associated with the occurrence of hair balls in the stomach, which impair feed intake (Patton *et al.*, 1983). The relationship between fat metabolism and ketonemia (blood ketone bodies) in rabbits has been studied by Jean-Blain and Durix (1985). Green (1937, 1938) described pregnancy toxemia symptoms, including fatty liver, an enlarged, extended gallbladder, and excretion of ketones in the urine.

VII. OTHER DISEASES WITH A NUTRITION INVOLVEMENT

Nutritional status influences a number of other pathological states besides those described above. Abortions, resorbed fetuses, and small, weak litters at birth, with a high mortality of kits during the first week of life, are common problems. Dietary inadequacy is a basic cause. Any severe type of stress, including nutritional stress, can result in the doe terminating pregnancy. This has survival value in the wild. For continuation of the species, survival of the adult is more important than that of a particular litter. If there is a low energy intake, reflecting a poor feed supply, it is of survival value for the female to cease reproduction, and resume it when conditions improve and survival of the young is more likely. This is accomplished, apparently by a neurohormonal involvement, by either resorbing the fetuses, generally before day 20 of gestation, or aborting them. Thus resorption–abortion can be linked to inadequate nutrition involving virtually any nutrient. Cheeke *et al.* (1984) found that excess vitamin A (see Chapter 9) can result in these symptoms, as can vitamin A deficiency. Probably deficiencies and toxicities of other nutrients can exert similar effects. Hydrocephalus, as previously described, is also a symptom of either vitamin A deficiency or toxicity.

An important problem in rabbits is fur chewing (fur pulling, fur eating). Sometimes rabbits will pull fur out of the hair coat of other rabbits in the same

cage or in an adjacent cage. Besides being unsightly, it diminishes the value of the skin, and results in a reduced price obtained for meat rabbits. Fur chewing may result in hair balls (trichobezoars) forming in the stomach. These indigestible masses of hair may plug the pyloric sphincter, so food cannot move through the stomach. The animal goes off feed, loses weight, and eventually dies. It occurs frequently in does, perhaps associated with the normal hair pulling to make the nest. It is particularly important in Angora rabbits, in which "wool block" is a major problem. The feeding of a high-fiber diet, and particularly the feeding of long hay, greens, or other roughage may help to "sweep" hair out of the stomach before it can form a trichobezoar.

Fur balls can be treated by the administration of a source of proteolytic enzymes, such as bromelain and papain. These are protein-digesting enzymes found in pineapples and papaya, respectively. Oral dosing with about 10 ml of raw pineapple juice, given several times daily, will usually cause a hair ball to disintegrate and pass through the stomach. After feed intake resumes, the feeding of long hay will help to remove any remaining hair.

Nutritional status is related to respiratory disease, primarily through effects on the environment. Most respiratory disease in rabbits is caused by infection with *Pasteurella multocida*. This bacterial organism colonizes the nasal passages, leading to respiratory distress and ultimately pneumonia and breakdown of the lungs. A principal factor involved in *Pasteurella* infection is the presence of high ammonia levels and high humidity in the rabbitry. Water vapor in the air dissolves ammonia, and it attacks the mucous membranes of the nasal passages when the rabbit breathes. This destroys the normal resistance of the mucosa to bacterial infection, and allows the *Pasteurella* organisms to invade. Adequate ventilation is necessary to reduce both humidity and ammonia concentrations. The source of the ammonia is urea excreted in the urine. Bacteria in the manure convert the urea to ammonia, a volatile substance that is released into the air of the rabbitry. The ultimate source of the ammonia is the protein in the diet. Excess protein (amino acids) is metabolized in the liver, and the nitrogen is converted to urea. Urea is filtered out of the blood by the kidney, and excreted in the urine. Ammonia in the rabbitry can be controlled in part by ensuring that excess protein or protein with an imbalance of amino acids is not fed.

Both Patton *et al.* (1980) and (Morisse, 1979) have noted that it is quite difficult to infect rabbits with *Pasteurella* unless there is ammonia in the air. In a low-ammonia environment, millions of *Pasteurella* organisms can be sprayed into the nasal passages with no infection resulting. With high concentrations of ammonia, colonization readily occurs.

The main nutritional involvement in pasteurellosis is the relationship between high dietary protein and air ammonia levels in the rabbitry. A vitamin A deficiency would be expected to increase the susceptibility of the nasal epithelial tissue to infection, but, as discussed in Chapter 9, vitamin A deficiency in rabbits is unlikely under practical conditions if good quality alfalfa meal is used in the diet.

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13

Feed Analysis

Analysis of feedstuffs is useful to measure their nutrient content, and to determine the presence of toxic substances. Knowledge of the composition of feedstuffs is necessary to allow diets to be formulated that meet the nutrient requirements of the animals that will receive the feed. If problems occur with a particular batch of feed, analysis of it may help to track down the problem. The price of feed ingredients generally is dependent on their nutrient content. Large feed manufacturing plants usually have a quality control laboratory, where feed ingredients are analyzed and the manufactured feed monitored to ensure that it meets specifications.

For reasons of time and cost, it is not usually feasible to obtain a complete nutrient analysis of feedstuffs. While it is usually possible to get protein and fiber analyses done quickly at a reasonable cost, analysis of amino acids and vitamins may often not be practical. In this case, "book values" from tables of feed composition may be used. While book values are very useful, they are not "cast in stone." There is considerable variability in nutrient content of most feedstuffs, particularly for vitamins and trace elements. For many years, a system called the proximate analysis has been used to assess the nutritional value of feeds. The components of the proximate analysis scheme are listed below:

Dry matter
Crude protein
Ether extract
Ash
Nitrogen-free extract (NFE)

Each of these will be described briefly.

I. DRY MATTER

The dry matter content of a feed refers to the residue after all water is removed. Generally, dry matters are determined by drying a feed sample in an oven, usually at 100°–105°C. This procedure is adequate with most feedstuffs,

with the exception of materials such as silage, which may contain large amounts of volatile material such as the volatile fatty acids (VFA).

A common problem encountered is distinguishing between feed analyses expressed on a dry matter basis and on a "wet weight" or "as is" basis. In the laboratory, feeds are analyzed on a dry matter basis. They are dried, and then kept in a desiccator to ensure that they do not absorb moisture from the air. The importance of this is that for many analyses, only small sample sizes are used. Depending on the humidity of the laboratory on a particular day, a feed will take up or give off moisture. A sample of 100 mg of a feed today may weigh only 90 mg tomorrow or may weigh 125 mg the day after. Thus to get accurate results, it is necessary to sample the dry matter, which is protected against moisture, so its weight will not fluctuate with atmospheric conditions. The livestock producer, however, does not feed on a dry matter basis. The feed is used "as is," as it comes out of a bin or sack. Confusion frequently arises concerning how to convert values from a laboratory report into "as is" values for the feed. Conversions from each basis may be made as follows:

1. To convert values from a dry matter basis to a "wet weight" or "as is" basis, multiply by the percentage dry matter divided by 100.

Example: On a dry matter basis, an alfalfa sample contains 16.5% crude protein. The dry matter content is 92%. The protein content on an "as is" basis is

$$16.5 \times \frac{92}{100} = 15.2\%$$

Note that on an "as is" basis, the nutrient content will always be lower than on a dry matter basis, because of the dilution with moisture.

2. To convert from a "wet weight" basis to a dry matter basis, multiply by a factor of 100 divided by the percentage dry matter.

Example: A wheat sample contains 11.2% crude protein on a wet weight basis, and contains 96% dry matter. The protein content on a dry matter basis is

$$11.2 \times \frac{100}{96} = 11.7\%$$

II. CRUDE PROTEIN

By definition, crude protein is equal to nitrogen content multiplied by a factor of 6.25. This factor is derived from the general relationship that most proteins contain about 16% nitrogen. The nitrogen is that of the amino groups of the amino acids. Thus, 16 g of nitrogen come from 100 g of protein, or 1 g of nitrogen comes from 100/16 = 6.25 g of protein. There are several inaccuracies

in the estimation of crude protein. One is that the factor of 6.25 is an average value; for a particular protein source, it may not be completely accurate. The other thing to bear in mind is that the crude protein determination does not actually measure protein, but measures nitrogen. The assumption is made that all of the nitrogen in the feed is associated with protein. This assumption is not necessarily always correct. However, it would be virtually impossible to measure each individual type of protein in a feed, so the measurement of nitrogen is a necessity on a practical basis.

The procedure used to measure crude protein is known as the Kjeldahl analysis, after the Danish chemist who developed it in the nineteenth century. Feed samples are digested by boiling in concentrated sulfuric acid, until the sample is totally broken down. The nitrogen in the protein is converted to ammonium ion (NH_4^+). The digested material is then made alkaline by the addition of concentrated sodium hydroxide; this converts the NH_4^+ to ammonia, NH_3. Passage of steam through the sample results in the distillation of NH_3 in the steam, which is passed through a boric acid solution. The boric acid traps the ammonia by forming a complex with it; the amount of ammonia is then determined by a titration procedure. With the appropriate equipment, large numbers of samples can be run at one time, so the procedure is relatively quick and easy to perform.

III. CRUDE FIBER

The crude fiber content is determined by boiling an ether-extracted feed sample in dilute acid, then in dilute alkali, drying, and burning in a furnace. The difference in weight before and after burning is the crude fiber fraction. It is an old procedure that was developed to mimic the acid conditions of the stomach followed by the alkaline condition of the small intestine. The crude fiber determination is required by most regulatory agencies, so in most states of the United States a crude fiber guarantee must appear on the feed tag. Unfortunately, crude fiber is often a very poor predictor of feed fiber. In recent years, the term "modified crude fiber" has come into use. This is the same as crude fiber except that the ashing step is omitted.

Fiber is a term used to refer to the structural cell wall components of plant cells, as opposed to the nonfiber cellular contents of proteins and sugars. The main chemical constituents of the cell wall are cellulose, lignin, hemicellulose, pectins, and silica. The problems associated with the use of crude fiber are that it does not accurately correlate with these cell wall constituents.

The crude fiber fraction is basically the residue remaining after alternate boiling in acid and alkali. This procedure dissolves some of the cell wall components, so it is not a true measure of fiber. For example, Van Soest (1982) notes that as much as 28% of the cellulose in forages and 30–80% of the lignin may be

dissolved in the crude fiber procedure, and so cannot be measured. The inadequacies of the crude fiber procedure have been known for many years; however, it is still widely used because of the inertia of regulatory agencies in requiring the listing of crude fiber on feed tags.

Crude fiber has been widely replaced by a system developed by P. J. Van Soest at Cornell University, involving the use of detergent solutions. The detergent system is intended to differentiate the highly digestible cell contents of plant tissue from the less digestible cell wall constituents. Extraction of a feed sample with a neutral (pH 7) solution of detergent (sodium lauryl sulfate) dissolves the cell contents, leaving a residue of cell wall constituents—cellulose, hemicellulose, lignin, and silica. Samples containing grains should be treated with amylase to dissolve starch. The residue from this procedure is called neutral detergent fiber (NDF). The acid detergent fiber (ADF) is the residue remaining after extraction of the feed sample with acid (1 *N* H_2SO_4) detergent (cetyl trimethylammonium bromide). This procedure dissolves hemicellulose, so NDF − ADF = hemicellulose content.

Probably the most suitable estimate of fiber in rabbit nutrition is ADF. This is primarily cellulose and lignin, so would be a good estimate of indigestible fiber.

Italian workers (Pagano Toscano *et al.*, 1986) studied relationships between crude fiber, ADF, and NDF in rabbits. They used 45 rabbit feeds and feed ingredients, with a range of ADF values from 21.20 to 40.59%. The relationship between crude fiber and ADF was described by the equation:

$$\% \text{ ADF} = 9.432 + 0.912 \ (\% \text{ crude fiber})$$

A rearrangement gives the following equation for calculation of percentage crude fiber when percentage ADF is known:

$$\% \text{ crude fiber} = \frac{\% \text{ ADF}}{0.912} - 10.342$$

Similar equations relating NDF to crude fiber were derived:

$$\% \text{ NDF} = 28.924 + 0.657 \ (\% \text{ crude fiber})$$

$$\% \text{ crude fiber} = \frac{\% \text{ NDF}}{0.657} - 44.02$$

Values for ADF and NDF, calculated using these equations, are shown for a range of crude fiber values from 12 to 30% (Table 13.1). It should be recognized that these values are "ball park estimates" only, because there is no sound chemical basis relating crude fiber to ADF and NDF. For specific ingredients, there may be a good relationship between crude fiber and the detergent fibers. For forages, there is a good relationship between NDF and ADF (Fig. 13.1).

TABLE 13.1

Comparison of Crude Fiber, ADF, and NDF Percentages in Rabbit Feeds[a]

Crude fiber	ADF	NDF
12	20.37	36.81
14	22.20	38.12
16	24.02	39.44
18	25.85	40.75
20	27.67	42.06
22	29.49	43.38
24	31.32	44.69
26	33.14	46.01
28	34.97	47.32
30	36.79	48.63

[a]Calculated using the equations of Pogano Toscano *et al.*, 1986.

Because of the importance of fiber in rabbit nutrition, techniques used to assess dietary fiber should be standardized. It appears that ADF provides the best estimate for indigestible fiber for rabbits.

IV. ETHER EXTRACT

The ether extract is a measure of the fat content of feeds. Feed samples are extracted with ether, and the ether-extracted material is weighed after evaporation of the ether. Alternatively, the loss of weight of the feed sample after extraction with ether can be used to estimate the weight of fat. Actually, this procedure measures lipids, which are defined as constituents of plant and animal tissue that are soluble in organic solvents such as ether. Most lipids in feeds are fats and oils. Other lipids include chlorophyll, various plant pigments, waxes, essential oils, and resins. Normally the concentration of these substances is not high enough to affect the fat determination significantly.

Ether extraction does not remove saponified fats. Saponification involves formation of soaps, which are mineral (sodium, potassium, calcium, magnesium) salts of fatty acids [e.g., $(CH_3—(CH_2)_n—COO^-)_2Ca^{2+}$]. According to Parigi-Bini *et al.* (1974), the presence of saponified fat in the feces may result in an overestimation of the digestibility of fat in rabbits. Extraction with a more polar solvent (e.g., acetone) will remove soaps. Another procedure to solubilize saponified fats is to use a 6-hr hydrolysis with 3 *N* HCl prior to ether extraction.

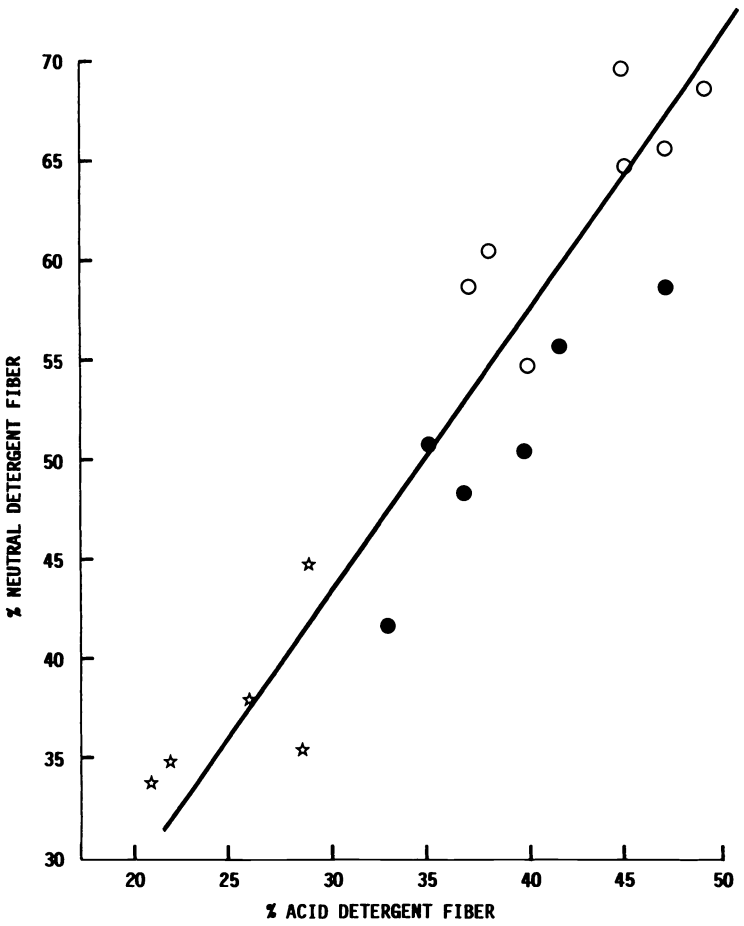


Fig. 13.1 Relationship between ADF and NDF for tropical woody legume (☆), nonwoody legume (●), and grass (○) forages used in rabbit feeding (data from Raharjo *et al.*, 1986).

V. ASH

The ash content of feeds is the residue remaining after the sample is completely burned (oxidized) in a furnace at a high temperature (500–600°C). The ash value represents the total mineral content. It is useful mainly as an indicator of contamination with inert materials such as soil, or the addition of excess levels of mineral supplements such as salt or limestone. Some minerals like iodine and selenium are volatilized during the ashing process, but their concentrations are so small that the loss of these components does not appreciably affect the ash value. Principal constituents of ash of most feeds are silica, calcium, and phosphorus.

The levels of individual minerals in the ash fraction can be measured using specific techniques for the minerals in question. A procedure called atomic absorption spectrometry is used to analyze for a number of specific mineral elements.

VI. NITROGEN-FREE EXTRACT (NFE)

The NFE represents the sum of the components not measured directly by the other analyses discussed above, as well as the sum of the errors in the other determinations. In equation form, % NFE = 100 − (% crude protein + % crude fiber + % ether extract + % ash). NFE is composed primarily of starch and other readily available carbohydrates. Since it is determined by difference, and because the crude fiber procedure solubilizes some of the components of fiber such as hemicellulose, the NFE value is not a precise estimate of starch content, but does provide a reasonable estimate of the readily available carbohydrate fraction of feeds.

VII. ESTIMATION OF FEED ENERGY

As discussed earlier, (Chapter 5) the energy content of feeds is determined by bomb calorimetry. Digestible energy (DE) values are commonly used in formulation of rabbit diets and expression of energy requirements. The metabolizable energy (ME) content of feeds for rabbits is reported by Fekete and Gippert (1986) to be 94.5% of DE.

Because DE or ME can be measured experimentally only in a metabolism trial involving facilities and resources that are often unavailable to feed analysis laboratories and feed companies, it is desirable to be able to estimate DE or ME from more easily obtained analytical data. The TDN scheme (Chapter 5) is a technique designed to add up the total content of energy providing nutrients, using proximate analysis data. The digestibility of each component must be measured or an assumed value used, limiting the usefulness of the TDN procedure. A variety of equations have been developed, using proximate analysis values and experimentally determined DE values on the same feeds, for the calculation of DE. Two of these are presented below.

Equation	References
DE (kcal/kg) = 4253 − 32.6 (% crude fiber) − 144.4 (% ash)	Fekete and Gippert (1986)
DE (kcal/g) = 4.36 − 0.0491 (% NDF)	Fonnesbeck *et al.* (1974)

VIII. FEEDING TRIALS

While laboratory analyses are useful in determining the nutritional quality of feeds, in the final analysis it is the performance of the animals that eat the feed which determines its ultimate value. With rabbits, feeding trials are conducted to evaluate feeds and feed ingredients. Frequently, weanling rabbits are used as the test animals. This is appropriate, because of their rapid growth rate and high nutritional requirements. A period of 28 days is adequate to assess the feeding value of the test diets. For statistical analysis, it is desirable to use individually caged animals, because the cage, rather than the individual animals within a cage, is considered to be the experimental unit. This is particularly important for statistical analysis of feed intake and feed conversion, because unless animals are individually caged, individual feed intakes cannot be determined. While it is desirable from a statistical point of view to have individually caged animals, it can be argued that results obtained in this manner might not be directly applicable to practical conditions in a rabbitry, where fryers are kept in group cages. Differences in responses due to competition for feeder space, peer influence on feeding behavior, and so on, could result in different responses to the same feed for individually caged versus group-caged animals.

If a feed ingredient has an adverse effect on palatability, growth reduction may be a consequence of reduced feed intake rather than being associated with a nutritional deficiency. The "pair-feeding" technique can be used in this situation. Animals of similar size are paired up, so that the control animal's feed intake is restricted to the same quantity as is consumed by its pair animal that is fed free choice. If the growth rate is similar for both groups, on the same quantity of feed, then the problem with the feed is low palatability, and not a metabolic problem.

IX. DIGESTIBILITY TRIALS

The determination of digestibility of nutrients in feedstuffs is very important in assessing their nutritional value. Digestibility refers to the fraction of the feed or individual components (protein, fiber, energy, etc.) that is digested and absorbed. The digestive tract can be regarded as an exterior tube, and nutrients in feeds are not useful unless they can be taken up from the tube into the blood. For example, if the digestibility of crude protein in a sample of alfalfa meal is 70%, it means that 70% of the alfalfa protein is digested and absorbed, and 30% is excreted in the feces, and so of the total protein consumed, only 70% of it is potentially useful to the rabbit.

Several methods may be used for determination of digestibility. The total collection method is the most accurate. Animals are housed individually in cages with a screen allowing the collection of feces uncontaminated with urine. An adjustment period of 1 week on the test diet is sufficient to adjust the animals to the diet, and to ensure that no residue of the previous diet remains in the digestive tract. The adjustment period is followed by a 1-week collection period during which feed intake is accurately measured and fecal excretion is collected and measured. The feed and feces are analyzed for constituents of interest, and the percentage digestibility determined by calculating the percentage of the nutrient in question that was excreted in the feces. If, for example, 28% of the consumed crude protein was excreted in the feces, then the digestibility of the protein was 72% (100 − 28).

Another method that can be used for calculation of digestibility involves the use of indicators or markers. These are indigestible compounds such as chromic oxide. By measuring the concentration of the marker in the feed and feces, the digestibility can be determined. Since the marker is not absorbed, the extent to which it becomes concentrated in the feces reflects the degree to which the feed was "concentrated" by absorption of nutrients during the passage through the gut. Indigestible components of the feed, such as chlorophyll, lignin, and acid-insoluble ash have also been used in digestibility trials. The advantage of the indicator technique is that total collection of the feces and accurate measurement of feed intake are not necessary; only representative samples are needed. A formula by which percentage digestibility can be calculated, and an example showing its use, are as follows:

$$\%\ \text{digestibility} = 100 - \left(100 \times \frac{\%\ \text{indicator in feed}}{\%\ \text{indicator in feces}} \times \frac{\%\ \text{nutrient in feces}}{\%\ \text{nutrient in feed}} \right)$$

Example: Calculate the percentage digestibility of crude protein (CP) in a feed to which 1% chromic oxide was added. Data collected were as follows: % CP in feed = 18; % CP in feces = 20; % chromic oxide in feed = 1; % chromic oxide in feces = 5.

$$\begin{aligned} \%\ \text{CP digestibility} &= 100 - (100 \times 1/5 \times 20/18) \\ &= 100 - 22.2 = 77.8\% \end{aligned}$$

A. Variability in Apparent Digestibility Values

It is characteristically observed in rabbit digestibility trials that the digestibility of fiber components is quite variable. For example, the following values for apparent digestibility of crude protein and ADF in barley were obtained (Cheeke, 1974):

Rabbit number	Digestibility of crude protein (%)	Digestibility of ADF (%)
1	83.9	16.5
2	86.0	15.7
3	84.1	8.1
4	90.6	51.8
5	86.0	40.9

Others have reported wide variations in fiber digestibility (Lang, 1981). The variability in the fiber digestibility values may relate to the mechanisms of selective excretion of fiber and cecotrophy. It is possible that some fiber may be held in the cecum for a time and then evacuated. Depending on the stage of the digestibility trial when this occurred, apparent fiber digestibility values could be markedly skewed in either direction, and negative values may sometimes be observed.

B. True versus Apparent Digestibility

Digestibilities calculated by simply measuring the intake and fecal excretion of a nutrient are referred to as apparent digestibilities. True digestibility is calculated by subtracting the endogenous secretions of the animal. These corrections are of most significance in calculating true digestibilities of protein, amino acids, and energy. In the case of fiber, there is no endogenous excretion of fibrous components.

The endogenous fraction of the feces refers to excretion of components that did not arise directly from the diet. Endogenous losses include digestive enzymes, bacteria, and cells sloughed off the lining of the intestine. In the case of protein digestibility, some of the nitrogen in the feces comes from these endogenous sources (enzymes, bacteria, cellular debris) rather than being the indigestible residue of the dietary protein. The endogenous loss is measured in several ways. One is by feeding a series of different levels of dietary protein, measuring fecal excretion, and extrapolating to zero protein intake. Another method is to feed the animals a protein-free diet, and measure fecal N losses, which then arise entirely from endogenous losses. Neither method is entirely satisfactory. In practical terms, apparent digestibilities are more readily measured than true digestibilities, and are satisfactory estimates of nutrient availability.

X. MEASUREMENT OF TRANSIT TIME

The flow of digesta through the digestive tract can be measured by various techniques. An indigestible marker, such as chromic oxide, can be administered

with the diet and its appearance in the feces measured. Animals can be killed at various times after the administration of the marker, and the concentrations measured in different segments of the gut. A modification of this technique is to administer materials such as barium sulfate or radioopaque plastic particles and observe their passage rate through the digestive tract using X rays.

In using markers, it is assumed that their flow rate is similar to that of feed particles. Solids and liquids move through the gut at different rates, and the passage rate of solids is a function of their particle size. Liquid markers can be used to trace the movement of soluble material. Radioactive polyethylene glycol (PEG) and ethylenediaminetetraacetic acid (EDTA) are two liquid markers that can be employed (Pickard and Stevens, 1972). The markers are administered, and their concentrations in various portions of the digestive tract determined at intervals after dosing. These authors studied the movement of solids by administering hollow plastic particles of different sizes and colors, and tracing their movement through the gut.

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14

Feedstuffs for Rabbits

I. PROPERTIES AND CLASSIFICATION OF FEEDSTUFFS

Feedstuffs are dietary ingredients that provide nutrients or contribute other desirable properties such as bulk or palatability factors. They can be classified into several groups according to their major contributions: roughages, concentrates, mineral and vitamin supplements, and nonnutritive feed additives.

A. Roughages

These bulky feeds are high in fiber and low in digestible energy. Examples include alfalfa meal, hay, pasture, silage, straw, chaff, corncobs, cottonseed hulls, rice hulls, bagasse, and wood.

B. Concentrates

Concentrates are feeds low in fiber, and with a high energy or protein content. They are primarily the cereal grains and plant protein supplements.

1. Energy Sources

Examples include cereal grains (corn, wheat, barley, milo, rye, triticale), other noncereal seeds such as amaranthus grain and buckwheat, grain milling by-products (wheat bran, rice bran, wheat mill run, wheat middlings, etc.), beet pulp, citrus pulp, molasses, fats and oils, brewer's and distiller's grains, and tubers (e.g., cassava meal, potatoes).

2. Protein Sources

These are concentrates that contain over 20% crude protein. Examples include soybean meal, cottonseed meal, rapeseed meal, canola meal, sunflower meal, fish meal, and dried milk by-products.

C. Mineral Supplements

These are used to supply specific mineral elements. Examples include limestone, dicalcium phosphate, salt, and trace mineral mixtures.

D. Vitamin Supplements

These are sources of specific fat-soluble and water-soluble vitmains.

E. Nonnutritive Feed Additives

A variety of additives are used for purposes other than providing nutrients. Some common additives include antibiotics, antioxidants, bacterial preparations (probiotics), colors and flavors, emulsifying agents, enzymes, hormones, and pellet binders.

Some of the major feedstuffs in these categories will be discussed, with major consideration given to results obtained in feeding trials with rabbits.

II. ROUGHAGES

Roughages are bulky, coarse-textured feeds that have a low weight per unit volume. Forages are crops that are grown specifically for feeding to animals as roughage sources. Examples of forages include alfalfa, clovers, and grasses. The term "herbage" is sometimes used; it refers to all types of leafy or woody plants consumed by animals. Besides encompassing forages, herbage also includes browse plants, such as leafy trees and shrubs, which are consumed by browsing animals (e.g., sheep and goats). Browse plants may also be harvested by hand for feeding to rabbits. This is common in tropical countries and is referred to as a "cut and carry" system.

A. Types of Forages

Forage crops grown for animal feeding are of three general types: legumes, grasses, and forbs. Some of the general nutritional properties of these types of forages are different, so a brief discussion of them is given below.

1. Legumes

Legumes are plants of the botanical family Leguminosae. The name is derived from the characteristic fruit pod of plants of this family. A very important characteristic of legumes is that most have nitrogen-fixing bacteria associated with their roots. The bacteria, called rhizobia, infect the young roots and form

colonies. These develop into large visible masses called nodules. In the nodules, the bacteria take nitrogen out of the air in the upper layer of soil and convert it into nitrogen-containing compounds. The nitrogen is trapped by a hemoglobinlike pigment called leghemoglobin, which is a red or pink color. Nodules that are actively fixing nitrogen are pink when cut open. The atmospheric nitrogen is converted to ammonia, and then to amino acids. These amino acids can be used by the plant to make its own protein.

The nitrogen-fixing ability of legumes is of tremendous importance. Leguminous plants store an abundance of protein in their leaves, stems, and seeds. This protein is provided "free" from the air; legumes do not need to be fertilized with nitrogen. Often the roots will shed nodules, fertilizing nonlegume crops being grown with the legume, such as in a grass–clover pasture. The crop residues from legumes add nitrogen to the soil, fertilizing succeeding crops. Legumes thus are soil builders, and are often grown as "green manure crops" to improve soil fertility.

Most legumes have a typical cloverlike leaf that is readily recognized. Common legumes include alfalfa, clovers, peas, beans, vetch, peanuts, kudzu, lespedeza, trefoil, and a number of tropical legumes such as leucaena. Typically legumes are superior to other forages in their protein, mineral, and vitamin contents. They are excellent sources of calcium, phosphorus, and potassium. A negative characteristic of temperate-zone legumes is that many of them cause bloat in cattle and sheep. Bloat is caused by an accumulation of gas bubbles in the rumen. Foaming agents in the forage cause the formation of a stable foam. Bloat of this type does not occur in rabbits.

2. Grasses

Grasses belong to the Gramineae family, which includes the forage grasses as well as the cereal grains. The forage grasses include both temperate and tropical types. Grasses tend to be of lower nutritional value to animals than are legume forages, as they are usually lower in crude protein, vitamins, and minerals. Tropical grasses are often quite low in feeding value, being higher in fiber and lower in protein than temperate grasses.

3. Forbs

Forbs are broadleaf, nonwoody plants providing herbage to animals. They are of most importance to grazing animals. Forbs that might be employed to some extent in rabbit feeding include comfrey, amaranthus, and common weeds such as dandelions.

4. Tree Leaves

The leaves of many broad-leaved trees can be used in rabbit feeding. This would be practical only under conditions of small-scale backyard rabbit produc-

tion, particularly in tropical countries where leafy trees are abundant and labor is readily available. A variety of tropical trees, including *Leucaena, Sesbania, Albizia,* and *Calliandra* species have nutritious leaves. Mulberry leaves have been used with good success as major feedstuffs for rabbits in India and Africa. Black locust leaves are an important forage for rabbit feeding in parts of China. Tree leaves often contain tannins, which adversely affect the availability of protein.

5. Fibrous Crop Residues

Nonforage roughages include materials like straw and bagasse, which are residues of crop processing. Straw is the residue of stems remaining when the seed (grain) of crops like wheat, barley, and oats is harvested. Straw has a very low nutritional value. It is very low in protein and high in fiber. Bagasse is the residue of sugarcane stems after the sugar is extracted, and has very little nutritional value. Corncobs are another example. These products are sometimes used as sources of indigestible fiber for rabbits, and also as nest-box bedding.

Grain processing by-products can be considered as roughage sources. Oat, rice, and cottonseed hulls are high-fiber ingredients that can be used to increase the fiber content of rabbit diets.

B. Nutritive Value of Forages

The leaves of forages are generally higher in protein and lower in fiber than the stems, and so have a higher feeding value. This is illustrated in Table 14.1.

Fertilization, particularly with nitrogen, tends to increase the protein and

TABLE 14.1

Protein and Fiber Content of the Leaves and Stems of Common Forages[a]

Forage	Crude protein (%)	ADF (%)	Lignin (%)
Alfalfa			
Leaves	27.1	11.6	2.6
Stems	11.1	43.3	11.8
Comfrey			
Leaves	21.2	22.6	10.2
Stems	11.3	27.4	9.9
Sudan grass			
Leaves	17.7	32.6	7.6
Stems	12.7	33.5	3.5

[a]From Cheeke and Carlsson (1978).

reduce the fiber content. As forages become mature, the protein level decreases, the structural carbohydrates (fiber) increase, and the nutritive value decreases. The forage becomes increasingly less digestible as it matures. At full maturity it becomes straw, with a very low protein and very high fiber content. Forage maturity is associated with an increasing proportion of stems to leaves, and a greater degree of lignification of the stems. Forages fertilized with organic fertilizer (e.g., manure) and those treated with chemical fertilizers do not appear to differ in feeding value to rabbits (McSheehy, 1975).

C. Conservation of Forages

1. Hay and Dehydrated Forages

Except for a limited amount of greens feeding, rabbits generally are fed forage as a component of dry, mixed pelleted feed. The two major processes used to prepare the forage are field curing to produce hay, and artificial dehydration. Curing crops for hay involves cutting the crop and allowing the water to be removed by the action of sunlight and wind. Forages should be cut in the early-bloom stage, to maximize total yield without compromising nutritive value. There are often extensive losses of protein and vitamins associated with field curing, particularly if the hay is excessively bleached or rain-damaged during the curing process. With alfalfa, there may be a considerable loss of leaves from shattering during field curing, reducing the nutritional value of the product.

To avoid these losses, herbage is often artificially dried. In the United States, alfalfa is the principal crop that is dehydrated, but sometimes grasses or whole corn or milo plants are artificially dried. In Europe, grass and grass–clover mixtures are dried, with relatively less alfalfa used. Dried grass is a common European feedstuff. In the dehydration process, field-chopped alfalfa or grass is fed through rotating drums heated by combustion of natural gas. With careful control of the temperature, a high-quality product very high in vitamin activity can be produced. Excessive heating will reduce protein availability and degrade carotene and vitamin E. After drying, the dehydrated crop is usually stored under an inert gas (N_2) to prevent vitamin oxidation. An antioxidant such as ethoxyquin is usually added, as is a small amount (0.5–3%) of fat to reduce dustiness. The increasing cost of natural gas has resulted in a reduction in the amount of dehy (dehydrated alfalfa) produced. There is now a greater amount of field wilting used, to reduce moisture content prior to dehydration.

Machines to produce cubes or wafers from forages are available. These products might have some application in rabbit feeding, as alfalfa cubes can be given as a supplementary fiber source if needed.

2. Soilage and Silage

Soilage is also called green chop. It is forage that is cut and chopped in the field and then fed directly to livestock. It is used mainly with dairy cattle. It might have some application in large commercial rabbitries, if automated feeding systems for green chop were developed.

Silage is the product produced by a controlled anaerobic fermentation of material high in moisture. The forage crop (alfalfa, grass, corn, etc.) is green-chopped and packed into either an upright or horizontal silo. The first stage of fermentation is the depletion of oxygen, followed by a lactic acid fermentation. Bacteria that produce lactic acid as a waste product proliferate. This increases the acidity (lowers the pH), which stabilizes the mixture by inhibiting the activity of bacteria that cause rotting.

There has not been much work with silage for rabbit feeding. Small experimental silos have been made from large plastic bags or garbage cans for studying silage fermentation. It might be possible to utilize this concept in making silos of an appropriate size for a rabbitry. Another system, used in the dairy industry, is ensiling forage in long plastic bags, using a special machine.

Partridge *et al.* (1985) evaluated grass silage (perennial ryegrass and timothy) as a feedstuff for weanling rabbits. As the proportion of silage in the diet increased, dry matter intake and growth rate decreased. Visual observation of the feces indicated that many long particles were passing through the digestive tract undigested, in agreement with the observation of Cheeke *et al.* (1985) that the cellular structure of grasses is somewhat resistant to breakdown during mastication and digestion in the rabbit.

3. Tropical Forage Conservation

In tropical countries, there is generally a wet season when forage is abundant, and a dry season when it is not. For efficient rabbit production, it would be desirable to conserve excess forage in the wet season for feeding during the dry season. Effective means of doing this have not yet been developed. Preparing hay is difficult for climatic reasons, and has not been a part of traditional farming as it is in temperate areas. Labor-intensive techniques are available for making hay during wet weather, but have not been used in tropical areas. Making silage might have possibilities, although most tropical grasses do not produce good silages. Many are low in sugar, tend to be coarse, do not pack well, and have a high moisture content. Fermentation losses are accelerated with high environmental temperatures. Perhaps the best strategy is conservation of forage "on the vine." Deep-rooted, drought-resistant plants, especially trees, can be used as sources of forage during dry periods. Leucaena and mulberry leaves, for example, can be harvested for this purpose. One deep-rooted grass species successful-



Fig. 14.1 Guatemala grass is a useful forage for rabbits in tropical areas because it remains productive in the dry season. (Courtesy of Dr. S. D. Lukefahr, Alabama A and M University, Normal.)

ly used in parts of Central America and Africa is Guatemala grass (*Tripsacum paxum*), which produces forage in the dry season (Fig. 14.1).

D. Roughage Sources

The roughages discussed here are those that are usually fed dry, either as hay or incorporated into a pelleted diet. Many can also be fed as greens.

1. Alfalfa

Alfalfa (Fig. 14.2) is known as the "Queen of the Forages." It has the highest feeding value of all commonly grown forages and, with particular types of processing, can approach concentrates in feeding value. Alfalfa is called lucerne in English-speaking countries other than the United States and Canada and in some other languages (e.g., *la luzerne* in French). Alfalfa originated in Southwest Asia and was originally cultivated in Iran. It is now grown in all temperate regions of the world. It has a long taproot, which gives it the ability to survive in drought conditions but makes it susceptible to poor drainage. The major alfalfa-growing areas of the United States are in the West and Midwest. There is an extensive alfalfa dehydration industry in a number of states, including Kansas, Nebraska, California, and parts of eastern Washington and Oregon. Dehydrated

alfalfa is produced in the western provinces of Canada. Alfalfa meal is a very desirable feed for rabbits and, in much of the world, is the largest single component of rabbit feeds.

Alfalfa can produce several times as much protein per acre as any other crop. This protein is in a form that is not readily utilized by most nonruminant animals, including humans. When the alfalfa level in the diet exceeds 5–10%, the performance of poultry and swine is reduced. In part this is due to low palatability to these species. Rabbits, on the other hand, readily consume high-alfalfa diets, and perform well on them. Studies at the Oregon State University Rabbit Research Center have demonstrated good results with diets in which alfalfa replaced the grain component entirely (see examples of diet formulas, Chapter 17). Because of the unique characteristics of its hindgut, the rabbit is very efficient in extracting (digesting) the protein in alfalfa and other forages.

In addition to being an excellent source of protein, alfalfa is a good source of phosphorus and is very high in calcium and potassium. It provides indigestible fiber, which helps prevent enteritis. It is the richest common plant source of vitamin A activity (Table 9.3); dehydrated alfalfa meal may have over 60 times as much carotene as yellow corn, and over 4 times as much as carrots. Alfalfa is palatable to rabbits. Thus, it has many qualities that will ensure its continuing use as a rabbit feed. In areas where alfalfa does not grow and so is expensive, it is a challenging task to find suitable feed ingredients to use in its place.



Fig. 14.2 Alfalfa is a leafy perennial forage legume. The dried forage (alfalfa meal) is one of the major ingredients in rabbit diets in North America and Europe.

TABLE 14.2

Composition of Various Forms of Alfalfa

Nutrient	Content of nutrient (as-fed basis)			
	Fresh alfalfa	Dehydrated alfalfa meal	Sun-cured alfalfa meal	Alfalfa hay
Dry matter (%)	24	92	91	89
DE (kcal/kg)	620	2350	2200	2200
TDN (%)	14	53	50	50
Crude protein (%)	4.9	17.4	17.6	17.7
Lysine (%)	0.26	1.01	1.0	1.0
Methione + cystine (%)	0.14	0.55	0.54	0.54
Crude fiber (%)	6.5	23.9	27.3	24.9
Fat (%)	0.8	2.7	2.1	2.4
NFE (%)	10.0	38.1	34.1	37.3
Ash (%)	2.2	9.8	9.6	8.1
Calcium (%)	0.45	1.32	1.3	1.33
Phosphorus (%)	0.08	0.28	0.28	0.28
Vitamin A activity (IU/g)	56.4	146.6	63.6	64.0

Besides its feeding value, alfalfa has other desirable attributes relevant to agriculture in general. It is a legume, so it does not require nitrogen fertilization. It is a perennial, so the energy costs associated with its production are less than for many annual crops. It improves the soil, adding organic matter and reducing erosion. Alfalfa meal is not consumed directly by humans, so its use by livestock is complementary, rather than competitive, in relation to human food needs. One negative attribute is that it does require large quantities of water, which may make its production in the irrigated areas of the western United States less attractive in the future.

The composition of alfalfa, showing nutrients of major significance in rabbit feeding, is shown in Table 14.2.

Alfalfa meal has been extensively tested as a feedstuff for rabbits. A few representative trials will be discussed. Data of Pote *et al.* (1980) have already been presented (Table 6.10), showing no decrease in gains of fryers when alfalfa meal completely replaced cereal grain in the diet. Harris *et al.* (1981b) evaluated diets containing 23, 54, and 74% alfalfa meal in gestation–lactation diets. Total litter weight and litter size at 56 days of age were greater with the 54% and 74% alfalfa levels than with the 28% alfalfa diet, with the best total production with the 54% alfalfa level.

Harris *et al.* (1983a) reported better results with sun-cured alfalfa meal and chopped alfalfa hay than with the dehydrated product (Table 14.3), when they were incorporated into a diet containing 54% alfalfa. In a feed preference study,

TABLE 14.3

Performance of Fryer Rabbits Fed Diets Containing 54% Alfalfa, with Different Types of Alfalfa Products[a]

Form of alfalfa	Average daily gain (g)	Average daily feed intake (g)	Feed/gain	Mortality (%)
Chopped hay	35.3	121	3.42	18.8
Sun-cured meal	32.5	116	3.59	18.8
Dehydrated meal	27.1	113	4.71	37.5

[a]From Harris *et al.* (1983b).

rabbits offered the three diets free choice consumed the diet with sun-cured alfalfa meal at the highest rate (61% of total intake), followed by chopped alfalfa (34% of total intake), with only 5% of total feed intake consisting of the diet containing dehydrated alfalfa meal (dehy). In a subsequent study (Table 14.4), no differences in performance were noted when sun-cured meal and dehy were used (Harris *et al.*, 1984b). These inconsistent results suggest that variations between batches of alfalfa products make generalization of the type of expected response difficult. Dehydrated alfalfa meal often has a greater degree of bitterness than the sun-cured meal, which may lead to a lower palatability in many instances.

Lebas *et al.* (1975) evaluated the effect of drying conditions on the feeding value of dehydrated alfalfa meal for rabbits. Inlet air temperatures of 1050°, 850°, and 650°C, and corresponding outlet temperatures of 140°, 125°, and 110°C in the dryer were used, with two drum rotation speeds of 2.8 and 4.8 turns per minute. Quality of the meal, as assessed by growth of rabbits fed diets with

TABLE 14.4

Performance of Fryer Rabbits Fed Diets Containing 54% Alfalfa, with Various Proportions of Dehydrated and Sun-Cured Alfalfa[a]

Diet	Average daily gain (g)	Average daily feed intake (g)	Feed/gain	Mortality (%)
0% Dehy–100% sun-cured	37.8	136	3.63	3.7
25% Dehy– 75% sun-cured	38.5	137	3.52	9.2
50% Dehy– 50% sun-cured	37.7	135	3.61	5.6
75% Dehy– 25% sun-cured	38.0	134	3.56	0
100% Dehy– 0% sun-cured	39.1	136	3.49	3.7

[a]From Harris *et al.* (1984b).

65% alfalfa meal, was best with the lowest dryer outlet temperature; inlet temperature and roller turn rate did not affect the quality of the alfalfa meal.

2. Clovers

Clovers are similar to alfalfa in feeding value for rabbits, being high in protein, calcium, and vitamin A activity. Clovers are highly palatable, often being more palatable than alfalfa. Good-quality clover hay can be substituted for alfalfa in rabbit rations, so long as adjustments, if necessary, are made to correct for any differences in protein content. Clovers tend to have somewhat lower protein levels than alfalfa (Table 14.5).

In the United States, clover meals comparable to alfalfa meal are not generally commercially available, so the opportunity to use clover in pelleted diets for commercial rabbit production is not usually available. For backyard rabbit production, clover can be grown and fed in the fresh form. In most areas, red clover would be the most suitable species for this purpose. It is a short-lived (2–4 years) perennial, which grows in an upright manner and is readily harvested. White clover is a low-growing pasture species, not amenable to ready harvest for feeding to rabbits. Crimson clover is a fall-seeded winter annual that is similar to red clover in growth habitat. It produces an abundance of forage for a limited period in the spring and early summer.

3. Other Legume Forages

Alfalfa and clovers are the main leguminous forages used in rabbit feeding. Under certain conditions, other forage legumes might be of interest. A number of these will be listed and briefly discussed.

Birdsfoot trefoil is a perennial forage legume grown in many parts of the world, including the northeastern United States such as New York State. It is inferior to alfalfa in yield, so is generally grown on the more poorly drained soils where alfalfa does not thrive. It should make a satisfactory rabbit feed.

Crown vetch is extensively grown in the eastern United States and the Mid-

TABLE 14.5

Composition of Clovers, on an "as Fed" Basis

Clover type	Dry matter (%)	DE (kcal/kg)	Crude protein (%)	Crude fiber (%)
Fresh red clover	22.7	600	4.2	5.0
Red clover hay	87.0	2170	14.1	25.5
Fresh white clover	17.6	500	5.0	2.8
White clover hay	90.7	2200	17.0	22.0
Fresh crimson clover	17.6	500	3.0	4.9
Crimson clover hay	88.8	2190	14.8	24.6

TABLE 14.6

Comparative Digestibility of a Number of Forages[a]

Forage type	Digestibility (%)			
	Dry matter	Crude protein	Crude fiber	NFE
Legumes				
Alfalfa	67.5	80.7	29.8	81.9
Clover, red	55.1	64.4	26.5	68.2
Clover, white	72.7	68.2	57.4	83.1
Kudzu	38.0	62.5	16.1	55.8
Lespedeza, common	44.7	66.7	10.6	59.3
Lespedeza, sericea	31.5	28.7	7.3	46.5
Peanut hay	47.1	55.0	25.0	65.9
Soybean hay	41.3	67.1	16.6	58.9
Sweet clover	56.9	79.0	6.5	73.4
Grasses				
Bluegrass	45.2	74.4	12.6	41.0
Oat hay	29.1	61.0	10.4	35.5
Sudan grass	53.8	68.1	26.6	64.1
Others				
Cabbage	100	98.6	88.5	100
Kale	76.0	81.1	59.5	83.4

[a]Adapted from Voris *et al.* (1940).

west as a ground cover for highway embankments and other disturbed areas. It contains glycosides that are toxic to some types of livestock. It should be used with caution in rabbit feeding until the toxicity aspect has been studied.

The lespedezas are important legumes in the southeastern states. They contain tannins, which sometimes adversely affect palatability and feeding value. Voris *et al.* (1940) reported that the digestibility of protein, energy, and fiber by rabbits was much lower for lespedeza than for alfalfa (Table 14.6).

Kudzu is a coarse, rapidly growing vine (Fig. 14.3), native to Asia. that was introduced into the United States as an ornamental. It has become a pest in the southeastern states, where it may climb trees and other vegetation and smother them. In a study with fryers, kudzu produced lower growth rates when used in place of alfalfa (Gomez de Varela *et al.*, 1983). Average daily gain was 39.7 g with a diet containing 40% alfalfa, and 31.6 g with a diet with 40% dried kudzu.

4. Tropical Legumes

A wide variety of forage legumes grow in the tropics, many of them vines, shrubs, and trees. The leaves are generally high in protein and are suitable rabbit

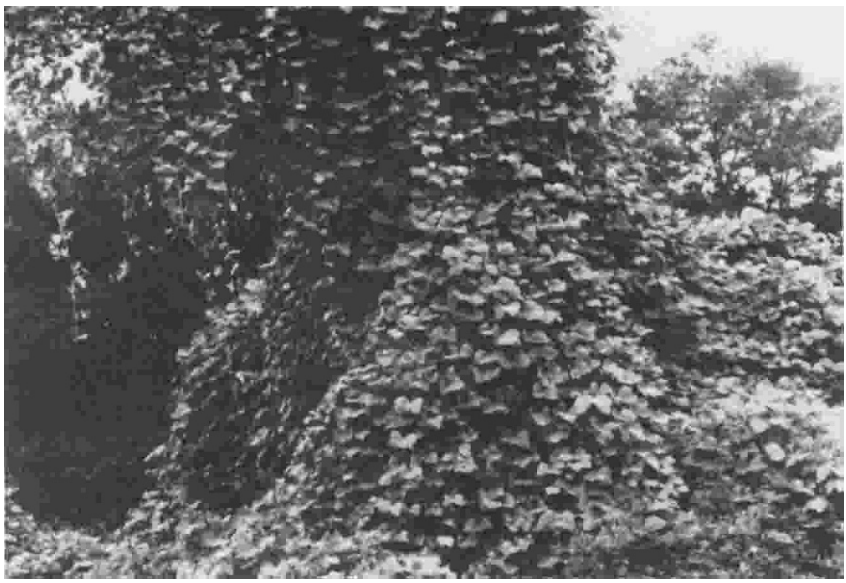


Fig. 14.3 Kudzu is a semitropical leguminous vine, common throughout the southern United States. It can be used as a green feed for rabbits.

feedstuffs. The tropical legume that has been most widely studied as a rabbit feed is *Leucaena leucocephala*, which contains the toxic amino acid mimosine (Cheeke and Shull, 1985). Mimosine toxicity causes poor growth and alopecia (loss of hair). In ruminants, mimosine is converted in the rumen to dihydropyridone (DHP), which is goitrogenic. In spite of the presence of the toxin, fresh leucaena is highly palatable to rabbits (Raharjo *et al.*, 1985).

Several feeding trials have shown that growth of rabbits is reduced when moderate levels of leucaena meal are fed. Some comparative results are shown in Table 14.7. Tangendjaja *et al.* (1986) used a treatment involving mild heat treatment by which mimosine in leucaena leaves was largely converted to DHP. However, performance with the treated meal was inferior to that with untreated leaf meal (Table 14.7), suggesting that DHP is toxic to rabbits. Szyszka *et al.* (1984) fed diets containing various levels of purified mimosine to rabbits. Growth was not impaired with 0.13 or 0.26% mimosine, but was reduced with 0.39% mimosine. Their study indicated that growth was not impaired until mimosine intake exceeded 0.23 g/kg body weight per day. It is apparent from these results that levels of leucaena meal in excess of 10% of the diet may result in growth depression.

The digestibility of leucaena meal has been studied by several groups. Results of Parigi Bini *et al.* (1984) are shown in Table 14.8, showing a reduction in the apparent digestibility of most proximate constituents when leucaena constituted



Fig. 14.4 Leaves and seedpods of *Leucaena leucocephala,* a tropical leguminous tree. The leaves are high in protein, but their use in rabbit feeding is limited because of the presence of mimosine, a toxic amino acid. (Courtesy of Dr. R. J. Jones, CSIRO, Australia.)

TABLE 14.7

Growth and Feed Intakes of Rabbits Fed Various Levels of Leucaena Meal

References	Leucaena in diet (%)	Average daily gain (g)	Average daily feed intake (g)
Parigi Bini *et al.* (1984)			
	0	43.1	140
	10	44.5	157
	20	37.1	139
	30	37.0	154
Tangendjaja *et al.* (1986)			
	0	23.7	100
	20	17.4	103
	40	9.4	97
	60	5.9	85
	20[a]	16.0	107
	40[a]	11.9	98
	60[a]	0.7	92

[a]Treated to reduce mimosine by conversion to dihydropyridone.

TABLE 14.8

Apparent Digestibilities and Nitrogen Retention in Rabbits Fed Various Levels of Leucaena Meal[a]

Item	Leucaena meal in diet (%)			
	0	10	20	30
Apparent digestibility (%)				
Dry matter	66.3	61.9	59.8	53.7
Organic matter	67.2	63.1	61.4	55.4
Crude protein	77.8	71.1	63.8	52.4
Crude fiber	11.3	9.3	7.9	9.6
Ether extract	85.1	81.9	76.8	66.3
NFE	72.8	70.1	70.5	66.2
N balance (g/day)				
N intake	4.14	4.55	4.28	4.56
N in feces	0.92	1.32	1.54	2.18
N in urine	1.72	1.72	1.47	1.34
N retained	1.49	1.52	1.27	1.05

[a]From Parigi-Bini *et al.* (1984).

30% of the diet. With 0 and 60% leucaena, apparent digestibility of protein was 73% and 41%, and of energy, 65% and 53%, in the work of Tangendjaja *et al.* (1986). Lower crude protein digestibility for leucaena than for alfalfa meal was reported by Harris *et al.* (1981d).

Raharjo *et al.* (1986) evaluated a number of tropical forages in Indonesia, including several tree legumes, as rabbit feedstuffs. Their composition is shown in Table 14.9. The apparent digestibility of crude protein and energy in tropical legumes was in general quite high, whereas comparable values for tropical grasses were usually very low (Table 14.10).

The black locust (*Robinia pseudoacacia*) is a temperate leguminous tree, which can be grown as a forage source. Black locust leaf meal is grown commer-

TABLE 14.9

Composition of Tropical Forages[a]

Forage	Gross energy (kcal/kg)	Percentage composition (dry matter basis)				
		Crude protein	ADF	NDF	Ca	P
Woody legumes						
Albizia falcata	4326	16.3	26.4	38.0	0.65	0.17
Calliandra calothyrus	4756	21.8	29.1	44.7	1.71	0.18
Leucaena leucocephala	4206	21.9	21.8	35.0	1.34	0.21
Sesbania formosa	4469	19.9	20.8	34.1	0.73	0.37
Sesbania sesban	4254	17.8	29.1	35.4	0.75	0.37
Nonwoody legumes						
Cassia rotundifolia	3991	15.0	47.0	59.3	0.76	0.25
Centrosema pubescens	3885	21.4	35.3	51.4	0.74	0.23
Desmodium heterophyllum	3752	13.4	37.1	48.5	0.73	0.22
Neonatonia wrightii	3442	13.1	43.3	55.8	1.52	0.23
Pueraria phaseoloides	3872	15.6	39.9	50.7	0.74	0.36
Stylosanthes guianensis	3107	14.8	33.1	41.6	1.24	0.22
Grasses						
Brachiaria brisantha	2820	6.7	36.8	59.3	0.47	0.16
Chloris gayana	3705	7.6	44.6	70.2	0.30	0.18
Panicum maximum cv. Green Panic	3537	5.8	48.7	69.4	0.33	0.19
Panicum maximum cv. Guinea	3585	6.6	47.1	66.2	0.70	0.21
Paspalum plicatulum	4230	6.5	44.7	65.1	0.50	0.15
Pennisetum purpureum	3824	12.0	38.2	61.4	0.29	0.36
Setaria splendida	2629	6.9	39.7	55.4	0.46	0.20
Agricultural by-products						
Manihot esculenta (tops)	4804	16.8	28.2	38.9	1.76	0.28

[a]Adapted from Raharjo *et al.* (1986).

TABLE 14.10

Digestibility of Tropical Forages in Rabbits[a]

Forage	Digestibility (%)				
	Dry matter	Energy	Crude protein	ADF	NDF
Woody legumes					
Albizia falcata	74.7	70.3	73.4	58.0	63.1
Calliandra calothyrus	49.5	51.4	49.8	12.5	25.6
Leucaena leucocephala	74.2	69.5	75.9	37.8	54.5
Sesbania formosa	69.5	65.8	64.2	30.9	46.5
Sesbania sesban	79.3	77.5	83.9	62.3	62.6
Nonwoody legumes					
Cassia rotundifolia	41.6	40.1	57.5	22.7	26.8
Centrosema pubescens	43.0	54.2	72.9	29.3	32.5
Desmodium heterophyllum	28.1	48.7	52.1	13.4	13.6
Neonatonia wrightii	49.4	39.8	56.6	36.7	38.7
Pueraria phaseoloides	46.4	44.3	62.6	21.1	27.4
Stylosanthes guianensis	43.4	55.1	53.9	23.3	18.5
Grasses					
Brachiaria brisantha	16.7	24.5	17.8	4.2	11.3
Chloris gayana	38.9	36.3	32.4	33.2	41.9
Panicum maximum cv. Green Panic	15.7	12.6	5.6	10.3	12.5
Panicum maximum cv. Guinea	12.3	10.7	13.0	7.8	7.3
Paspalum plicatulum	35.0	33.7	21.2	25.7	29.6
Pennisetum purpureum	46.3	45.2	64.7	34.6	42.8
Setaria splendida	15.0	9.4	6.2	16.1	9.0
Agricultural by-products					
Manihot esculenta (tops)	49.9	47.0	42.0	25.6	33.0

[a]From Raharjo *et al.* (1986).

cially in China as a feedstuff. Harris *et al.* (1984a) evaluated black locust leaf meal as an ingredient (40%) of a pelleted diet for weanling rabbits. A diet with 40% alfalfa meal served as the control. Results (Table 14.11) indicate that black locust leaf meal is inferior to alfalfa meal as a feed for rabbits. Growth rate and the digestibilities of protein, fiber, and energy were reduced.

Singh and Negi (1986) similarly found that feeding black locust leaves to Angora rabbits resulted in lowered crude protein digestibility and reduced wool production compared to those receiving a control diet. They suggested that the adverse effects were associated with tannins in black locust leaves.

The winged bean (*Psophocarpus tetrogonolobus*) is a tropical legume that has been widely promoted since 1975 as a potential answer to protein deficiency in developing countries. It produces beans in a seed pod, protein-rich leaves that

TABLE 14.11

Growth Rate of Rabbits and Nutrient Digestibility with Diets Containing 40% Black Locust Leaf Meal or Alfalfa[a]

Item	Black locust leaf meal	Alfalfa meal
Average daily gain (g)	28.2*[b]	40.0**
Average daily feed intake (g)	114*	96**
Feed/gain	4.37	2.39
Digestibility (%)		
Crude protein	54.6*	75.8**
ADF	6.8*	24.6**
NDF	40.4*	51.2**
Diet DE (kcal/kg)	2808*	3074**

[a]From Harris *et al.* (1984a).
[b]* Different from ** ($p < 0.05$).

can be used as a forage, and a tuber that can be consumed by humans and animals (Fig. 14.5). In areas where the winged bean is produced, leaves could be collected and used in backyard rabbit production. The potentials of the winged bean were outlined in a National Research Council (1975) publication. Henry *et al.* (1985) described some negative factors about the winged bean, in an article provocatively entitled "The winged bean. Will the wonder crop be another flop?" Negative factors include the need for a prolonged cooking time, which increases fuel requirements. In many tropical areas, fuel sources are in critically short supply. At any rate, the forage of the winged bean may have application in rabbit feeding. Harris *et al.* (1981a) found that the average daily gain and the percentage digestibility of protein were lower in fryers fed winged bean meal as compared to controls fed alfalfa meal.

The pigeon pea (*Cajanus cajan*) is a tropical perennial woody shrub, producing seeds used as human food, and abundant foliage that can be used as a forage for livestock. It should be an excellent green feed for rabbits in tropical areas. Feeding trials in Hawaii during the Second World War, when rabbit production was being considered as a means of increasing local meat production, demonstrated that the pigeon pea was the only forage tested that would support growth of rabbits when used as the sole feed (Beaumont, 1943).

5. Grasses

Grasses are usually somewhat lower in crude protein than legumes and often have a higher fiber content. The composition of a number of temperate grasses is shown in Table 14.12. The tropical grasses differ in structure and nutritional value from temperate grasses, and so will be discussed separately.

There are few studies involving the utilization of grasses by rabbits. Harris *et*



Fig. 14.5 The winged bean produces an edible seedpod, and abundant forage that can be used in rabbit feeding. (Courtesy of Dr. G. E. Matzke, Oregon State University, Corvallis.)

al. (1981c) found that Kentucky bluegrass meal, when used at 40% of the diet, supported a daily gain of 37 g, which was equivalent to that obtained with alfalfa meal. Two reports suggest that Coastal Bermuda grass (*Cynodon dactylon*) may give unsatisfactory results with rabbits. Borgman and Mitchell (1966) noted poor growth and high mortality in rabbits fed various levels of Coastal Bermuda grass (Table 14.13). The performance of the controls was quite poor, complicating interpretation of these results. Champe and Maurice (1983) compared rabbit growth with diets containing alfalfa meal or Coastal Bermuda grass, at equivalent crude fiber levels (Table 14.14). Daily gains were lower and mortality

TABLE 14.12

Composition of Some Temperate Grasses

Grass	Percentage composition (as-fed basis)		
	Dry matter	Crude protein	Crude fiber
Bermuda grass, hay	92	11.0	27.6
Bromegrass, hay	91	8.9	29.1
Corn, leaves	25	4.3	6.7
Oats, hay	88	7.3	29.5
Orchard grass, fresh	25	3.8	6.2
Orchard grass, hay	89	9.8	30.0
Reed canary grass, hay	89	10.2	30.0
Ryegrass, fresh	22	2.0	6.6
Ryegrass, straw	89	3.8	33.0
Sudan grass, fresh	21	2.5	6.5
Tall fescue, hay	85	7.3	27.8
Timothy, hay	89	6.3	30.2

higher with the Bermuda grass. Champe and Maurice (1983) concluded that Coastal Bermuda grass was not a satisfactory fiber source and should not be used for growing rabbits. Coastal Bermuda grass is a warm-season grass, and has a low content of the highly digested mesophyll cells and a high content of the poorly digested epidermis and parenchymal bundle sheaths (Table 14.15), which probably explains its low feeding value.

Grass meals are not commonly produced in the United States, and so are

TABLE 14.13

Effect of Various Dietary Levels of Coastal Bermuda Grass on Performance of Weanling Rabbits[a]

Dehydrated grass in diet (%)	Average weight change per rabbit per week (g)		Mortality (%)
	0–4 Weeks	4–8 Weeks	
0	32	38	20
20	−38	93	30
40	−46	42	40
60	−54	67	30
80	−103	88	70
100	−132	−134	100

[a]Adapted from Borgman and Mitchell (1966).

TABLE 14.14

Response of Weanling Rabbits to Diets Containing Alfalfa Meal or Coastal Bermuda Grass at Various Crude Fiber Levels[a]

Dietary crude fiber (%)	Forage (%)	Average daily gain (g)	Average daily feed intake (g)	Mortality (%)
Alfalfa diets				
3	2.55	12.2	39.9	54
6	18.40	18.8	61.7	33
9	31.30	26.6	76.7	31
12	45.00	24.4	88.6	11
Bermuda grass diets				
3	2.00	16.3	46.0	57
6	13.80	4.0	36.5	71
9	23.44	14.1	73.4	54
12	33.85	13.0	57.7	47

[a]Adapted from Champe and Maurice (1983).

seldom available for incorporation into rabbit diets. Provided that adjustments are made for the lower crude protein level as compared to alfalfa, most temperate grasses (orchard grass, ryegrass, bluegrass) can probably be used in place of alfalfa meal with no deleterious effects.

Tropical grasses produce very large yields of low-quality forage (Fig. 14.6). They are known as C_4 plants, meaning that the first stable products of photosynthesis are compounds with four carbon atoms (oxaloacetic acid, malic acid, aspartic acid). Temperate grasses are C_3 plants, indicating that three-carbon compounds (e.g., phosphoglyceric acid) are the first product of photosynthesis. The C_4 plants make more efficient use of solar energy than do C_3 plants. The enzyme that synthesizes the C_4 compounds, phosphoenolpyruvic acid carboxylase, has a temperature optima of 30–55°C, whereas the enzyme involved in C_3 plants, ribulose diphosphate carboxylase, functions best at 20–25°C. Some crops (e.g., corn, sorghum, and amaranth) are C_4 plants, derived from tropical ancestors.

The low nutritive value of tropical grasses is related to the plant tissue structure. They have a high content of poorly digested tissues such as the epidermis, vascular tissue, and parenchyma bundle sheaths, and a low content of the readily digested mesophyll cells. Temperate grasses have a higher proportion of phloem and mesophyll cells, which are readily digested (Table 14.15). Tropical grasses are more highly lignified than temperate grasses, further reducing their digestibility. The mesophyll cells in tropical grasses are tightly packed, restricting access of digestive enzymes. These grasses often are coarse, with a tough epider-

mal layer, further resisting digestive breakdown. Cheeke *et al.* (1985), in a study of the microscopic breakdown of cellular integrity of forages during passage through the rabbit gut, found that a temperate grass, orchard grass, was less completely fragmented than a number of legume forages, indicating a less complete breakdown of the grass.

Feeding trials with tropical grasses as feedstuffs for rabbits confirm their low nutritive value. Harris *et al.* (1981a) found a very low digestibility of the ADF (1.5%) and cell wall constituents (5%) of guinea grass (*Panicum maximum*) in weanling rabbits, in contrast to values of 24.5% and 29.5% for ADF and cell wall constituent digestibility for the tropical legume *Clitoria ternata*. Raharjo *et*

TABLE 14.15

Percentage of Tissue Types in Leaves from Warm- and Cold-Season Grasses[a]

Grass	Total vascular tissue	Parenchyma bundle sheaths	Epidermis	Mesophyll
Warm season				
Cynodon dactylon cv. Coastal (Coastal Bermuda grass)	37	28	26	27
Coast cross 1 Bermuda grass	36	27	30	23
Paspalum notatum cv. Pensacola (Bahia grass)	18	11	25	52
Paspalum dilatatum (Dallis grass)	14	10	35	44
Digitaria decumbens cv. Pangola (digitgrass)	13	10	48	33
Digitaria sanguinalis	13	9	49	35
Bothriochloa caucasica (bluestem grass)	23	13	42	31
AVERAGE OF WARM-SEASON GRASSES	22	16	36	35
Cool season				
Bromus inermis (bromegrass)	20	7	19	53
Dactylis glomerata cv. Boone (orchard grass)	22	9	20	53
Phleum pratense cv. Clair (timothy)	13	5	26	55
Poa pratensis (Kentucky bluegrass)	11	4	17	65
Festuca arundinacea cv. Kentucky (tall fescue)	13	6	22	60
Festuca arundinacea cv. Kenhy	11	4	20	62
Lolium multiflorum (Italian ryegrass)	11	6	34	53
AVERAGE OF COOL-SEASON GRASSES	14	6	23	57

[a]Adapted from Akin (1982).



Fig. 14.6 Tropical grasses produce very high yields of dry matter. However, because of their cellular structure, they are high in fiber, low in protein, and of very low digestibility.

al. (1986) also found a low digestibility of tropical grasses as compared to tropical legumes (Table 14.10). These results suggest that some of these grasses, such as *Setaria, Brachiaria,* and Guinea grass, are of extremely low nutritive value to rabbits, and are useful primarily as sources of indigestible fiber. They might be used, for example, to supplement low-fiber feeds such as poultry mash or rice bran to provide adequate fiber. As major diet ingredients they are clearly inadequate.

The composition of a number of tropical grasses is shown in Table 14.9.

6. Other Forages

a. Comfrey. Comfrey (*Symphytum officinale*) is a coarse, broad-leaved perennial plant (Fig. 14.7) with a massive taproot. It forms large clumps, which

can be cut on a regular basis. It responds well to heavy fertilization, particularly with manure, so it can be grown in a patch near a rabbitry, and fertilized heavily with the rabbit manure. It is propagated by root cuttings. Comfrey has been the subject of considerable controversy. Various medicinal properties have been attributed to it, the most extreme being that it is a cure for cancer. These properties have been linked to the allantoin it is said to contain. These claims have no scientific basis. Allantoin is in fact a substance produced in animal metabolism and excreted in the urine. Its pharmacological properties are slight. Comfrey is also reported to contain vitamin B_{12}. However, the amount is so small, and vitamin B_{12} is so readily obtained from other sources (e.g., liver, meat), that this is of no consequence, particularly for rabbits, which do not have a dietary requirement for vitamin B_{12} (they obtain their vitamin B_{12} from coprophagy).

Comfrey contains some toxic and carcinogenic (cancer-causing) pyrrolizidine alkaloids (Culvenor *et al.*, 1980; Hirono *et al.*, 1978). For this reason, it may not be advisable for humans to consume comfrey products. Liver pathology has been linked with the consumption of comfrey products by humans (Ridker *et al.*, 1985). Since rabbits are not susceptible to the toxic effects of these alkaloids (Pierson *et al.*, 1977), there seems to be little danger in feeding comfrey to rabbits. It is comparable to alfalfa in its nutrient content.

Grobner *et al.* (1985) studied the effect of prolonged (4 months) feeding of



Fig. 14.7 Comfrey is a perennial herb grown as a forage for animal feeding. Its use is limited by its low palatability, and it should be used with caution because it contains toxic alkaloids.

fresh comfrey to rabbits receiving pelleted diets with 0 or 250 ppm supplemental copper. Pyrrolizidine alkaloids may cause elevated levels of liver copper (Cheeke and Shull, 1985), so it was of interest to determine if comfrey feeding in conjunction with the use of copper sulfate as a feed additive could result in liver copper accumulation. No evidence of liver abnormality was found in the animals fed comfrey, and liver copper was slightly lower in rabbits fed comfrey compared to those not receiving comfrey (440 versus 456 ppm).

For small rabbitries, comfrey does have some advantages. It is easy to harvest by hand and can be fed as a green forage to the rabbits. It is almost impossible to overfertilize it with manure, so the comfrey patch can receive all the animal waste from the rabbitry. It has a rapid rate of growth, and can be harvested frequently. Its main use is as a green feed; it is difficult to dry because of a thick, fleshy midleaf. It is covered with short, fuzzy hairs, making it prickly, so it tends to be unpalatable. However, if it is the only green offered, it will be readily consumed by rabbits. In short, comfrey is neither a miracle plant nor a curse (there are plenty of believers on each side), but a forage plant that is most suitable, by virtue of its agronomic features, for use on a garden or small-farm scale, rather than in large-scale commercial agriculture.

b. Brassica Species. *Brassica* species are plants of the cabbage family, and include a number of common vegetables, crops, and forages. Vegetable brassicas are cabbage, cauliflower, broccoli, brussel sprouts, and turnips. Crop species include rape and mustard, while forage brassicas are kale, forage rape, and Chinese cabbage.

Brassicas are normally fed to rabbits as greens. It is commonly believed by rabbit raisers that feeding these plants, particularly cabbage, causes diarrhea. Shqueir *et al.* (1985) studied the effect of feeding cabbage leaves on growth, diarrhea incidence, and fecal moisture content of weanling rabbits. The interpretation of the results (Table 14.16) is complicated by a high incidence of enteritis in the control group, but in general the performance of rabbits receiving cabbage did not appear to be adversely affected. The growth rate of rabbits fed cabbage only was low, as would be expected from the high moisture content (81%) of the cabbage. Although during the 4-week trial all of the animals fed cabbage only showed signs of diarrhea, most of the time their fecal pellets were very small and hard, reflecting the very low amount of indigestible matter in the leaves. Partridge *et al.* (1985) evaluated cabbage and yellow turnip as succulents for rabbits. Increasing dietary levels of these plant materials decreased total dry matter intake and the rate of gain. Cabbage has a high starch content, so might cause diarrhea as a result of carbohydrate overload (see Chapter 12). Thus, it is probably a sound practice to feed cabbage or other brassica plants only as part of a mixture of greens, rather than as the sole green feed.

TABLE 14.16

Effect of Cabbage Feeding on Performance, Diarrhea, and Fecal Moisture Content[a,b]

Diet	Average daily gain (g)	Daily pellet intake (g)	Daily cabbage intake (g)	Incidence of diarrhea (%)	Mortality (%)	Fecal moisture (%)
Pellets only, free choice	30.3	68	—	40	30	41.7
Pellets, 100 g/day, cabbage	32.7	38	56	50	30	26.9
Pellets, 50 g/day, cabbage	31.9	40	57	40	30	33.8
Pellets, 25 g/day, cabbage	27.7	22	64	50	20	28.2
Cabbage only, free choice	12.5	—	84	100	25	15.9

[a]From Shqueir *et al.* (1985).

[b]Pellet and cabbage intakes on a dry matter basis. The amount of pellets consumed was less than the amount offered.

c. Crop Residue Roughage Sources. Cereal grain straws (wheat straw, barley straw, rice straw, etc.) are low-quality roughages with little value as nutrient sources for rabbits. However, because of the need to have 12–15% crude fiber in rabbit feeds, there may be application of these materials simply as a source of indigestible fiber.

Alkali treatment using sodium hydroxide (lye) or other strong alkali has been used to improve the nutritional value of low-quality straw for ruminants. The alkali dissolves lignin, an indigestible component of the fiber that encrusts the cellulose. Because cellulose digestion is low in rabbits, it is unlikely that alkali treatment of straw would markedly enhance its usefulness for rabbit feeding.

de Blas *et al.* (1979) fed alkali-treated cereal (unspecified) straw to growing rabbits at dietary levels of 0, 5, 10, and 15%, replacing alfalfa meal. No adverse effects on growth or digestibility were noted. Partridge *et al.* (1984) evaluated sodium hydroxide- and ammonia-treated barley straw at levels of 0, 15, 30, and 45%. Compared to the same levels of untreated straw, slight improvements in animal growth and nutrient digestibilities were noted with the treatments, but the authors concluded that "any small improvements in growth performance achieved are unlikely to warrant the increased cost of straw treatment."

Rice hulls are available in large quantity in parts of the United States and in many tropical countries. They have a very low digestible energy (DE) content, but can be used as a source of indigestible fiber. Rice hulls have a high silica content, which can have an abrasive effect on pelleting and feed-mixing machinery, and also may cause irritation and ulceration of the digestive tract. Rice hulls contain a substance that stimulates development of rancidity in feeds. For

TABLE 14.17

Digestibility Coefficients for Whole Corn Plant Pellets Fed to Rabbits[a]

Item	Digestibility (%)
Dry matter	47.4
Crude protein	80.2
ADF	25.0
NDF	36.7
Ether extract	93.9
Ash	36.4
Gross energy	49.3

[a]From Schurg *et al.* (1977).

these reasons it is probably advisable not to use more than 10% rice hulls in rabbit diets. Oat bulls and cottonseed hulls may also be used as fiber sources.

d. Dehydrated Cereals. The same equipment used to dry alfalfa artificially to prepare dehy can be used to dry other crops, including whole cereals such as corn and milo, and grasses. Sometimes these products are prepared mainly to keep the equipment operating during periods when alfalfa is not available. These dehydrated products can be used in rabbit diets in place of alfalfa meal, with appropriate adjustment depending on the protein and fiber contents. Schurg *et al.* (1977) studied the nutritive value of whole corn plant pellets for rabbits. The product contained 6.2% crude protein and 30.8% ADF. Digestibility coefficients for the product (Table 14.17) indicate a fairly low nutritive value; the DE content was 1873 kcal/kg.

7. Greens

Fresh greens are relished by rabbits. For backyard production, and in developing countries where labor costs are low, feeding greens as a supplement may help in reducing costs of production. Many different leafy materials may be used, including vegetable leaves, weeds, tree leaves, and common grass and legume forages.

Pote *et al.* (1980) determined the effect of free-choice feeding of greens on performance of weanling rabbits various quantities of pelleted feed. With supplementary greens, the amount of pelleted feed could be reduced to about 50% of normal pellet intake without adversely affecting growth. Ramchurn (1979), in the African country of Mauritius, demonstrated similar results with tropical forages. When rabbits were fed 50% of the pellet intake of those receiving only

pellets free choice, supplementation with sugarcane, leucaena, or elephant grass maintained normal growth. Response to various degrees of pellet restriction, with supplementation with cabbage leaves and with mixed greens (clover, vegetables, grape leaves, comfrey) are shown in Fig. 14.8. Below 50% of normal pellet intake, growth rate declined markedly.

Harris *et al.* (1983b) studied the palatability of various greens by allowing individually caged rabbits access to 100 g of a particular fresh plant material for a 4-hr period. Consumption of the offered material was measured. Sunflower leaves, green bean vines, red clover forage, carrot tops, and cauliflower leaves were highly palatable; 90–100% of these materials were consumed. Dandelion leaves, white clover, Swiss chard, corn leaves, and amaranthus leaves were of intermediate palatability (60–90% were consumed). Orchard grass, grape leaves, and black locust leaves were of low palatability (40–60% were con-

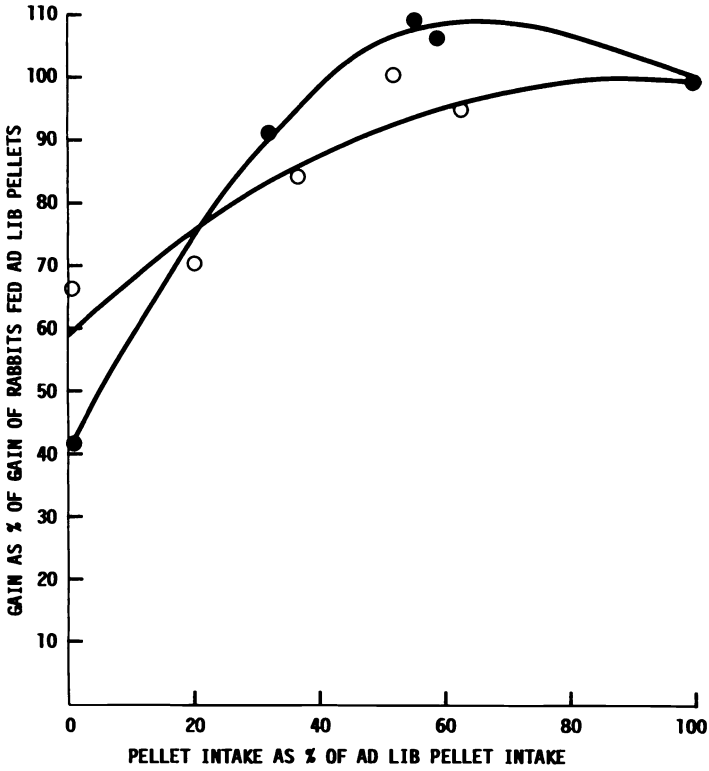


Fig. 14.8 Performance of weanling rabbits fed various levels of pelleted diet with free-choice greens. Normal gains are maintained with greens feeding when pellet intake is not restricted below 50% of feed intake of animals given only pellets. (○, Data from Pote *et al.*, 1980, for mixed greens; ●, Schqueir *et al.*, 1985, for cabbage.)

TABLE 14.18

Evaluation of Pigweed (*Amaranthus retroflexus*) and Lamb's-Quarters (*Chenopodium album*) in Diets for Weanling Rabbits[a]

Dietary component	Average daily gain (g)	Average daily feed intake (g)	Feed/gain	Mortality (%)
Alfalfa meal	38.9*[b]	102	2.63	0
Lamb's-quarters	23.5**	104	4.41	0
Pigweed	14.7**	49	3.30	50

[a]From Harris *et al.* (1980).
[b]*Different from ** ($p < 0.05$).

sumed). Of lowest palatability was comfrey; only 35% of the amount offered was eaten.

Raharjo and Cheeke (1985) tested the palatability of a number of tropical forages for rabbits by offering them in feed preference tests. Sweet potato (*Impomoea batatas*) foliage was the most preferred green feed tested. Other highly palatable species included *Leucaena leucocephala* and *Albizia falcataria*. *Sesbania grandiflora* and *Erythrina lithosperma* were moderately palatable, while *Calliandra calothyrsus* and *Gliricidia sepium* were unpalatable.

Pigweed (*Amaranthus retroflexus*) and lamb's-quarters (*Chenopodium album*) are common garden weeds that might be used in rabbit feeding. Harris *et al.* (1980) evaluated these as feeds for weanling rabbits, incorporating them into pelleted diets at a level of 40% of the diet. Results (Table 14.18) show that both

TABLE 14.19

Performance of Weanling Rabbits Fed Diets Containing 40% *Amaranthus hypochondriacus*[a]

Dietary component	Average daily gain (g)	Average daily feed intake (g)	Feed/gain	Mortality (%)
Alfalfa meal	39.2	111	2.83	30
Amaranthus leaves	24.6	83	3.36	10
Amaranthus whole plant	23.1	74	3.21	0
Amaranthus stems	23.1	85	3.68	0
Amaranthus seed heads (white seeds)	20.8	66	3.15	20
Amaranthus seed heads (black seeds)	14.0	—[b]	—	80

[a]From Harris *et al.* (1981c).
[b]Not measurable because of excessive feed wastage.



Fig. 14.9 Amaranthus is a grain and forage plant with potential as a human and animal feed. Feeding trials with rabbits have yielded poor results because of low palatability.

weeds gave markedly reduced gains as compared to the control diet with 40% alfalfa meal. With the pigweed diet, 50% of the animals died from cecal impaction. In a subsequent study (Harris *et al.*, 1981c), leaves, stems, and seed heads of *Amaranthus hypochondriacus* were evaluated, at 40% of the diet. Very poor performance was observed (Table 14.19). Schamber and Misek (1985) fed pigweed (*A. retroflexus*) to a group of rabbits for 28 days. While severe weight loss occurred from lack of sufficient feed intake, there was no evidence of kidney damage (acute tubular necrosis, perirenal edema, renal oxalosis) that commonly accompanies pigweed toxicosis in other species (Cheeke and Shull, 1985). *Amaranthus* spp. (Fig. 14.9) appear to be unsuitable feedstuffs for rabbits.

In tropical countries, aquatic weeds might have potential as rabbit feed. Water hyacinth (*Eichhornia crassipes*) is a free-floating freshwater plant (Fig. 14.10) that has become a major pest in lakes, reservoirs, and streams in tropical countries and the southern United States. It clogs waterways and may seriously restrict boat travel. Because of its incredibly rapid growth rate and its removal of soluble nutrients from water (nitrogen and phosphorus), it has potential as a source of feed and also as a means of water purification. Gerard and Troncoso (1980) evaluated water hyacinth as a feed for rabbits. Composition and digestibility are shown in Table 14.20. In a growth trial, with 25 and 50% dried water hyacinth in a pelleted diet, average daily gains were reduced as compared to the controls (Table 14.21). Arsenic levels in the tissues, particularly liver and



Fig. 14.10 Water hyacinth is a vigorously growing aquatic weed. It may have potential as a rabbit feed in some areas.

TABLE 14.20

Composition and Digestibility in Rabbits of Water Hyacinth[a]

Results	Fresh hyacinth, without roots	Fresh hyacinth, with roots
Dry matter (%)	6.1	4.9
Dry matter digestibility (%)	35.6	—
Crude protein (%)[b]	17.1	21.2
Crude protein digestibility (%)	42.9	—
Ash (%)[b]	16.7	21.2
Ash digestibility (%)	47.4	—
Crude fiber (%)[b]	15.4	21.2
Crude fiber digestibility	9.9	—

[a]Adapted from Gerard and Troncoso (1980).
[b]Percentage of dry matter.

TABLE 14.21

Growth Rate and Tissue Arsenic Levels of Rabbits Fed Water Hyacinth[a]

Results	Water hyacinth in diet (%)		
	0	25	50
Average daily gain (g)	27.6	21.7	18.0
Average daily feed intake (g)	117	118	117
Feed/gain	4.23	5.29	6.51
Diet arsenic (ppm)	0	0.390	0.531
Muscle arsenic (ppm)	0	0.363	0.685
Liver arsenic (ppm)	0	0.328	1.421
Kidney arsenic (ppm)	0	0.640	2.474

[a]Adapted from Gerard and Troncoso (1980).

kidney, were elevated (Table 14.21); water hyacinth tends to accumulate heavy metals. These results show that water hyacinth is not a high-quality feedstuff for rabbits but may have application at levels of 25% or less of the diet. Other aquatic plants might be useful rabbit feeds in developing countries. For example, in China the water peanut (*Alternanthera philoxeroides*) and water lettuce (*Pistia stratiotes*) are used as feedstuffs with good results.

In tropical countries, a variety of types of tree leaves can be used for rabbit feeding. Fomunyam (1984), in Cameroon, fed banana (*Musa sopientum*) and plantain (*Musa paradisica*) leaves as part of a complete diet. Weanling rabbits fed 30% banana or plantain leaves had an adequate rate of gain for tropical conditions of 20 g/day. Banana leaves contain moderate levels of toxic oxalates (Martin *et al.*, 1977).

Ramie (*Boehmeria nivea*) is a semitropical perennial plant (Fig. 14.11) that has been grown as a fiber crop. Fiber made from ramie is similar to linen in properties. Because of the high labor requirements for its production, ramie has not become a major fiber crop, although it is still grown commercially to some extent in Asia and South America. Rabbit raisers in Brazil have found that ramie is an excellent green feed for rabbits. It is very palatable, and produces a large quantity of forage. The plant may reach 8 ft in height and is easily propagated from root cuttings. It presumably would have a high fiber content, which may be helpful in maintaining normal digestive function. In a Brazilian study (Mendes *et al.*, 1980), the average daily gains with 0, 25%, and 50% ground ramie in the diet were 22.3, 22.1, and 6.5 g, respectively. Feed intakes were 99.3, 95.9, and 47.3 g/day, suggesting that at high dietary levels, ramie is unpalatable.

Arrowroot (*Maranta arundinacea*) is a herbaceous, perennial plant grown in the tropics as a source of starch for human consumption. Erdman (1986) investi-



Fig. 14.11 Ramie is a crop grown in some countries as a source of fiber. It is widely used in Brazil as a green feed for rabbits.

gated the use of arrowroot tops and rhizomes as feeds for rabbits. Growth rate was depressed when high levels (60–100%) of arrowroot were fed, but this may have been a consequence of the low dietary protein levels (6–15%). Further work is necessary to evaluate arrowroot adequately.

The fibrous residue remaining after extraction of leaf proteins from green plants to produce leaf protein concentrates may be suitable as a rabbit feed ingredient. Omole and Oke (1979) used the residual fibrous pulp after fractionation of *Amaranthus caudatus* and obtained adequate rabbit growth up to a level of 20% pulp. At 30% dried pulp growth rate was reduced.

The Jerusalem artichoke (*Helianthus tuberosa*), a member of the sunflower family, is occasionally of interest as a source of forage and tubers. The tubers are unique in that instead of starch they contain inulin, a polysaccharide composed of fructose. Although animals do not produce an enzyme that digests inulin, it is hydrolyzed in the acidic environment of the stomach (Graham and Aman, 1986). Jerusalem artichokes appear to have limited if any potential in rabbit feeding.

8. Other Roughage Sources

Sawdust and wood products such as ground aspen (*Populus tremuloid*) have been studied as feeds for ruminant animals. Because wood is a cellulose-based product, it is somewhat comparable to forages as a feedstuff for herbivorous

animals with microbial digestion. Wood products might have potential as sources of indigestible fiber and fermentable nutrients for rabbits. There are few if any studies on the nutritive value of wood products for rabbits, although sawdust and shavings have occasionally been added to feeds as fiber sources. Softwoods (cedar, pine, fir, etc.) contain resins and oils that may have toxic effects, so probably only products from hardwood species (broad-leaved trees) should be used.

Baertsche *et al.* (1986) evaluated a number of fast-growing hardwood tree species for their biomass yield potential and nutrient composition. Those with the highest yield potential were (in decreasing order) poplar, aspen, honey locust, black locust, and black alder. Crude protein contents ranged from 13 to 24%, with leguminous species (e.g., black locust, honey locust) having biomass with a higher protein content than for the nonlegume species. Biomass refers to the total vegetative growth of the plant. Cultivation of fast-growing short-rotation hardwood trees (e.g., hybrid poplars) would involve growing them as modified forage plants, with dense plant spacing and frequent harvest. Additionally, in some areas trees such as aspen might be economically harvested and processed as feedstuffs.

Animal wastes are potential feedstuffs. Dried poultry waste (DPW) has been fairly extensively used as a feed for ruminants. The nitrogen it contains is in the form of uric acid. This can be converted to protein in the rumen but probably is not effectively utilized by rabbits. Dried rabbit manure has been successfully incorporated as a fiber source into rabbit diets on an experimental basis. Some concerns with waste recycling are the dangers of disease transmission, and the accumulation of toxic or undesirable levels of drugs or other additives.

Swick *et al.* (1978) evaluated dried rabbit manure as a feedstuff. A digestibility trial indicated that untreated manure had a very low DE content (Table 14.22), but manure soaked in 2% NaOH had a DE content of 1970 kcal/kg,

TABLE 14.22

Digestibility of Dried Rabbit Manure When Incorporated into a Pelleted Diet[a]

Treatment	Digestibility[b] (%)				DE (kcal/kg)
	ADF	NDF	CP	GE	
Dried rabbit manure	8.1	16.0	36.7	37.4	772
Autoclaved rabbit manure	16.8	23.9	50.6	—	
Manure soaked in 2% NaOH	39.4	41.7	50.4	58.8	1970
Manure soaked in 2% NaOH, then autoclaved	35.8	38.1	45.0	—	

[a]From Swick *et al.* (1978).

[b]ADF, Acid detergent fiber; NDF, neutral detergent fiber; CP, crude protein; GE, gross energy.

nearly equal to that of alfalfa meal. Gains with diets containing 10% manure exceeded 40 g/day.

Elemele *et al.* (1980) found that 10% rabbit excreta could be included in poultry (broiler) diets without adversely affected performance. Lall *et al.* (1984) fed 0, 15, and 30% dried rabbit manure to sheep. Growth rate and nutrient digestibility were depressed with the inclusion of the manure, suggesting it was not of much value as a feedstuff for sheep.

Ekpenyong and Biobaku (1986a,b) used 10% dried poultry manure and activated sewage sludge in rabbit diets, and found no adverse effects on performance or changes in serum enzymes such as transaminases and alkaline phosphatase. Products such as activated sewage sludge may contain toxicants (heavy metals, industrial chemicals, etc.), which on a long-term basis may have detrimental effects on animals when they are used as a feed (Kinzell *et al.*, 1977).

III. CONCENTRATES

A. Cereal Grains

Cereal grains are high in starch (Table 6.1) and are likely to promote enteritis in rabbits. There is some evidence that grains highest in starch (and DE) are the least satisfactory for rabbits. For example, Hall and Johnston (1976) compared growth and lactation responses with corn, wheat, barley, and oat-based diets, and found better performance with the low-energy grains, oats and barley, than with wheat and corn. Cheeke (1974), in feed preference trials, found that rabbits preferred barley to wheat or corn.

Some characteristics of major feed grains will be described. Cereal grains are members of the grass family, and include corn (maize), milo (sorghum), millet, wheat, barley, oats, rye, and triticale. In the United States, corn is the major feed grain. Barley and oats are grown to some extent in the western states, while milo is grown in the Southwest. Millet and rye are grown only to a very minor extent, while wheat is grown primarily for human consumption. Triticale is a synthetic grain, developed in Canada from a wheat–rye cross.

Corn (*Zea mays*) is usually called maize in countries other than the United States and Canada. Where well adapted, corn produces more digestible energy per acre than any other grain, thus explaining why it is the world's most important feed grain. While corn is an excellent source of energy, it has a low (8–9%) protein content, and the protein is of quite low quality, being low in lysine, methionine, and tryptophan. A high-lysine type of corn, called opaque-2, has been developed, but as yet the lower yields do not justify its production. Alone among the grains, yellow corn possesses vitamin A activity.

Although corn is considered the premier feed grain for most livestock, it may

not be so for rabbits. Its high energy content promotes enteritis, and it seems to be somewhat unpalatable. With diets high in corn, it is difficult to achieve adequate crude fiber levels.

Sorghum (*Sorghum vulgare*), usually referred to in the United States as milo, is a drought-resistant plant grown in semiarid areas too dry for corn production. Milo is susceptible to predation by wild birds, so in many countries bird-resistant cultivars are grown. These have a high tannin content, which reduces their palatability and feeding value. Milo has not been used extensively in rabbit feeds, but presumably should give adequate results.

Barley (*Hordenum vulgare*) is widely grown in the northern areas of North America, Europe, and Asia. In North America, it is grown mainly for use in the brewing industry. Barley has a higher protein content and better protein quality than corn; it is lower in starch and high in fiber. These characteristics make it suitable as a rabbit feed ingredient. It contains β-glucans which may provoke enteritis.

Oats (*Avena sativa*) is a relatively minor grain crop. Oats seem to be quite suitable for rabbits, being highly palatable and high in fiber. The starch content is the lowest and the fiber content the highest of the cereal grains. These qualities are useful in rabbit feeding. Oat hulls have been shown to contain a factor that protects swine from stomach ulcers; the effect, if any, of this factor in preventing enteritis in rabbits has not been fully investigated. Riggs *et al.* (1978) compared alfalfa, wheat straw, oat hulls, and beet pulp as fiber sources in fryer diets, at equivalent fiber levels. Average daily gain was lowest with the oat hull diet; no differences in enteritis incidence were noted.

Wheat (*Triticum* spp.) is grown primarily for human consumption. It is sometimes used in animal feeds when the price is competitive with corn or when it is damaged by rain or frost, making it unsuitable for milling. It has a somewhat higher protein content than corn, and like corn, is a high-energy, low-fiber grain. It has not been extensively used in rabbit feeding.

Other grains, such as triticale, rye, rice, and millet are very seldom if ever used in rabbit feeds.

B. Cassava Meal

While not a cereal grain, cassava is discussed here because it is a high-energy, high-starch concentrate feed. Cassava (*Manihot esculenta*) is a tropical plant that produces edible forage and has a starchy root (Fig. 14.12). Large quantities of cassava meal (the dried, ground root) are produced in Southeast Asian countries such as Thailand and Indonesia. Cassava is also extensively grown in Brazil and Nigeria. The fresh root contains about 35% dry matter; on a dry matter basis, the meal contains about 85% nitrogen-free extract (NFE) (mainly starch) and 3% crude protein.



Fig. 14.12 Roots of cassava, a tropical food and forage plant. Both the roots and tops can be used in rabbit feeding. (Courtesy of O. O. Tewe and S. K. Hahn, University of Ibadan, Nigeria.)

Because of its high starch content, cassava meal is likely to cause enterotoxemia when used at high levels in rabbit diets. Although data on optimal levels are lacking, it is probably advisable not to use more than 15% cassava meal in rabbit feeds.

Cassava contains a cyanogenic glycoside, which can cause cyanide poisoning. In normal methods of processing, most of the cyanide is removed. Chopping or slicing the roots liberates an enzyme that breaks the cyanogenic glycoside down to release HCN (hydrogen cyanide or prussic acid). During the drying process, the volatile HCN is dissipated into the air. Omole and Onwudike (1983) found that the addition of 5% palm oil to diets containing cassava peel meal reduced the toxic effects of cyanogens in the meal by increasing the urinary excretion of thiocyanate.

C. Cereal Grain Milling By-Products

Grains are milled to produce flour and other food or industrial products. The milling by-products are used in animal feeds. Some of these have excellent potential as rabbit feedstuffs.

Wheat milling by-products make up about 28–30% of the total grain, with the remainder being flour for human consumption. Wheat mill feeds have a variety

TABLE 14.23

Specifications on Nutrient Levels of Wheat Millfeeds[a]

Millfeeds	Minimum protein (%)	Minimum fat (%)	Maximum fiber (%)
Bran	13.5–15	2.5	12.0
Middlings	10–14	3	9.5
Mill run	14–16	2	9.5
Shorts	14–16	3.5	7
Red dog	13.5–15	2	4

[a]From Church (1986).

of names, and are classified according to fiber content (Table 14.23). Wheat bran is the outer covering of the wheat kernel. It has a very high phosphorus content and is a good source of protein. About 50% of the total wheat by-products consists of bran. Wheat middlings (midds) consist of the fibrous layers just under the bran layer of the wheat kernel. Wheat mill run is a mixture of bran and midds. Shorts are fine particles of bran, germ, flour, and tailings. Red dog is mill tailings with fine particles of bran, germ, and flour.

Wheat millfeeds are bulky (low density) and quite palatable. They are well utilized by rabbits. The fiber component is more digestible in rabbits than in swine or poultry, so the DE is nearly as high as for the grain itself. Wheat milling by-products are widely available. In many developing countries, wheat is imported and milled in the country, so wheat by-products are available. For example, a large rabbitry in Haiti uses a feeding system based on wheat midds and shorts, mixed daily with molasses, water, and a premix, and fed as a wet mash supplemented with fresh grass. The crude fiber of wheat by-products is quite digestible in rabbits, so should not be included in the calculation of the fiber content of the diet. McNitt *et al.* (1982), in a study with high dietary levels of wheat mill run, noted high mortality from enteritis (Table 14.24). Provision of a source of indigestible fiber, such as straw, along with the milling by-product should prevent this problem.

Similar by-products are produced from the milling of other grains. Hominy feed is a by-product of the dry milling of corn. Rice bran is available in large quantities in many tropical countries. It has a high oil content, which provides energy, but it is very susceptible to development of rancidity. The presence of rice hulls in the bran can reduce its energy content. The hulls are high in silica and may cause ulceration of the intestinal lining, causing bloody diarrhea. Rice bran is a major feed ingredient for rabbits in many tropical countries such as Indonesia.

TABLE 14.24

Effect of Various Dietary Levels of Wheat Mill Run on Performance of Weanling Rabbits[a]

Item	Dietary level of wheat mill run		
	25	55	85
Dietary crude fiber (%)	25.8	18.4	12.0
Average daily gain (g)	44.0	40.9	34.0
Average daily feed intake (g)	175	144	179
Feed/gain	3.97	3.53	5.25
Mortality (%)	13.6	26.1	56.5

[a]From McNitt *et al.* (1982).

Grain screenings are the by-products produced when grains are cleaned, and consist of weed seeds, soil, broken seeds, chaff, and dust. Screenings are of variable composition. They might be useful in rabbit diets because of their high fiber content.

Brewers and distillers grains are the residue remaining after fermentation of grains for alcohol and beer production. Because the fermentation process ferments the starch and sugars, the residual grains are enriched in protein and fiber. Thus the original protein and fiber in the grains is present, with less of the starch remaining, so the protein and fiber contents on a percentage basis are increased. Although little information on their value in rabbit feeding is available, it would appear that they should be acceptable feedstuffs. The reduction of the starch content of the original grains should be useful in helping to avoid enteritis. Omole and Ajayi (1976) in Nigeria fed 0, 15, 30, and 45% brewers dried grains to growing rabbits. Similar growth rates (13–15 grams per day) were obtained with all treatments.

D. Food Processing By-Products

1. Molasses

Molasses is a major by-product of sugar production, mainly from sugarcane and to a lesser extent from sugar beets. Molasses is highly palatable, because it contains 46–48% total sugars, mainly sucrose. It is useful in improving feed palatability, improving pelleting and pellet quality, and reducing fines in pelleted feeds. It has a high mineral content, giving it laxative properties. Potassium is the major mineral element in molasses. Levels of molasses in rabbit diets should not exceed 20%. A level of 3–6% is the maximum practical level in pelleted feeds.

2. Beet Pulp

Beet pulp is the residue remaining after sugar is extracted from sugar beets. It is dried and made available in shredded or pelleted form. The nutritional qualities of beet pulp have been reviewed by Kelly (1983). A number of studies have been performed evaluating beet pulp as a feed for rabbits. Harris and Johnston (1980) found that substituting 20% beet pulp for alfalfa meal reduced the growth rate of litters of does receiving the test diets; the average 8-week weight of fryers was 1.67 kg on the alfalfa diet and 1.49 kg on the beet pulp diet. Beet pulp appeared less palatable than alfalfa meal, safflower meal, and grape pomace in a feed preference test. Franck and Seroux (1980) compared beet pulp levels of 0, 10, 20, and 30% in a fryer trial. Results are shown in Table 14.25. Performance was adequate at all levels of beet pulp. Martinez Pascual and Fernandez Carmona (1980a) reported the metabolizable energy (ME) for beet pulp to be 3300 kcal/kg, while Maertens and DeGroote (1984) reported DE values of 3300–3400 kcal/kg and Fekete and Gippert (1986) determined a DE value of 3100 kcal/kg. Fekete and Gippert (1986) found the digestibility of beet pulp crude fiber to be 70%; the nature of the fiber in beet pulp is that it is low in cellulose and highly digestible. Beet pulp appears to be a very acceptable feedstuff for rabbits, so long as an adequate level of indigestible fiber is incorporated into the diet. The crude fiber content of beet pulp should not be considered when calculating the dietary fiber level, because it is so highly digestible.

3. Citrus By-Products

Citrus by-products are derived from the residue resulting from the manufacture of citrus juice. The residue is treated with calcium hydroxide, pressed to remove residual juice, and dried. Citrus by-products are palatable, low in protein (5–8%), moderately high in fiber (11–12%), and may be high in calcium. These products are produced in large amounts wherever citrus crops are grown. For

TABLE 14.25

Performance of Fryer Rabbits Fed Various Levels of Sugar Beet Pulp[a]

Item	Dietary beet pulp (%)			
	0	10	20	30
Average daily gain (g)	36.2	37.3	36.9	37.9
Average daily feed intake (g)	126	131	116	117
Feed/gain	3.39	3.41	3.04	3.03
Mortality (%)	5.3	6.3	6.1	4.5

[a]From Franck and Seroux (1980).

example, in the region of Valencia, Spain, 60,000 tons of dried citrus pulp are produced annually (Fernandez Carmona *et al.*, 1980; Martinez Pascual and Fernandez Carmona, 1980b). These authors evaluated dried citrus pulp as a feedstuff for rabbits. The effect of various levels of citrus pulp on gains and nutrient digestibility were examined. The results (Table 14.26) show a progressive decline in average daily gain with increasing levels of citrus pulp, but an increasing digestibility of dry matter and fiber. The digestibility results indicate that citrus pulp fiber is highly digestible, and the product has a high DE content. They explained the poor growth performance on the basis of poor protein quality. A large amount of sediment (calcium carbonate) in the urine was noted, arising from the high calcium content of the pulp. Based on this study, it appears that citrus pulp can be used with satisfactory results up to about 30% of the diet. Leto *et al.* (1984) reported no depression in performance when either orange pulp or lemon pulp was used at 20% of the diet.

4. Fruit Pomace

Fruit pomace is similar to citrus pulp, except it is derived from noncitrus fruits such as apples and pears when they are processed for juice production. Schurg *et al.* (1980) evaluated dried apple, grape, and pear pomace in rabbit diets. When used at 10% of the diet, all gave satisfactory gains. When used at higher levels, gains were decreased with apple pomace, but not with grape pomace (Table 14.27). Reductions in protein, energy, and fiber digestibility occurred with 50% apple or grape pomace.

Parigi-Bini and Chiericato (1980), in Italy, studied the utilization of grape pomace by rabbits. The product consists primarily of skins and stalks, and about

TABLE 14.26

Effect of Dietary Level of Citrus Pulp on Growth, Digestibility, and Nitrogen Balance[a]

Item[b]	Citrus pulp in diets (%)						
	0	15	30	45	60	75	100
Average daily feed intake[c]	80	82	73	72	62	53	31
Average daily gain (g)	35.3	33.7	29.0	22.4	14.6	11.9	−3.7
DM Digestibility (%)	65.0	64.3	66.4	63.4	68.1	74.0	88.1
CF Digestibility (%)	16.7	19.9	32.8	34.1	40.0	58.7	83.4
ADF Digestibility (%)	19.2	21.8	34.7	38.5	45.5	58.2	81.6
N Digestibility (%)	73.1	72.8	75.4	74.7	75.8	76.3	64.7
N Retention (%)	44.6	44.5	42.3	40.0	39.5	45.0	−2.1
N Balance (g/day)	1.99	1.95	1.72	1.64	1.41	1.17	−0.01
DE (kcal/kg)	2900	2900	3100	2700	3000	3300	3800
ME (kcal/kg)	2800	2800	3000	2500	2800	3100	3500

[a]From Martinez Pascual and Fernandez Carmona (1980b).

[b]DM, Dry matter; CF, crude fiber; ADF, acid detergent fiber; DE, digestible energy; ME, metabolizable energy.

[c]g DM/kg$^{0.75}$/day.

TABLE 14.27

Effect of Various Dietary Levels of Apple Pomace and Grape Pomace on Growth and Nutrient Digestibility[a]

Item	Dietary pomace[b] (%)							
	5% Apple	15% Apple	25% Apple	35% Apple	50% Apple	5% Grape	25% Grape	50% Grape
Average daily gain (g)	26.8	23.9	25.6	24.0	13.8	23.1	26.7	24.5
Average daily feed intake (g)	61	59	61	62	50	47	57	73
Feed/gain	2.3	2.5	2.4	2.6	3.6	2.0	2.1	3.0
kcal Digestibility (%)	85.0	84.3	82.4	80.0	78.4	82.3	76.6	59.6
Protein digestibility (%)	80.2	76.1	71.6	65.5	63.6	77.2	72.0	57.3
ADF digestibility (%)	45.1	43.9	42.5	38.1	37.2	33.2	31.9	17.0

[a]Adapted from Schurg *et al.* (1980).

[b]Two different trials were conducted: one with apple pomace and one with grape pomace.

TABLE 14.28

Effect of Grape Pomace on Growth and Nutrient Digestibility[a]

Results	Dietary pomace (%)					
	0	8	16	24	32	40
Average daily gain (g)	39.4	39.8	37.7	38.8	39.2	38.2
Average daily feed intake (g)	158	157	154	156	154	159
Feed/gain	4.00	3.94	4.09	4.05	3.94	4.17
Dry matter digestibility (%)	57.0	57.0	57.2	56.4	56.3	54.3
Crude protein digestibility (%)	73.3	68.5	69.0	63.6	60.9	55.1

[a]From Parigi-Bini and Chiericato (1980).

160,000 metric tons are produced each year in Italy. It contains about 15–16% crude protein, 19% ash, 11–12% crude fiber, and 56% ADF. Results of a growth trial are shown in Table 14.28. These authors concluded that grape pomace can replace alfalfa meal in rabbit diets. In contrast, Martinez Pascual and Fernandez Carmona (1980a) concluded from a digestibility trial that grape pomace had a very low DE and had no practical value as a feedstuff. Similarly, they reported that olive pulp had a very low ME content of about 450 kcal/kg. Olive pulp is considered of virtually no value as a feedstuff except as a source of indigestible fiber.

In tropical countries, bananas and plantains can be used for feeding. Reject bananas not suitable for export or in excess of local human food needs can be used as animal feed. Fresh whole banana contains about 80% water. On a dry matter basis, bananas contain about 4% crude protein, 1.1% fat, 1.6% crude fiber, and 2.7% ash. The major constituents are starch and sugars. Unripe bananas contain tannins, which reduce palatability.

IV. PROTEIN SOURCES

A. Oilseed Meals

Many of the plant protein supplements used in animal feeds are the residue remaining after oil is extracted from the seeds. The oil may be used for edible (salad oil, margarine) or industrial application. Most oils are removed by solvent extraction with hexane (solvent-extracted meals). In the past, the oil was often removed by mechanical means (expeller process), leaving some oil residue in the meal.

1. Soybean Meal and Soybeans

Soybean meal is the major plant protein supplement used for nonruminant livestock in the United States and in much of the rest of the world. Soybean meal is highly palatable and has a good amino acid balance. Although raw soybeans contain a number of toxic factors, these are inactivated when soybean meal is prepared.

While soybean meal is the main soybean product used in rabbit feeding, there is sometimes interest in the use of whole soybeans. These can be prepared by the extrusion process (Fig. 14.13). The raw beans are extruded through a die; the friction produces sufficient heat to inactivate the inhibitors (trypsin inhibitors, lectins—see Chapter 15). Sanchez *et al.* (1984a) demonstrated that raw soybeans are unsatisfactory for growing rabbits (Table 14.29); extruded soybeans gave results similar to those with soybean meal. Pancreatic enlargement, a sign of trypsin inhibitor activity in many animals, was not detected in the group fed raw

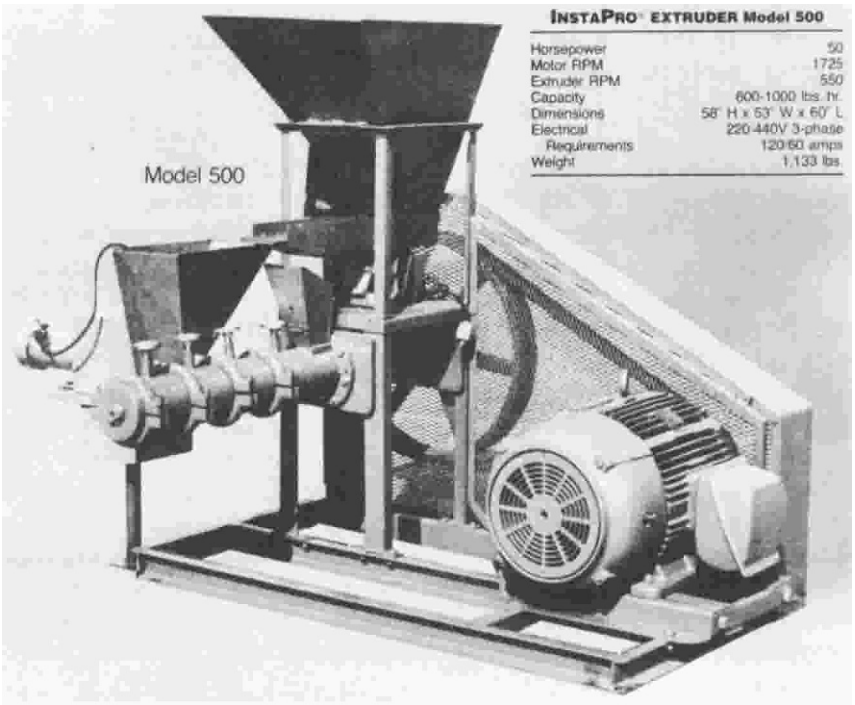


Fig. 14.13 An extruder, used in preparation of extruded soybeans and other extruded products. The feed is forced through a die; the pressure causes friction and heating, which break down the cellular structure and destroy heat-labile inhibitors. (Courtesy of Triple "F" Feeds, Des Moines, Iowa.)

TABLE 4.29

Performance of Weanling Rabbits Fed Various Soybean Products[a]

Product	TIU[b]	Soybean product in diet (%)	Average daily gain (g)	Average daily feed intake (g)	Feed/gain
Soybean meal	ND[b]	15	37.6*[c]	143	3.85*
Raw soybeans	70.0	20	27.6**	123	4.98**
Extruded soybeans	25.4	23	40.1*	135	3.38*
Low-TI soy flour	11.8	18	39.3*	140	3.56*
Low-fat, low-TI soy flour	6.8	13	36.6*	136	3.76*

[a]From Sanchez *et al.* (1984a).

[b]TIU, Trypsin inhibitor units/mg; ND, not determined; TI, trypsin inhibitor.

[c]* Different from ** ($p < 0.05$).

soybeans. The diffuse nature of the pancreas of the rabbit made it unfeasible to determine pancreas weight.

2. Cottonseed Meal

Cottonseed meal is the second most important plant protein supplement used in livestock feeding. The main concern with the use of cottonseed meal is that it contains a toxic phenolic compound called gossypol. Gossypol causes tissue damage, such as heart, liver, and lung lesions, and cardiac failure. In some species, gossypol interfers with spermatogenesis, resulting in male infertility. More information on gossypol is provided in Chapter 15.

McNitt *et al.* (1982) evaluated cottonseed meal (0.04% free gossypol) as a protein supplement for weanling rabbits. Normal growth rates were achieved with all levels of cottonseed meal (Table 14.30), and there was no response to supplementary lysine (the first limiting amino acid in cottonseed meal). In an earlier study, Cheeke and Amberg (1972) observed that gains were lower with cottonseed meal than with soybean meal supplementation of wheat-based diets; addition of an amino acid supplement of lysine and methionine to the cottonseed meal-containing diet eliminated the growth rate depression. McNitt (1981) reviewed the use of cottonseed meal in rabbit diets, and concluded that with free-gossypol levels of 0.04% or less, up to 15% cottonseed meal in the diet should be acceptable.

3. Rapeseed (Canola) Meal

Rapeseed meal is the residue remaining after oil is extracted from seeds of rape (*Brassica napus* and *B. campestris*). Rapeseed (Fig. 14.14) is a major crop in

TABLE 14.30

Growth Response of Weanling Rabbits Fed Various Levels of Cottonseed Meal[a]

Dietary cottonseed meal	Average daily gain (g)	
	No supplemental lysine	Supplemental lysine
0	40.2	36.2
4	37.0	41.8
8.2	38.6	39.0
16.5	38.9	40.5

[a]From McNitt *et al.* (1982).

Canada and is grown extensively in Europe and Asia. It is grown for both industrial and edible oil. The meal contains glucosinolates, compounds that inhibit the activity of the thyroid gland. Canadian plant breeders have developed cultivars low in glucosinolate content, producing nontoxic rapeseed meal. This low-glucosinolate meal is called canola meal, to distinguish it from the high-glucosinolate rapeseed meal.

Throckmorton *et al.* (1980) evaluated canola meal as a protein supplement for weanling rabbits. Satisfactory growth performance was obtained using canola meal as a complete replacement for soybean meal (Table 14.31). Lebas and Colin (1977) compared rapeseed meal and dehulled rapeseed meal (both were heat treated) as protein supplements, with a diet containing sunflower meal as the control. There were no differences in growth rate or evidence of thyroid enlargement (Table 14.32). From these reports, it would appear that canola or low-glucosinolate rapeseed meal can be used satisfactorily as the sole protein supplement for growing rabbits.

4. Sunflower Meal

Sunflowers (*Helianthus annuus*) are grown extensively as an oil crop in North America, Western and Eastern Europe. In the United States, sunflowers are grown mainly in the northern Great Plains states, such as North Dakota. Sunflower meal contains 30–35% crude protein and 22–25% crude fiber. Because of its high fiber content, it is of limited value for swine and poultry feeding, but might be quite suitable for rabbits. The work of Lebas and Colin (1977) suggests that it can support adequate growth (Table 14.32). Sunflower seeds, because of their high oil, protein, and fiber contents, might be quite suitable for rabbits. No studies on their use have yet been reported.



Fig. 14.14 A rapeseed plant. Rape is a member of the *Brassica* family, which includes such plants as mustard, cabbage, cauliflower, and turnips. Rapeseed meal is a major protein supplement in some areas. (Courtesy of J. M. Bell, University of Saskatchewan, Canada.)

TABLE 14.31

Growth Performance of Weanling Rabbits Fed Canola Meal[a]

Item	Replacement of soybean meal with canola meal			
	0	50	75	100
Dietary canola meal (%)	—	9.3	14.0	18.7
Average daily gain (g)	38.2	39.0	37.4	35.3
Average daily feed intake (g)	101	101	98	96
Feed/gain	2.53	2.59	2.62	2.73

[a]From Throckmorton *et al.* (1980).

5. Safflower Meal

Safflower (*Carthamus tinctorius*), a prickly plant much like a thistle in appearance, is an ancient oil crop. The meal is high in fiber and is deficient in lysine. Because of its composition (fairly low protein, high fiber), it is probably more suitable for rabbits than for other nonruminants. Harris and Johnston (1980) found safflower meal to be a satisfactory feedstuff for rabbits. In a feed preference trial, the safflower meal-containing diet was preferred over a similar alfalfa-based diet. Decorticated safflower meal is produced by mechanically separating the hull from the seed, to produce a higher protein, lower fiber product.

6. Other Oil Meal Protein Supplements

There are a number of other oil meals and plant protein supplements used to a minor extent in rabbit feeding. Linseed meal is the by-product of the extraction

TABLE 14.32

Responses to Rapeseed Meal and Sunflower Meal as Protein Supplements for Growing Rabbits[a]

Item	Protein source		
	Rapeseed meal	Dehulled rapeseed meal	Sunflower meal
Protein supplement in diet (%)	15.5	13	12
Average daily gain (g)	35.5	35.4	36.5
Average daily feed intake (g)	127	128	132
Feed/gain	3.61	3.64	3.63
Thyroid weight (g)	0.22	0.25	0.23

[a]From Lebas and Colin (1977).

of linseed oil from flax (*Linum usitatissimum*) seed. Because of its low lysine content, if should probably be fed in combination with a protein supplement of higher protein quality. It contains a vitamin B_6 (pyridoxine) antagonist, but because of the role of coprophagy in meeting vitamin needs of the rabbit, the antagonist (linatine) is unlikely to be of significance in rabbits.

Peanut meal (also called groundnut meal) is the residue remaining after extraction of the oil from peanuts. It contains 45–55% crude protein. Compared to soybean meal it is low in lysine and methionine, so it probably should not be used as the sole protein supplement. Peanuts are susceptible to infection by molds which produce aflatoxin, particularly in tropical climates. The potential for aflatoxin contamination should be considered in areas where storage conditions favor mold growth.

Sesame meal is produced to a minor extent in China, India, and Mexico. Sesame (*Sesamum indicum*) is one of the oldest known oil crops. The seeds are very small, and the seed capsules tend to shatter readily, so it is not easily harvested except by hand. Sesame meal is recognized as being very low in lysine and is often used experimentally to produce lysine-deficient diets. Lebas (1973) used sesame meal to study lysine requirements of rabbits. At various dietary protein levels, growth rate was less with sesame meal than with soybean meal.

Copra or coconut oil meal is the residue after oil extraction from dried endosperm of the coconut (*Cocos nucifera*). In many tropical areas, it is a readily available protein supplement. It contains 20–21% crude protein and 10–11% crude fiber. It probably is suitable for rabbits, but no reports on its use for this purpose are available. Palm kernel meal, the residue from oil extraction from the oil palm (*Elaeis* spp.), contains about 20% protein and is likely a suitable protein supplement for rabbits also.

Two new oilseed crops are meadowfoam (*Limnanthes alba*) and jojoba (*Simmondsia californica*). The oils of these plants have properties useful in industrial applications and cosmetics. Meadowfoam is adapted to poorly drained soils of the Pacific Northwest, while jojoba is a desert shrub of Arizona and other states of the Southwest. The meals remaining after oil extraction have been evaluated as feedstuffs for rabbits. Meadowfoam meal (MFM) contains a high concentration of glucosinolates, which are goitrogenic (see Chapter 15). Throckmorton *et al.* (1981) tested raw and steam-cooked MFM in diets for weanling rabbits. Levels of 20% and 40% raw MFM caused mild growth depression, but 40% steam-cooked MFM did not significantly reduce gains. At high (60 and 80%) steam-cooked MFM levels, growth was impaired and palatability of the diets was low.

Ngoupayou *et al.* (1985) tested the response of weanling rabbits to various dietary levels of jojoba meal, which contains a toxic glycoside called simmondsin. The raw meal caused pronounced growth depression. Treatment of the

meal to reduce the level of simmondsin resulted in improved performance. Levels of simmondsin below 0.05% of the diet produced little adverse effect.

Guar meal is the residue remaining after the extraction of galactomannan gums from guar (*Cyamopsis tetragonoloba*) seeds. Guar is a native of India and is grown commercially in that country and to a minor extent in the United States. The gums are used in food processing and for industrial purposes. The meal remaining after gum extraction contains about 35% crude protein. Schurg *et al.* (1986) evaluated guar meal as a feedstuff for rabbits. Levels of 0, 6, 13, 20 and 27% guar meal were fed; average daily gains of weanling rabbits were 33.9, 26.8, 19.6, 14.2 and 11.7 g, respectively. The results suggest that guar meal contains antinutritional substances which reduce growth, feed intake, and nutrient digestibility.

7. Full-Fat Oilseeds

The oil meals previously discussed are the residue remaining after the oil has been extracted for edible or industrial uses. Generally, the oil is more valuable and brings a higher economic return for these purposes than when used as animal feed. However, at times it may be economically feasible to utilize the full-fat seeds as feedstuffs. In general, the raw seeds contain toxins and must be heat treated prior to their use in feeds. With the whole seeds, this can be accomplished most readily by the use of the extrusion process, in which the seeds are extruded through a die. The friction involved builds up sufficient heat to inactivate heat-labile toxins.

Only limited work has been done with full-fat oilseeds as feedstuffs for rabbits, but their use would appear to have considerable potential as a means of increasing the dietary energy level without inducing carbohydrate overload. It is possible to use higher fat levels in pelleted feeds when it is contributed as part of an extruded ingredient than when it is simply added as a fat or oil.

Sanchez *et al.* (1984c) found that extruded soybeans gave growth results equal to those achieved with soybean meal in diets for fryer rabbits. Johnston and Berrio (1985) evaluated extruded soybean, safflower, cotton, and flax seeds as protein sources for lactating and growing rabbits. There were no significant differences in growth to 8 weeks of age of rabbits receiving the different oilseeds compared to the control treatment in which soybean meal was the protein supplement. The percentages of each seed in the diets were as follows: soybeans, 20%; cottonseed, 43%; safflower seed, 34%; flaxseed, 39%. It is of interest that such a high level of cottonseed was used without evidence of gossypol toxicity. Other whole oilseeds that might be considered in rabbit feeding are sunflower and rapeseed. A potential advantage of some of these seeds, particularly cottonseed and sunflower seed, is that they are high in protein, oil, and fiber, providing a

means of maintaining adequate protein and energy levels without depressing the dietary fiber content.

Another seed that has been evaluated is whole radish seed (Sanchez *et al.*, 1984c). Because of its high glucosinolate content, radish seed gave very poor growth when used at 20% of the diet, and appears unsuitable as a rabbit feed ingredient.

B. Grain Legumes

A number of grain legumes are grown throughout the world. These include soybeans, field beans (*Phaseolus* spp.), fava beans (*Vicia faba*), peas, and lupines (*Lupinus* spp.). Many are used directly for human consumption, and may also be used in animal feeds.

Field beans include kidney, pinto, and navy beans. They contain a number of toxicants, including trypsin inhibitors and lectins. Lectins are of major concern. Heat treatment of these beans by some process such as extrusion is necessary before they can be safely used. Sanchez *et al.* (1983) evaluated raw and heat-treated pinto beans in fryer diets. The results (Table 14.33) showed severe growth depression with raw beans, which was partially overcome by autoclaving. Lectins cause damage to the mucosa of the intestinal tract, leading to impaired nutrient absorption and diarrhea. Pinto beans (and probably kidney and navy beans) appear to be unsatisfactory as rabbit feeds.

Seroux (1984), in France, examined the use of peas, lupine grain, and field beans as rabbit feed. All of these grains could totally replace soybean meal without adversely affecting weight gains and feed conversion (Table 14.34). Maximum dietary levels employed were 30%, 21%, and 30% for peas, lupines, and beans respectively.

Lupine seeds are often high in manganese, particularly when the crop is grown on acid soils. Manganese toxicity symptoms, which include poor growth, depressed feed intake, and anemia, have been noted in swine and poultry fed lupine

TABLE 14.33

Performance of Rabbits Fed Raw and Autoclaved Pinto Beans[a]

Treatment	Average daily gain (g)	Average daily feed intake (g)	Feed/gain
Soybean meal	35.7*[b]	139*	3.9*
Raw pinto beans	14.4**	87**	6.1**
Autoclaved pinto beans	21.9**	94**	4.3*

[a]From Sanchez *et al.* (1983).

[b]* Different from ** ($p < 0.05$).

TABLE 14.34

Growth Responses of Weanling Rabbits Fed Grain Legumes[a]

Legume	Average daily gain (g)	Average daily feed intake (g)	Feed/gain
15% Soybean meal (control)	43.6	117	2.68
7% Lupin	43.7	117	2.68
14% Lupin	43.7	114	2.63
21% Lupin	44.0	114	2.60
15% Soybean meal (control)	39.0	113	2.89
10% Field bean	39.2	114	2.92
20% Field bean	38.8	114	2.94
30% Field bean	39.1	111	2.86
15% Soybean meal (control)	45.0	138	3.08
30% Winter peas	43.8	141	3.16
30% Spring peas	45.2	146	3.13

[a]From Seroux (1984).

seed. Elevated dietary manganese levels impair iron absorption and induce signs of iron deficiency such as anemia and lowered hemoglobin levels. Dietary manganese concentrations of 500–1000 ppm are potentially toxic.

C. Animal Protein Sources

Animal protein sources such as meat and bone meal, fish meal and feather meal are used quite extensively in swine and poultry feeding, but are seldom used in rabbit diets in the US. Fishmeal has been routinely utilized in rabbit diets in Britain. Because of the herbivorous nature of rabbits, and their strict vegetarian behavior in the wild, it is not surprising that animal protein sources might be overlooked in rabbit diet formulation.

Meat and bone meal is prepared from animal tissues obtained from slaughter houses and rendering plants. It contains about 50% crude protein, 8% fat, 10% calcium and 5% phosphorus. It tends to be somewhat variable in quality. Probably it should be limited to 5–10% of the diet.

Fish meals are generally too expensive to be utilized in rabbit feeds. They are very high in protein content (50–70%) and have an excellent amino acid balance. Fish meal should not be used in fattening diets, as it may impart a fishy flavor to the meat.

Feather meal is prepared by steam-cooking feathers, which are available in large quantity from poultry processing plants. Feather meal tends to be somewhat low in digestibility. Fekete and Hegedus (1986) found that 3% feather meal could be used with no adverse effects in fryer rabbit diets.

TABLE 14.35

Effects of Lysine and Methionine Hydroxy Analog Supplementation of Alfalfa-Based Diets for Weanling Rabbits[a]

Regimen	Average daily gain (g)	Feed/gain	Mortality (%)
Trial 1			
21% SBM[b]	38.4	3.01	0
21% SBM + 0.3% MHA	39.4	2.92	10
15% SBM	36.5	3.09	10
15% SBM + 0.3% MHA	39.9	3.09	0
9% SBM	39.1	3.03	0
9% SBM + 0.3% MHA	38.9	3.06	20
3% SBM	38.1	2.77	0
3% SBM + 0.3% MHA	37.3	3.06	0
Trial 2			
54% Alfalfa diet			
21% SBM	34.4	3.51	15
0% SBM	33.9	3.81	10
0% SBM + 0.3% MHA	33.5	3.79	10
74% Alfalfa diet			
21% SBM	32.6	3.76	10
0% SBM	31.9	3.86	10
0% SBM + 0.3% MHA	34.1	3.91	10
Trial 3			
21% SBM	39.7*[c]	3.45*	6
0% SBM	39.1*	3.84**	0
0% SBM + 0.3% lysine	35.9**	3.97**	6
0% SBM + 0.3% lysine + 0.3% MHA	38.5*,**	3.73**	0

[a]From Sanchez *et al.* (1984b).

[b]Diet contained 54% alfalfa meal, 20% wheat mill run, and 21% SBM. In other diets, SBM was replaced with wheat mill run. SBM, Soybean meal; MHA, methionine hyroxy analog.

[c]* Different from ** ($p < 0.05$).

D. Synthetic Amino Acids

Two amino acids, lysine and methionine, are widely used in the feed industry, especially in poultry feeds. The forms in which they are commonly used are L-lysine, DL-methionine, and methionine hydroxy analog (MHA). Supplementary methionine is used to a limited extent in rabbit diets, as a means of meeting the sulfur amino acid requirement. With alfalfa and wheat mill run-based diets, supplementation with lysine and/or methionine has not been effective in improving performance (Sanchez *et al.*, 1984b), and lysine depressed performance (Table 14.35). Of particular interest in these studies was the finding that the

protein supplement (soybean meal) could be completely removed from the diet, with all the dietary protein provided by alfalfa meal and wheat mill run, with no detrimental effect on growth and no response to supplementary amino acids.

V. NONNUTRITIVE FEED ADDITIVES

A number of feed additives are used in animal feeding for purpose other than providing nutrients. These include growth stimulants (antibiotics, hormones), preservatives (antioxidants, mold inhibitors), enzymes, feed flavors, and pellet binders. Some of those most likely to be used in rabbit feeding will be discussed.

A. Antibiotics

Antibiotics are natural substances, produced by molds and fungi, which inhibit the growth of bacteria. Since the discovery by Sir Alexander Fleming of penicillin in moldy bread, antibiotics have truly been the wonder drugs of the twentieth century, saving perhaps millions of people from death by infectious diseases.

In the late 1940s, it was demonstrated that inclusion of antibiotic production fermentation residues in the diet of chicks improved their growth. Subsequent studies demonstrated that the growth response was caused by residual antibiotics in the fermentation products. Since the early 1950s, antibiotics have been extensively used as growth promotants in livestock feeds. The mode of action of antibiotics in improving growth is not completely understood. One obvious effect might be the control of pathogenic bacteria in the gut. Other postulated modes of action include modifications of gut bacteria populations to favor nutrient-synthesizing organisms, reduction of toxin production by bacteria, and improvements in nutrient absorption. It has been demonstrated that there is a thinning of the intestinal wall of animals fed antibiotics, which might favor increased absorption of nutrients. Some of the antibiotics that have been used in the feed industry include chlortetracycline (Aureomycin), oxytetracycline (Terramycin), penicillin, bacitracin, streptomycin, chloramphenicol, tylosin, flavomycin, lincomycin, monensin (rumensin), neomycin, oleandomycin, and virginiamycin.

The use of antibiotics and other drugs is carefully regulated by the Food and Drug Administration (FDA). In recent years, there has been concern expressed that the use of antibiotics in feeds may result in the contamination of the human environment with antibiotic-resistant bacteria. While there is little conclusive evidence that this has ever occurred, it is a possibility. The best long-term solution will be the development of antibiotics for animal feeding that are not

used in human medicine. Virginiamycin is an example of such a drug, used only in livestock.

The only antibiotic approved for use in rabbit feed in the United States is oxytetracycline, at a level of 10 g/ton. Rabbits are quite sensitive to a variety of antibiotics. Enteritis can be induced by a number of antibiotics, as a result of disturbances in bacterial populations. For example, lincomycin, clindamycin, ampicillin, and tylosin can cause diarrhea and mortality (Loliger *et al.*, 1984; Katz *et al.*, 1978).

Borriello and Carman (1985) have suggested that bacitracin might be effective in prevention of enterotoxemia caused by *Clostridium spiroforme*. In support of this suggestion, Casady *et al.* (1964) found that 50 mg zinc bacitracin per kilogram of diet reduced the incidence of enteritis.

B. Probiotics

The term probiotics has been coined to describe bacterial organisms that are added to feeds with the intention of having these organisms colonize the gut. *Lactobacillus acidophilus* is an organism that has been used for this purpose, with variable results. A disadvantage of this organism, and most other probiotics, is that it is killed by heat and so cannot be used in pelleted diets.

A spore-forming organism, *Bacillus toyoi,* has the advantage that the spores are resistant to heat, and can be used in pelleted feeds. According to Hattori *et al.* (1984), this probiotic when fed in the diet will colonize the rabbit hindgut, and by competitive inhibition, control the growth of undesirable organisms such as *Escherichia coli.* An intriguing possibility is that probiotics could be fed along with high-energy diets, and prevent the proliferation of *E. coli* and *Clostridium* species, which cause enteritis.

C. Buffers

Buffers are substances that resist changes in acidity. They have been extensively used in diets for feedlot cattle, to prevent development of acidosis. Commonly used buffers include sodium bicarbonate, ground limestone, and magnesium oxide. Some feedstuffs, such as alfalfa meal, have considerable buffering capacity.

With cattle, it has been suggested (Wheeler and Noller, 1977) that starch that escapes digestion in the rumen may not be completely digested in the small intestine because the intestinal pH may be too low for maximal amylase activity. The addition of buffers to the diet has been shown to improve postruminal starch digestion (Wheeler, 1980). Harris *et al.* (1982a) hypothesized that buffers in rabbit diets might increase starch digestion in the small intestine and thus avoid enteritis induced by carbohydrate overload of the hindgut. They tested the effects

TABLE 14.36

Effect of Dietary Buffers on Growth and Enteritis Mortality on Weanling Rabbits[a]

Buffer type	Average daily gain (g)	Feed/gain	Mortality (%)
Control	42.9	2.77	13.4
1% Magnesium oxide	35.3	2.55	6.7
5% Sodium bicarbonate	34.6	2.91	26.7
3% Limestone	37.3	2.60	26.7
3% Limestone + 3% sodium bicarbonate	35.1	4.33	40.0

[a]From Harris *et al.* (1982a).

of the addition of sodium bicarbonate, limestone, and magnesium oxide on growth and enteritis. The results (Table 14.36) did not suggest advantageous effects of the addition of buffers. Mortality from enteritis was highest in the groups receiving buffers, except with magnesium oxide. In view of the evidence that increased cecal pH favors the proliferation of *E. coli* and *Clostridium* species (Morisse *et al.*, 1985), it is probable that the buffers used would increase the likelihood of enteritis. It would appear that buffers are not useful additives in rabbit diets.

Zeolites are clay minerals that have ion exchange and buffering capacities. Mumpton and Fishman (1977), in a review of zeolites, suggested that these compounds may lower the pH of the intestinal tract and reduce enteritis in livestock. Grobner *et al.* (1982) fed two levels of zeolite (1.5 and 3%) in high-fiber (54% alfalfa) and low-fiber (20% alfalfa) diets for weanling rabbits. Average daily gain was significantly greater for rabbits fed the high-alfalfa diets, but there was no significant effect of zeolite on growth rate. Zeolite had no apparent effect in reducing enteritis, and in one treatment (54% alfalfa + 1.5% zeolite), enteritis mortality was significantly greater than with the other treatments.

D. Flavoring Agents

Feed flavors have been promoted as a means of increasing feed intake of animals. Normally, feed intake is regulated by animals in accordance with their metabolic needs, particularly for energy. An increased feed intake above normal voluntary intake would probably just result in the storage of the extra intake as body fat, rather than in a true stimulation of tissue growth. With unpalatable feedstuffs, it is possible that feed flavors might enhance feed intake. An important effect of increased feed palatability to rabbits would be a reduction in feed spillage. To date, there are no data available on the effect of commercial feed flavors on rabbit performance.

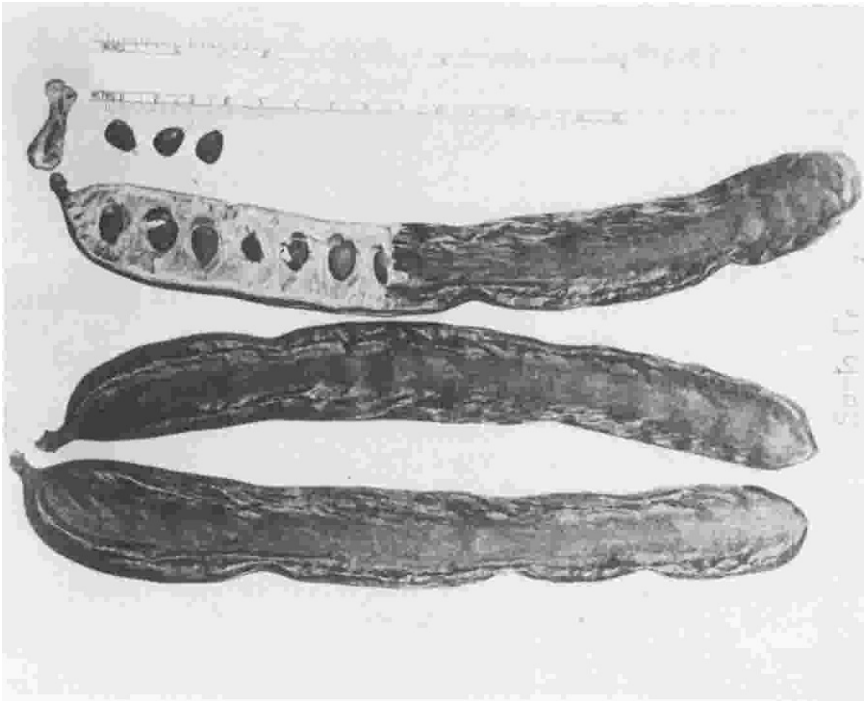


Fig. 14.15 Seeds and pods of carob. Carob meal is used in several European countries as an additive in rabbit feeds to improve palatability. (Courtesy of C. A. Schroeder, University of California at Los Angeles.)

Thyme (*Thymus vulgare*) is an herb in the mint family, which is said to be attractive to rabbits (B. L. Bradley, Chicago, Illinois, personal communication). Some evidence to support this belief is the report of Fekete and Lebas (1983), who compared performance of rabbits fed a control diet with those fed the same diet with 150 or 300 mg thyme extract per kilogram. Average daily gain was increased ($p < 0.05$) from 35.9 g (control) to 44.3 g (300 mg thyme extract/kg). In a feed preference trial, rabbits consumed a greater quantity of the thyme-containing diets than of the control diet. This study suggests that thyme might be a useful additive to increase acceptability of rabbit diets, particularly when ingredients of low palatability are used.

Carob meal, prepared from the seedpods of the carob tree (*Ceratonia siliqua*), is often used in Italy and other southern European countries to increase the palatability of rabbit diets. The carob is a leguminous tree, grown in the Mediterranean area. The pods and seeds (Fig. 14.15) are rich in sugar and are used as a chocolate substitute. The attractive taste and aroma of the carob meal impart positive effects on the palatability of diets containing it.

E. Pellet Binders

Good-quality pellets and a low content of fines are desirable for rabbits. With poor-quality pellets that crumble and produce a lot of dust or fines, rabbits waste large amounts of feed by scratching it out of the feeders. Pellet binders can aid in producing a hard, firm pellet. Bentonite, a type of clay, is probably the most commonly used pellet binder, at a level of about 2% of the diet. Grobner *et al.* (1983) evaluated the effect of 5% dietary sodium bentonite on rabbit performance and incidence of diarrhea, in response to concerns of rabbit raisers that bentonite in the feed might be causing cecal impaction. No effects of bentonite on growth rate were seen (Table 14.37). There was a slight increase in the incidence of cecal impaction. Because the level of bentonite was deliberately selected to be higher than that used as pellet binder, and no significant adverse effects were seen, it was concluded that bentonite is a suitable pellet binder for use in rabbit feeds.

F. Acidifying Agents

The pH of the hindgut increases during an enteritis episode (see Chapter 12). It is not entirely clear if the change in acidity precedes the enteritis or is a consequence of it. Morisse *et al.* (1985) hypothesized that a diet low in fermentable carbohydrate results in a lowered VFA production in the cecum, causing the pH to increase, followed by a proliferation of *E. coli* and *Clostridium* organisms. Morisse *et al.* (1979) found that administering acid in the drinking water increased the acidity of the cecum and reduced the incidence of enteritis. If it is advantageous to increase the acidity of the digestive tract, there are several organic acids that can be used as feed additives. Falkowski and Aherne (1984) reported on the effectiveness of fumaric and citric acids as feed additives in diets for baby pigs. The addition of 1% or 2% fumaric or citric acid had a slight

TABLE 14.37

Effect of 5% Dietary Sodium Bentonite on Performance of Weanling Rabbits[a]

Treatment	Average daily gain (g)	Feed/gain	Mortality (%)	Cecal impaction (%)
20% Alfalfa diet	38.7	2.57	23.2	2.9
20% Alfalfa diet + bentonite	37.5	2.64	23.8	11.4
54% Alfalfa diet	38.7	3.30	18.6	0
54% Alfalfa diet + bentonite	36.1	3.31	29.9	5.7

[a]From Grobner *et al.* (1983).

beneficial effect on growth rate and feed efficiency. The effectiveness of these additives in rabbit diets has not been evaluated, but would appear to be worthy of investigation.

G. Herbs

There is little scientific information on the effect of various herbs on rabbit performance or health. As previously mentioned, Fekete and Lebas (1983) observed that thyme is stimulatory to feed intake in rabbits. King (1983) tested the effect of ginseng extract when offered in the water on growth of weanling rabbits. There was a slight effect on growth, with average daily gain of 21.9 g for rabbits receiving ginseng as compared to 20.5 g for controls receiving water.

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15

Toxins in Feeds

Most feedstuffs contain factors that can be toxic to animals. Cheeke and Shull (1985) define a toxin (also referred to as a toxicant) as a substance that, under practical conditions, can impair some aspect of animal metabolism and produce adverse biological or economic effects in animal production. There are few if any feed ingredients that do not contain substances that are potentially toxic to animals. In many cases, the toxins do not represent a significant hazard, because they are present at low concentration, are inactivated during feed processing, or are detoxified by animals.

I. NATURAL VERSUS SYNTHETIC TOXINS

The only toxins in rabbit diets that are usually of concern are natural substances occrring in feeds. Synthetic substances such as pesticides, herbicides, and other agricultural chemicals as contaminants of feeds have rarely if ever been linked to any problem in rabbit production.

Why do plants contain toxins? It appears that toxins have evolved as defense mechanisms of plants against diseases and being eaten by herbivores such as insects and other animals. Upon reflection, it is apparent that a plant that did not contain any toxins would be unlikely to survive. Insects and animals would relish it, preventing it from reproducing, and the plant would become extinct. Humans have developed crops that have very low levels of toxins, but they can survive only with our help. We protect these plants against pests by cultivation and spraying with pesticides, fungicides, and antibacterial agents. Without human involvement, corn, wheat, lettuce, and so on could not survive and would quickly become extinct in only a few growing seasons. Natural toxins are nature's pesticides (Fig. 15.1).

Animals possess enzymes, particularly in the liver, that can inactivate many natural toxins. As plants develop compounds that deter predators, the insect and mammalian predators evolve detoxification mechanisms. This process is called coevolution. It is most advanced in the insect world, because of the short generation interval and huge numbers of organisms involved. If 99.995% of a popula-

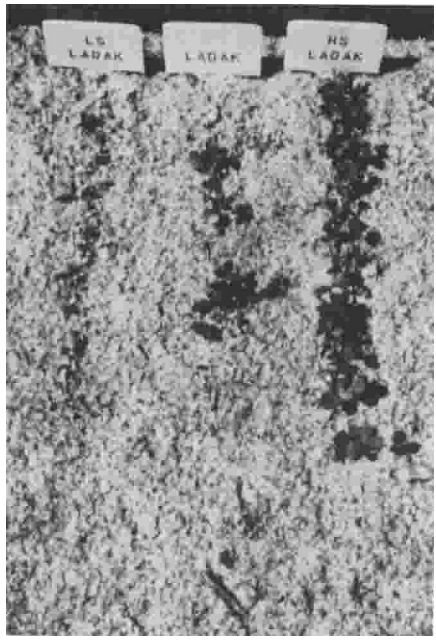


Fig. 15.1 Natural toxins are nature's pesticides. Alfalfa seedlings of a low-saponin selection of the Ladak cultivar have been decimated by the pea aphid (left), while seedlings of a high-saponin strain are untouched (right). Selection of crops for increased resistance to pests almost inevitably reduces their feeding value for animals. Conversely, selection of crops for increased feeding value usually reduces their resistance to pests and increases the need for pesticide use. (Courtesy of Dr. E. L. Sorensen, Kansas State University.)

tion of flies is susceptible to DDT, and only 0.005% have an enzyme that detoxifies DDT, it does not take long for the resistant group to become dominant when the population is sprayed with DDT. On a longer time scale, mammals can evolve similar resistance. As an example, some plants in western Australia contain a deadly poison, fluoroacetate (also known as compound 1080, widely used in the past as a coyote poison in the United States). Kangaroos and opossums in western Australia are highly resistant to 1080, having enzymes that detoxify it, whereas the same species of animals in eastern Australia, which have not been exposed to the 1080-containing plants, are highly susceptible (King *et al.*, 1978). Coevolution in the insect world has resulted in some insects now having a metabolic requirement for certain plant toxins. The cinnibar moth, a species that feeds on alkaloid-containing *Senecio* species (e.g., tansy ragwort), requires these alkaloids for the synthesis of essential hormones, and cannot survive on plants that do not contain these alkaloids. Some plants can even fight off other plants with chemicals! The black walnut produces a compound called

juglone, which is secreted from its roots; this compound inhibits the growth of other plants, freeing the black walnut tree from competition for nutrients. This is known as allelopathy.

Selection of crops for low levels of toxins has been successful. Examples of some include low-saponin alfalfa, low-gossypol cotton, low-glucosinolate rapeseed, and low-trypsin inhibitor triticale. As a general rule, those plants selected for low toxin levels have a higher feeding value for animals, but are more difficult to grow than regular varieties, requiring more pesticide application because they lack nature's pesticides.

Further information on the fascinating roles of plant toxins in deterrence of herbivores and on the processes of coevolution can be found in books by Cheeke and Shull (1985), Grant (1984), and Rosenthal and Janzen (1979).

II. METABOLISM OF TOXINS BY ANIMALS

Most toxins are fat-soluble substances. Detoxification reactions involve modification of the chemical structure of the toxins to make them water soluble, allowing excretion in the urine. The liver is the major site of this metabolism, involving a set of enzymes variously known as the hepatic drug-metabolizing enzyme system, the cytochrome *P*-450 system or the mixed-function oxidase system. In this system a hydroxyl (-OH) group is added to an aromatic structure. The hydroxyl group is chemically reactive, and can react with water-soluble substances such as glutathione, glucuronic acid, and certain amino acids, resulting in the toxin molecule becoming water soluble and excretable in the urine. This process of reacting with another compound via the hydroxyl group is called conjugation. There are marked animal species differences in susceptibility to different toxins. This is largely a result of differences in liver-detoxifying enzyme activity.

III. CLASSES OF NATURAL TOXINS

Cheeke and Shull (1985) have classified natural toxins into the following categories:

1. Alkaloids
2. Glycosides
3. Proteins
4. Amino acids
5. Carbohydrates
6. Lipids
7. Glycoproteins
8. Glycolipids
9. Metal-binding substances
10. Phenolics
11. Mycotoxins
12. Miscellaneous toxins

Those toxin categories that have significance in rabbit nutrition will be discussed.

A. Alkaloids

Alkaloids are alkaline substances that contain nitrogen. They usually are bitter tasting, and most are toxic. They are very widely distributed in the plant kingdom.

Pyrrolizidine alkaloids (PA) are among the most toxic alkaloids. They are hepatotoxins, causing irreversible liver damage. Plants containing PA include pasture weeds of the *Senecio* genus (e.g., *S. jacobaea* or tansy ragwort), *Crotalaria* species, which are broad-leaved legume weeds, and comfrey (*Symphytum officinale*), an herb and forage plant. *Crotalaria* seeds may be contaminants of grain used in rabbit diets, while comfrey is often deliberately fed as a green feed.

The PA are metabolized in the liver to very reactive compounds called pyrroles. The pyrroles react with DNA and enzymes, interfering with cell division and enzymatic functions of the liver. The liver becomes small and fibrotic. Signs of toxicity are those of liver failure, and include jaundice, accumulation of fluid in body cavities (ascites), and neurological signs (abnormal behavior). The livers of PA-poisoned animals may accumulate high levels of copper, and in some cases, chronic copper toxicity develops as a result of PA exposure.

There are considerable species differences in susceptibility to PA. Among livestock, cattle and horses are highly susceptible, while sheep and goats are very resistant to PA toxicosis (Cheeke and Shull, 1985). Rabbits are also quite resistant (Pierson *et al.*, 1977), probably because of efficient PA excretion in the urine (Swick *et al.*, 1982). Grobner *et al.* (1985) fed comfrey, a PA-containing plant, to rabbits for 4 months and observed no signs of toxicity or elevations in liver copper. Swick *et al.* (1982) found that feeding a source of *Senecio* PA to rabbits in a diet containing 100 ppm added copper resulted in elevated liver copper concentration compared to controls not fed PA.

Comfrey contains at least eight PA (Culvenor *et al.*, 1980). Hirono *et al.* (1978) fed comfrey to rats; with dietary levels of 0.5% comfrey root and 8% comfrey leaves, liver cancer was produced. While it is not advisable for humans to consume comfrey because of its hepatotoxic and carcinogenic properties, it does not appear to represent a hazard to rabbits because of their lack of sensitivity to PA.

Another class of alkaloids found in feeds is the ergot alkaloids, produced by fungi that parasitize the seed heads of various grasses and grains. The term "ergot" is used to refer to the purplish black structure formed in the seed head (Fig. 15.2). Fungal spores infect the seed head as it is flowering, and grow to produce the ergot. Cool, damp weather delays pollination and favors infection of grains with ergot fungi. Some grains, such as rye and triticale, are highly suscep-

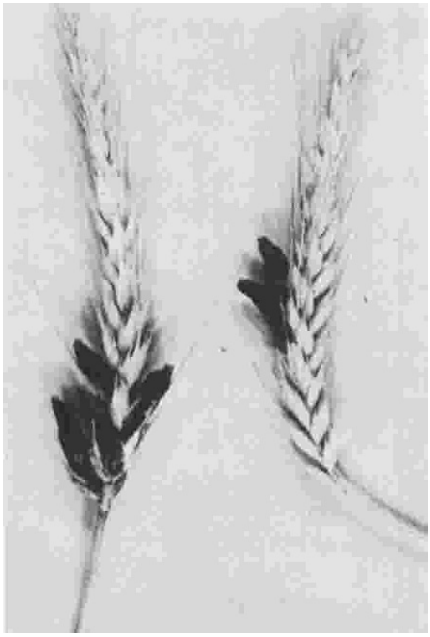


Fig. 15.2 Ergot infection of triticale seed heads. The purplish black ergot body contains toxic alkaloids.

tible to ergot infection because they are cross-pollinated, and have an extended flowering period. Ergot may enter the feed of animals when ergotized grains are used in feed preparation. Levels of 0.1% ergot in mixed feeds are sufficient to have detrimental effects on animals.

Signs of ergot toxicity are a result of the effect of ergot alkaloids in stimulating smooth muscle contraction. This causes restriction of the blood supply to the extremities (legs, ears), leading to death of these tissues and gangrene. Early signs of ergot poisoning are lameness and stamping of the feet, indicative of pain. Reproductive problems, including abortion and depressed lactation, also occur.

Lupines (*Lupinus* species) are grown as grain crops in Europe, Australia, and some parts of the United States. Lupines contain quinolizidine alkaloids. Most varieties of lupines currently grown have been selected for low alkaloid levels, and so are unlikely to cause toxicity problems.

Potato and tomato vines contain steroid alkaloids that can cause poisoning. Green potato tubers have a high alkaloid content. These products should not be fed to rabbits.

Red clover forage may be infected with a fungus causing black patch disease. Hay made from infected clover can be toxic, causing weight loss, abortion, and

profuse salivation. The condition in cattle and horses is called slobbers. The causative agent has been identified as an indolizidine alkaloid called slaframine. Guinea pigs have been used as experimental animals in studies of slaframine metabolism; they show profuse salviation after receiving the alkaloid.

Tall fescue is a vigorous perennial grass widely grown as a forage. It contains a variety of alkaloids, including some PA apparently produced in association with fungal infection of the grass. Daniels *et al.* (1984) in Arkansas have shown that administration of toxic tall fescue extracts to pregnant rabbits caused an increased respiration rate, abortion, stillbirths, and agalactia (lack of milk production).

B. Glycosides

Glycosides are toxic substances containing a carbohydrate linked to a toxic noncarbohydrate substance by an ether bond. The noncarbohydrate compound is called an aglycone. Glycosides are found in various plants; when the plant tissue is damaged by wilting, freezing, or mastication, plant enzymes are released that hydrolyze glycosides, releasing the toxic aglycones.

Cyanogenic glycosides are those that yield hydrogen cyanide (prussic acid) when the glycoside is hydrolyzed. Plants noted for their cyanide-producing potential are forage sorghums (Sudan grass, Johnson grass), cassava, linseed meal, white clover, and the seeds of apples, almonds, peaches, and apricots. These seeds contain laetrile, a cyanogenic glycoside that at one time was claimed to have anticancer properties, but this has been disproven. The main rabbit feedstuffs likely to have toxic levels of cyanide are the leaves and roots of cassava. Cassava roots can be processed to eliminate the cyanide. If they are macerated or grated, an enzyme is released that breaks the glycoside down, yielding cyanide. The cyanide can be removed by soaking the cassava in water, or by sun-drying the material.

Glucosinolates are glycosides with sulfur-containing aglycones, which are goitrogenic, causing inhibition of the thyroid gland. They occur mainly in plants of the genus *Brassica,* such as cabbage, kale, rape, mustard, and turnips. The occurrence of goitrogens in plants was first demonstrated in 1928, when Chesney *et al.* (1928) observed that prolonged feeding of cabbage to laboratory rabbits resulted in goiter (enlarged thyroid gland). It is unlikely that rabbits would normally be fed sufficient cabbage or other *Brassica* greens to cause goiter. Rapeseed meal contains glucosinolates at a sufficient level to cause enlarged thyroids and growth depression. However, many of the rapeseed cultivars now grown are of the low-glucosinolate type, so the meal from these varieties (canola meal) is nontoxic, and is a satisfactory protein supplement for rabbits (Throckmorton *et al.*, 1980).

Some plants contain cardiac glycosides, which may on occasion be important

in rabbit nutrition. The garden foxglove (*Digitalis purpurea*) contains potent cardiac glycosides that are used in medicine (digitalis drugs—e.g., digitonin). Feeding foxglove leaves (Fig. 15.3) to rabbits will kill them. Oleander (*Nerium oleander*) is an ornamental shrub widely grown in the southern United States. It contains potent cardiac glycosides; a single leaf is sufficient to kill a rabbit. Milkweeds (*Asclepias* species) contain cardiac glycosides, which can poison rabbits if they are fed hay or straw contaminated with milkweed. Templeton (1968) termed this condition "head-down disease." An interesting example of coevolution is that of the larvae of the monarch butterfly, which feed on milkweeds and accumulate the glycosides in their tissues. These compounds protect the butterfly from birds. The glycosides cause birds to vomit and avoid the monarch butterfly thereafter.

Saponins are glycosides found in legumes such as alfalfa. They are bitter substances, and are major factors in reducing the palatability of alfalfa to animals (Cheeke and Shull, 1985). Low-saponin strains of alfalfa have been developed. Low-saponin alfalfa meal in the diet at various levels has been shown to be more palatable and to give better growth responses with rats and swine (Cheeke *et al.*, 1977, 1978; LeaMaster and Cheeke, 1979) than similar alfalfa with a high-saponin content. The better growth performance appears to be primarily a result



Fig. 15.3 The leaves of the garden foxglove contain a potent cardiac glycoside which is very poisonous to rabbits and other animals.

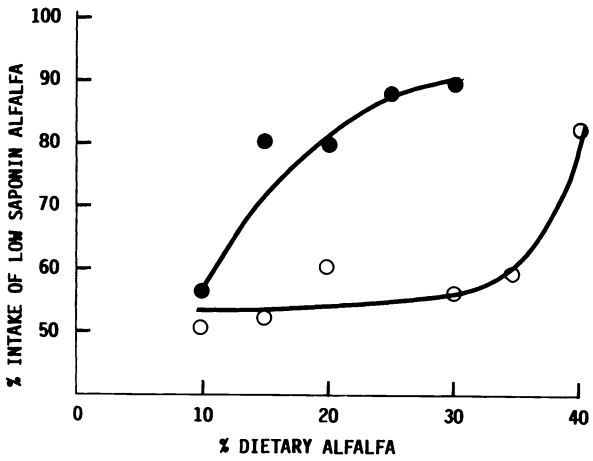


Fig. 15.4 Rabbits (○) are quite tolerant of the bitterness of saponins in alfalfa, and do not show an aversion to high-saponin alfalfa until a dietary level of 35% alfalfa. Consumption by rats (●) is shown for comparison. (Data from Cheeke *et al.*, 1977.)

of increased feed intake due to the higher palatability of the low-saponin alfalfa meal.

Cheeke *et al.* (1977) evaluated low- and high-saponin alfalfa meal with rabbits for palatability and feed preference. Rabbits showed no discrimination between diets containing high- or low-saponin alfalfa until dietary levels of 35% alfalfa (Fig. 15.4). Above this level they preferred the low-saponin type. This indicates a much higher tolerance to saponins in terms of palatability response than rats or swine, which prefer the low-saponin type at dietary alfalfa levels of 10% (Cheeke *et al.*, 1977) and 1% (LeaMaster and Cheeke, 1979), respectively. Thus it appears that rabbits are more tolerant of saponins in alfalfa than are other nonruminants, including poultry (Cheeke *et al.*, 1983). The saponin content of alfalfa increases with high environmental temperatures, so is usually higher for second-cutting than for first- and third-cutting alfalfa. This may be a factor in the generally poorer animal performance with second-cutting alfalfa (Cheeke and Shull, 1985).

Saponins form insoluble complexes with cholesterol, and reduce cholesterol absorption and serum cholesterol levels (Malinow *et al.*, 1979). This may account for the serum cholesterol-lowering property of dietary alfalfa in rabbits (Barichello and Fedoroff, 1971). Cheeke (1970, 1976) suggested that feeding sources of saponins might be a means of lowering the cholesterol content of meat. However, Holmes *et al.* (1984) observed no differences in the cholesterol levels of meat from rabbits fed low-, medium-, and high-alfalfa diets.

The yucca plant has a high saponin content of a type known as sarsaponins. These have been suggested as having beneficial effects in control of environmen-

tal ammonia levels in broiler houses (Johnston *et al.*, 1981), either by feeding the sarsaponin in the diet or sprinkling it on the litter. The effectiveness of this treatment in rabbits has not been evaluated.

Phytoestrogens are glycosides in plants that have estrogenic activity. Subterranean clover (*Trifolium subterran*), a widely grown forage crop in Australia, is well known for its estrogenic effects on livestock. The symptoms of "clover disease" include a dramatic decrease in the fertility of sheep, and signs of feminization in males such as teat enlargement. Alfalfa contains a phytoestrogen called coumestrol that has sometimes caused decreased fertility and irregular estrous cycles in dairy cattle. The effects of phytoestrogens in alfalfa and other legumes on rabbits has not been investigated, but because of the responses seen with other livestock, possible adverse effects on reproduction in rabbits could be anticipated.

C. Proteins and Amino Acids

Two important types of toxic proteins in feeds are trypsin inhibitors and lectins. They are both commonly found in legume seeds, particularly beans of various types.

Raw soybeans contain trypsin inhibitors, toxic proteins that inhibit the digestive enzyme trypsin and other protein-digesting enzymes such as chymotrypsin. Feeding raw soybeans to nonruminants such as swine and poultry results in poor animal performance, including reduced growth, poor feed conversion, and, in some species, an enlarged pancreas. Pancreatic enlargement with the feeding of raw soybeans is related to the normal pancreas size (Table 15.1). Those

TABLE 15.1

Relationship between Pancreatic Size and Hypertrophic Response to Trypsin Inhibitors

Species	Pancreas weight (as % of body weight)	Pancreatic hypertrophy[a]
Mouse	0.6–0.8	+
Rat	0.5–0.6	+
Chick	0.4–0.6	+
Rabbit	0.22–0.27[b]	–
Dog	0.21–0.24	–
Human	0.09–0.12	?
Calf	0.06–0.08	–

[a]Liener and Kakade (1980).
[b]Latimer and Sawin (1957).

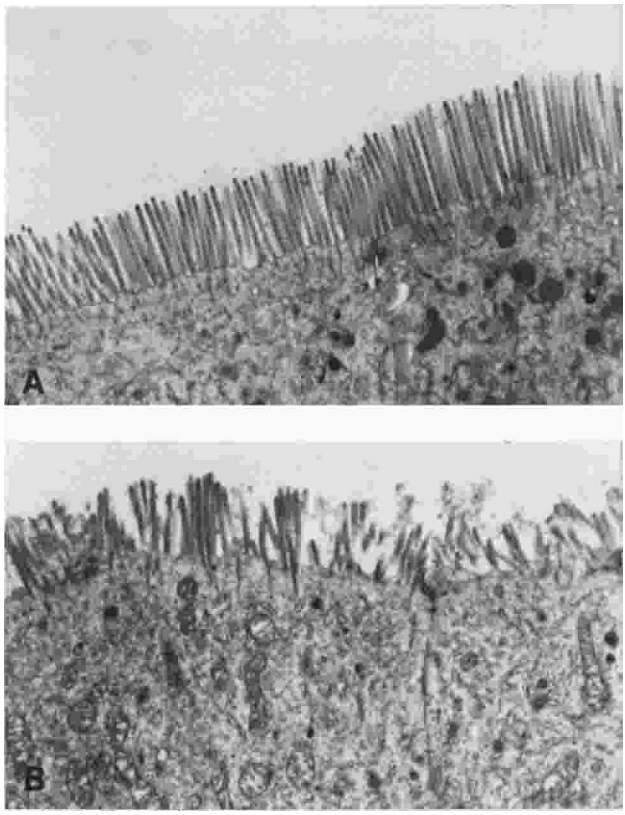


Fig. 15.5 Effect of lectins on the microvilli of the intestinal mucosal cells. In contrast to the normal microvilli (A), the microvilli from a section of the small intestine of a pig fed raw kidney beans have been extensively damaged (B), markedly impairing digestion and absorption. (Courtesy of R. Begbie and T. P. King, The Rowett Research Institute, Aberdeen, Scotland.)

animals that normally have a large pancreas (>0.3% of body weight) develop pancreatic enlargement (hypertrophy) when fed trypsin inhibitors, whereas those with a normal pancreas size of less than 0.3% of body weight do not show pancreatic hypertrophy. Sanchez *et al.* (1984) attempted to determine the effect of raw soybeans on pancreas weight in rabbits, but found that the diffuse nature of the gland prevented accurate measurement of pancreas weight. Microscopic evaluation did not reveal any discernible abnormalities in the pancreatic tissue.

Raw soybeans inhibit growth in rabbits (Sanchez *et al.*, 1984). Heat treatment, such as by extrusion, eliminates the toxic effect by destruction of the heat-labile trypsin inhibitors. Rabbit trypsin and chymotrypsin are very sensitive to soybean protease inhibitors (Rascon *et al.*, 1985).

Lectins are another type of toxic protein in beans, particularly in kidney beans. Lectins bind to the intestinal mucosa, and cause extensive damage to the microvilli (Fig. 15.5). This results in impaired nutrient absorption and invasion of the gut lining by pathogenic bacteria. Sanchez *et al.* (1983) observed that feeding raw pinto beans in the diet of weanling rabbits produced marked growth depression and induced diarrhea. Heat treatment of the beans partially overcame the effects.

Other plants that contain lectins include the castor bean (*Ricinus communis*) and the black locust (*Robinia pseudoacacia*). The seeds and foliage of castor beans are highly toxic; the lectin they contain, ricin, is one of the most toxic substances known. The black locust is a leguminous tree that is of some interest as a potential forage source. It is grown quite extensively in China as a source of leaf meal for poultry feeding. Harris *et al.* (1984) reported that replacement of 40% alfalfa meal with black locust leaf meal resulted in pronounced growth depression of weanling rabbits, and reduced crude protein digestibility (Table 14.11). In a feed preference study with various forages, Harris *et al.* (1983) found black locust leaves to be of very low palatability to rabbits. It is likely that these negative effects are associated with the black locust lectins.

Plants contain a number of amino acids that are toxic to animals. The most significant of these is mimosine, an amino acid in leucaena (*Leucaena leucocephala*). Leucaena is widely grown in tropical countries as a fuel and forage crop. It is a tree legume, which can be kept in a shrubby form by repeated cutting. The leaves of leucaena are high in protein, and are highly palatable to rabbits.

Mimosine toxicity causes alopecia (hair loss) in animals (Fig. 15.6), as well as skin lesions and poor growth. Mimosine is converted to a metabolite, dihydroxypyridone (DHP), in the rumen and also by plant enzymes in the leaves them-

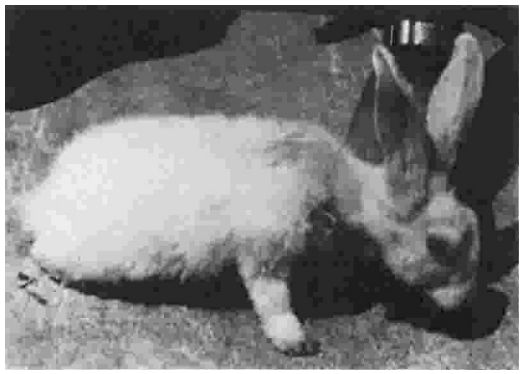


Fig. 15.6 Mimosine toxicity in a rabbit fed *Leucaena leucocephala*, showing alopecia (loss of hair) and dermatitis.

selves (Lowry *et al.*, 1983). Tangendjaja *et al.* (1986) showed that conversion of mimosine to DHP by dipping leucaena in hot water for 10 min, followed by sun-drying, did not eliminate the toxicity of leucaena meal to rabbits.

Brassica forages, such as kale and rape, contain a toxic amino acid, *S*-methyl cysteine sulfoxide (SMCO). This amino acid is known as the brassica anemia factor. In ruminants, SMCO is metabolized in the rumen to dimethyl disulfide, which is absorbed. This compound is an oxidant that damages the red blood cell membranes, causing hemolysis and excretion of hemoglobin pigments in the urine. In rabbits, it is likely that SMCO is absorbed before reaching the site of fermentation (the cecum), so it is probable that the brassica anemia factor is not toxic to rabbits. This is corroborated by the reports of Greenhalgh *et al.* (1969) and Partridge *et al.* (1985), indicating that kale SMCO does not cause anemia in rabbits.

D. Tannins

Tannins are phenolic compounds found in a number of feedstuffs. The term "tannin" is derived from the use of plant extracts containing these compounds for the tanning of leather. Oak leaves were at one time used for this purpose. Tannins react with proteins to modify their structure and make them resistant to digestion. Tannins are astringent (unripe fruit is rich in tannin) because they react with proteins in taste buds in the mouth. These compounds play a major role in protecting plants from animals, insects, and diseases. The durability of many types of wood is due to the presence of tannins, which inhibit growth of fungi and bacteria. In animal nutrition, the major concerns with tannins are that they have adverse effects on feed intake, they reduce availability of proteins, and they may impair some aspects of animal metabolism.

A grain well known for its tannin content is sorghum or milo. Milo grain is produced in an open panicle that is very susceptible to predation by wild birds. Bird-resistant cultivars of milo have been developed that are high in tannin content and unpalatable to wild birds. Of course, they are also of low palatability to domestic animals. Most high-tannin sorghum varieties have brown or pigmented seeds. The yellow milo grown in the United States has a low tannin content, and is similar to corn in nutritional value.

Sunflower meal and leaves contain tannins. Harris *et al.* (1981) found that sunflower leaf meal gave poor results when used at a level of 40% in a diet for weanling rabbits, as a replacement of alfalfa meal. Average daily gain was 16 g for rabbits fed the sunflower leaf meal diet and 40 g for the control group. Pronounced hair chewing (Fig. 15.7) was noted in the animals fed the sunflower leaf meal diet; this probably resulted from the induction of a protein deficiency by the tannins in sunflower leaves.

Forages contain tannins and other phenolic compounds. These phenolics are

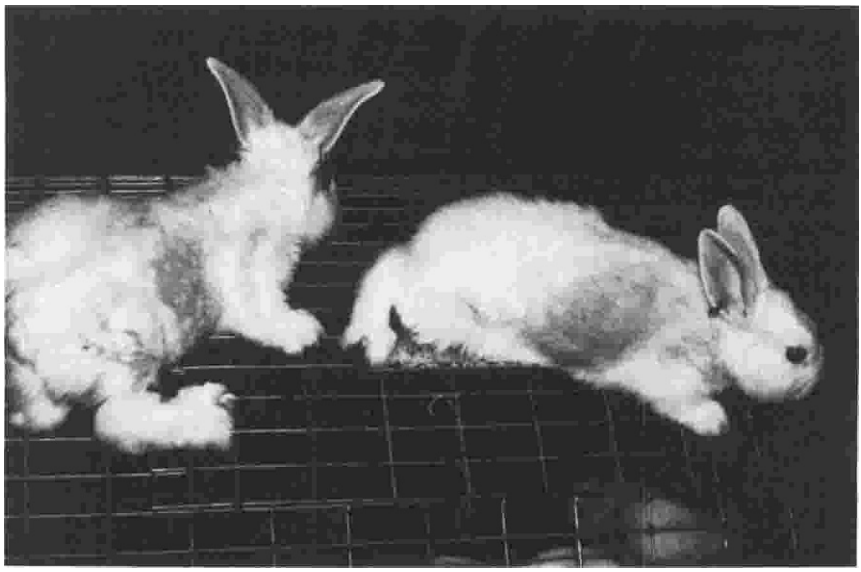


Fig. 15.7 Hair pulling in rabbits fed a diet containing sunflower leaf meal. Sunflower leaves contain tannins, which bind protein and create a protein deficiency.

conjugated with amino acids in the liver and excreted in the urine. The reddish orange pigmentation of rabbit urine appears to be in large part due to the excretion of phenolics.

Lespedeza, a forage grown in the southern United States, has a high tannin content. It has a low digestibility, particularly of protein, because of the adverse effects of tannins.

An interesting effect of some phenolic compounds in plants is that they may influence the reproductive activity of animals. Berger *et al.* (1977, 1981) reported that the reproductive behavior of meadow voles is controlled by dietary cues. In the spring, new grass contains a phenolic compound called 6-methoxybenzoxazolinone (6-MBOA), which triggers reproductive activity in voles, stimulating ovarian development. 6-MBOA is chemically similar to melatonin, a hormone with a role in the regulation of seasonal breeding behavior. In late summer, plants contain other phenolic compounds (e.g., cinnamic acid) that depress reproductive activity. Limited evidence suggests that these compounds may have physiological activity in rabbits (M. A. Grobner, P. R. Cheeke, and N. M. Patton, unpublished observations). This could have important implications. For example, first-cutting alfalfa might have stimulatory effects on reproduction, while third- or fourth-cutting alfalfa might have adverse effects. This hypothesis requires experimental verification. Wallage-Drees (1983) observed that wild rabbits begin breeding abruptly when succulent plant species begin to grow,

regardless of the time of year. This could suggest an involvement of dietary cues, or conversely, could reflect an improvement in dietary energy intake. Wallage-Drees (1983) concluded that the growth of grasses is a trigger for the first successful conceptions of the breeding season. If indeed these phenolic compounds in early grass growth are reproduction stimulators, the use of sprouted grains as a supplement might be an effective means of stimulating reproduction of rabbits when breeding depression occurs. Epstein *et al.* (1986) found that a short photoperiod and cool temperatures maximized 6-MBOA production in sprouted wheat.

Gossypol is a phenolic substance in cottonseed meal. It causes various adverse effects on animals, including depressed appetite, weight loss, lung and heart lesions, and anemia. In chickens, gossypol causes an olive green pigmentation of the egg yolk (Fig. 15.8). Gossypol has been evaluated in China as a birth control agent, following the discovery that low dietary gossypol levels cause infertility of men. Administration of gossypol to male rats and hamsters caused sterility (Chang *et al.*, 1980), whereas male rabbits were not affected. McNitt *et al.* (1982) observed no adverse effects on semen quality or fertility when bucks were fed a high cottonseed meal level (20%) for an extended period. Thus it appears that cottonseed meal can be used in rabbit diets without adversely affecting reproduction. McNitt (1981) recommended that with meal containing 0.04% free gossypol or less, up to 15% cottonseed meal can be safely used in rabbit diets. This corresponds to a level of 60 ppm gossypol as an upper limit. Levels above 100 ppm (0.01% free gossypol) are likely to be toxic. Free gossypol is that which is not bound to protein. The bound form is nontoxic, so analytical results are usually expressed in terms of free gossypol.

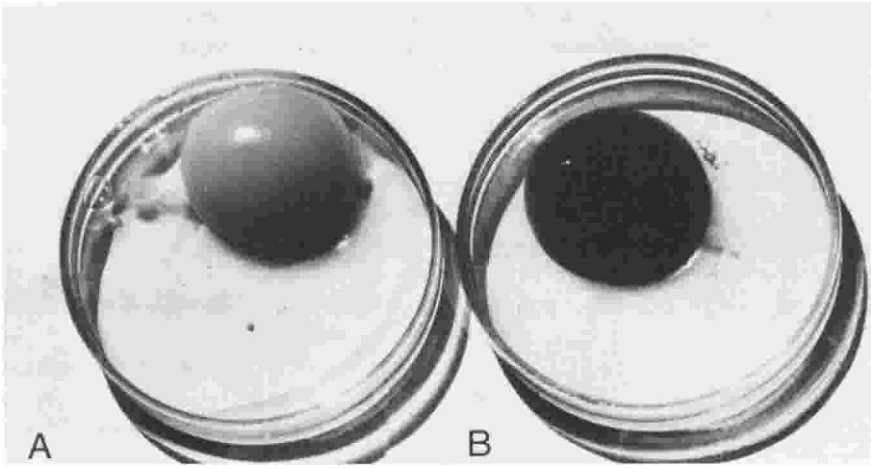


Fig. 15.8 One of the most sensitive indicators of adverse effects of gossypol is the olive green yolk in eggs from hens fed cottonseed meal. (A) Normal control; (B) control plus gossypol.

E. Mycotoxins

Mycotoxins are toxic substances produced by molds growing on plants and in feeds during storage. Since the early 1960s, when mycotoxins were first recognized, they have been of increasing concern in animal nutrition, both in terms of toxicity to animals and presence of mycotoxins in meat, milk, and eggs.

Aflatoxins are mycotoxins produced by the molds *Aspergillus flavus* and *Aspergillus parasiticus*. They were discovered in 1960, during an investigation of a huge loss in Great Britain of turkeys that had been fed moldy peanut meal. Aflatoxins are produced in corn and other grains both before and after harvest. Certain environmental conditions, such as drought stress and insect damage, predispose crops to infection with fungi. Storage of feed ingredients under warm, humid conditions can result in explosive growth of *Aspergillus* fungi.

Aflatoxins are metabolized in the liver, and this organ is the principal tissue affected by toxicity. Acute aflatoxin poisoning causes extensive liver damage and death from liver failure. There are marked species differences in susceptibility to aflatoxins. Sheep and rats are much less sensitive than rabbits and ducklings. These differences are related to the activity of liver enzymes, which metabolize aflatoxin to more toxic metabolites. Rabbits have a very high activity of these enzymes. Clark *et al.* (1980, 1982) studied chronic aflatoxicosis in rabbits. Signs of toxicity included loss of appetite, reduced weight gain, lethargy, emaciation, dehydration, jaundice, and death. Extensive liver damage was noted. Daily doses of 0.025 and 0.0375 mg/kg body weight aflatoxin B_1 for 24 days caused no discernible problems, whereas doses of 0.05 and 0.0625 mg/kg were toxic. Naturally occurring aflatoxicosis in rabbits in the United States has not been reported, but in India, 4000 Angora rabbits in a 7000-animal herd died from aflatoxin contamination of the feed (Mehrotra and Khanna, 1973). Levels of more than 2 ppm aflatoxin in the diet are likely to cause toxicity problems in rabbits.

Several other mycotoxins are important contaminants of feeds. Zearalenone is a toxin produced by *Fusarium* fungi that may infect grains. Swine are especially sensitive to zearalenone, which causes hyperestrogenic effects such as vaginal prolapse, enlargement of the vulva, and swelling of the mammary glands. Zearalenone is toxic to rabbits and causes hyperestrogenic effects as it does in swine (Pompa *et al.*, 1986). These workers showed that the major metabolite of zearalenone in rabbits is α-zearalenol, which has pronounced estrogenic activity. Administration of a total dose of 1 mg zearalenone per kilogram of body weight to female rabbits over a 12-day period resulted in a significant increase in uterine weight. Levels of zearalenone in feed of 1-2 ppm could presumably interfere with rabbit reproduction when fed for only a few (8–10) days (Pompa *et al.*, 1986).

Another group of toxins produced by *Fusarium* species are the trichothecenes.

One of the most important of these is T-2 toxin. T-2 toxin produces lesions of the mouth and digestive tract, feed refusal, vomiting, diarrhea, and hemorrhaging. Gentry (1982) studied T-2 toxicity in rabbits, and found marked impairment of blood-clotting mechanisms. The T-2 toxin did not appear to function as a vitamin K antagonist. Another trichothecene of concern is vomitoxin. Swine are particularly sensitive. Contamination of the feed with vomitoxin results in feed refusal, or if feed is consumed, vomiting and gastric irritation. Vomitoxins have caused losses of swine and poultry in the United States, but have not been implicated in toxicoses in rabbits. Khera *et al.* (1986) studied the effect of vomitoxin (4-deoxynivalenol) on reproduction in rabbits. A level of 0.024% vomitoxin in the diet caused a 100% incidence of fetal resorption. No teratogenic effects were observed. A no-observed-effect level was 0.6 mg vomitoxin per kilogram body weight, equivalent to 0.0015% vomitoxin in the diet.

Two other mycotoxins found in grains are ochratoxin and citrinin. Both of these toxins cause kidney damage. Hanika *et al.* (1984, 1986) administered citrinin to rabbits, and noted diarrhea and kidney damage.

Probably the major mycotoxin of concern in rabbit feeds is aflatoxin. The widespread occurrence of aflatoxin contamination of corn, soybeans, and cottonseed meal in the United States, and the high sensitivity of rabbits to aflatoxin, suggest that the potential for outbreaks of aflatoxicosis is ever present.

F. Other Toxins

Nitrates in feeds are sometimes of concern. Plants may accumulate nitrates when they are heavily fertilized with nitrogen, or stressed by drought. Nitrate accumulates mainly in vegetative tissue (leaves and stems) rather than in seeds. Levels of 0.5% (5000 ppm) nitrate in feeds are potentially dangerous, with acute poisoning likely if the level exceeds 1%. Acute toxicity involves interference with the ability of hemoglobin to transport oxygen in the blood, resulting in symptoms of labored breathing, bluish mucous membranes of the mouth, nose, and eyes, and rapid death. The blood is dark brown or chocolate-colored, because of the conversion of hemoglobin to methemoglobin. Chronic nitrate toxicity in livestock has been linked to reduced growth, abortions, and infertility. There are no specific data on these effects in rabbits.

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16

Ration Formulation

In formulating diets for livestock, the objectives should be to design diets that meet the nutrient requirements of the animals and return the maximum economic benefit to the livestock owner. In the case of animals raised for exhibition purposes or as pets, the economic factor is not as critical. Nevertheless, nearly all people who raise animals would like to use diets that meet the animals' needs and maintain them in good health, at a reasonable cost. Diets that meet the requirements, with neither nutrient deficiencies nor marked excesses, are said to be balanced. The following types of information are required to formulate diets: (1) the nutritional requirements of the animal; (2) the nutrient composition of the feedstuffs available; (3) the availability of nutrients in the feedstuffs; (4) nonnutrient characteristics of the feedstuffs, such as palatability and pelleting properties; and (5) the costs of available feedstuffs.

I. NUTRIENT REQUIREMENTS OF RABBITS

Factors influencing the requirements for nutrients have been discussed earlier in the appropriate chapters. In ration formulation, it is necessary to have specific numbers for major nutrients: are you formulating a diet to contain 16% crude protein or 18% crude protein? In some cases, where reasonable excess of a nutrient is neither harmful nor expensive, a minimum requirement can be stated and it is not of great concern if the requirement is substantially exceeded.

The standard sources of information on nutrient requirements for livestock are the National Research Council (NRC) publications in the series "Nutrient Requirements of Domestic Animals." The most recent "Nutrient Requirements of Rabbits" was published in 1977. The NRC requirements are given in Table 16.1. It is immediately apparent from the table that quantitative data on requirements, especially for functions other than growth, are lacking. Less apparent, but no less important, is the fact that many of the figures are derived from experiments conducted many years ago, using diets and with animal performance that are clearly inadequate by today's standards. In many cases, very small numbers of animals per treatment were used. In some cases purified or semipurified diets

that were unpalatable were used, resulting in very low growth rates even for the control animals. The French rabbit nutritionist Francois Lebas has established a set of nutrient requirements that is more closely oriented toward modern commerical rabbit production needs (Table 16.2).

In using nutrient requirement figures, a knowledge of what is truly important is needed. There is no point in trying to meet exactly the requirement for chlorine or riboflavin, for example. The chlorine requirement is met simply by using 0.5% added salt, and riboflavin is obtained by cecotrophy, so the likelihood of producing a riboflavin deficiency is remote. The nutrients of particular concern in rabbit diets are crude protein, digestible energy (DE), and indigestible fiber. As discussed earlier, there is no specific energy requirement in terms of kilocalories per unit diet, because over a wide range of energy levels, animals will adjust

TABLE 16.1

Nutrient Requirements of Rabbits Fed *ad Libitum*[a,b]

Nutrients[c]	Growth	Maintenance	Gestation	Lactation
Energy and protein				
Digestible energy (kcal)	2500	2100	2500	2500
TDN (%)	65	55	58	70
Crude fiber (%)	10–12[d]	14[d]	10–12[d]	10–12[d]
Fat (%)	2[d]	2[d]	2[d]	2[d]
Crude fiber (%)	16	12	15	17
Inorganic nutrients				
Calcium (%)	0.4	—[e]	0.45[d]	0.75[d]
Phosphorus (%)	0.22	—[e]	0.37[d]	0.5
Magnesium (mg)	300–400	300–400	300–400	300–400
Potassium (%)	0.6	0.6	0.6	0.6
Sodium (%)	0.2[d,f]	0.2[d,f]	0.2[d,f]	0.2[d,f]
Chlorine (%)	0.3[d,f]	0.3[d,f]	0.3[d,f]	0.3[d,f]
Copper (mg)	3	3	3	3
Iodine (mg)	0.2[d]	0.2[d]	0.2[d]	0.2[d]
Iron	—[e]	—[e]	—[e]	—[e]
Manganese (mg)	8.5[g]	2.5[g]	2.5[g]	2.5[g]
Zinc	—[e]	—[e]	—[e]	—[e]
Vitamins				
Vitamin A (IU)	580	—[e]	>1160	—[e]
Vitamin A as carotene (mg)	0.83[d,g]	—[h]	0.83[d,g]	—[h]
Vitamin D	—[i]	—[i]	—[i]	—[i]
Vitamin E (mg)	40[j]	—[e]	40[j]	40[j]
Vitamin K (mg)	—[k]	—[k]	0.2[d]	—[k]
Niacin (mg)	180	—[l]	—[l]	—[l]
Pyridoxine (mg)	39	—[l]	—[l]	—[l]
Choline (g)	1.2[d]	—[l]	—[l]	—[l]

(*continued*)

TABLE 16.1 (*Continued*)

Nutrients[c]	Growth	Maintenance	Gestation	Lactation
Amino acids (%)				
Lysine	0.65	—[i]	—[i]	—[i]
Methionine + cystine	0.6	—[i]	—[i]	—[i]
Arginine	0.6	—[i]	—[i]	—[i]
Histidine	0.3[d]	—[i]	—[i]	—[i]
Leucine	1.1[d]	—[i]	—[i]	—[i]
Isoleucine	0.6[d]	—[i]	—[i]	—[i]
Phenylalanine + tyrosine	1.1[d]	—[i]	—[i]	—[i]
Threonine	0.6[d]	—[i]	—[i]	—[i]
Tryptophan	0.2[d]	—[i]	—[i]	—[i]
Valine	0.7[d]	—[i]	—[i]	—[i]
Glycine	—[e]	—[i]	—[i]	—[i]

[a]National Research Council (1977).

[b]Percentage or amount per kilogram of diet.

[c]Nutrients not listed indicate dietary need unknown or not demonstrated. TDN, Total digestible nutrients.

[d]May not be minimum but known to be adequate.

[e]Quantitative requirement not determined, but dietary need demonstrated.

[f]May be met with 0.5% NaCl.

[g]Converted from amount per rabbit per day using an air-dry feed intake of 60 g/day for a 1-kg rabbit.

[h]Quantitative requirement not determined.

[i]Probably required, amount unknown.

[j]Estimated.

[k]Intestinal synthesis probably adequate.

[l]Dietary need unknown.

their voluntary feed intake to meet their energy needs. As a general rule, the DE should be in the range of 2500–3000 kcal/kg for rabbits. At lower levels, feed intake may be limited by gut capacity. At high energy levels, hindgut dysfunction may occur, with enterotoxemia or cecal impaction developing.

The level of indigestible fiber is important. Low levels of fiber are associated with cecal-colonic hypomotility and the development of diarrhea. Probably the best analytical measure of indigestible fiber is acid detergent fiber (ADF). A minimum level of 13% crude fiber or 21% ADF should be used for all classes of rabbits.

II. MATHEMATICS OF RATION FORMULATION

It is a routine practice to use computers in diet formulation. Programs are available for microcomputers for ration formulation. Modern feedmills are computerized, so that the entire operation, including the weighing out of ingredients,

TABLE 16.2

Nutrient Requirements of Rabbits Recommended by Lebas (1980)[a]

Nutrient	Class of rabbit				
	Growing 4–12 weeks	Lactation	Gestation	Maintenance	Does and litters fed one diet
Crude protein (%)	15	18	18	13	17
Amino acids (%)					
Sulfur amino acids	0.5	0.6	—	—	0.55
Lysine	0.6	0.75	—	—	0.7
Arginine	0.9	0.8	—	—	0.9
Threonine	0.55	0.7	—	—	0.6
Tryptophan	0.18	0.22	—	—	0.2
Histidine	0.35	0.43	—	—	0.4
Isoleucine	0.60	0.70	—	—	0.65
Valine	0.70	0.85	—	—	0.8
Leucine	1.05	1.25	—	—	1.2
Phenylalanine	1.20	1.40	—	—	1.25
Crude fiber (%)	14	12	14	15–16	14
Indigestible fiber (%)	12	10	12	13	12
Digestible energy (kcal/kg)	2500	2700	2500	2200	2500
Metabolizable energy (kcal/kg)	2400	2600	2400	2120	2410
Fat (%)	3	5	3	3	3
Minerals					
Calcium (%)	0.5	1.1	0.8	0.6	1.1
Phosphorus (%)	0.3	0.8	0.5	0.4	0.8
Potassium (%)	0.8	0.9	0.9	—	0.9
Sodium (%)	0.4	0.4	0.4	—	0.4
Chlorine (%)	0.4	0.4	0.4	—	0.4
Magnesium (%)	0.03	0.04	0.04	—	0.04
Sulfur (%)	0.04	—	—	—	0.04
Cobalt (ppm)	1	1	—	—	1
Copper (ppm)	5	5	—	—	5
Zinc (ppm)	50	70	70	—	70
Iron (ppm)	50	50	50	50	50
Manganese (ppm)	8.5	2.5	2.5	2.5	8.5
Iodine (ppm)	0.2	0.2	0.2	0.2	0.2
Vitamins					
Vitamin A (IU/kg)	6000	12,000	12,000	—	10,000
Carotene (ppm)	0.83	0.83	0.83	—	0.83
Vitamin D (IU/kg)	900	900	900	—	900
Vitamin E (ppm)	50	50	50	50	50
Vitamin K (ppm)	0	2	2	0	2
Vitamin C (ppm)	0	0	0	0	0
Thiamin (ppm)	2	—	0	0	2
Riboflavin (ppm)	6	—	0	0	4
Pyridoxine (ppm)	40	—	0	0	2
Vitamin B_{12} (ppm)	0.01	0	0	0	—
Folic acid (ppm)	1	—	0	0	—
Pantothenic acid (ppm)	20	—	0	0	—

[a]From Lebas (1980).

is computer controlled. The advantages of using computer formulation are that many simultaneous equations can be solved, allowing the calculation of the least expensive combination of ingredients that will meet the requirements. For each nutrient, a minimum and a maximum level can be specified. You might, for example, put 13% crude fiber as a minimum and 16% as a maximum. The level of ingredients can be controlled. You might want to use at least 10% wheat bran but not more than 25%. These minimum and maximum constraints can be specified. Normally, least-cost diet formulation is used, so that the least expensive ration is developed.

Diets can be hand-formulated, and because of the simple nutrient requirements of rabbits, it is probably adequate in many cases simply to calculate the composition using a hand calculator. The following example will illustrate the process:

Formulate a diet containing 18% crude protein, using 40% alfalfa meal, which is 16% crude protein (CP), and barley (11% CP) and soybean meal (45% CP) to make up the remainder of the diet. The diet will contain 0.5% trace mineralized salt.

Solution

The barley and soybean meal (SBM) will add up to 59.5%. The 40% alfalfa meal provides $40 \times 0.16 = 6.4\%$ CP. Therefore, the barley and SBM must provide $18 - 6.4 = 11.6\%$ CP.

Let the amount of barley $= x$.
Then the amount of SBM $= 59.5 - x$.
The amount of protein from barley $= 0.11x$.
The amount of protein from SBM $= 0.45\ (59.5 - x)$.
The sum of the barley and SBM protein is 11.6.
Therefore, $0.11x + 0.45(59.5 - x) = 11.6$

$$0.11x + 26.775 - 0.45x = 11.6$$

Solving for x: $-0.34x = 11.6 - 26.775$

$$= -15.175$$

Multiply by -1 to remove the negative signs:

$$(-1)\ (-0.34x) = (-1)\ (-15.175)$$

$$0.34x = 15.175$$

$$x = 15.175/0.34 = 44.6$$

Therefore, the amount of barley is 44.6% and the amount of SBM is $59.5 - 44.6 = 14.9\%$. The composition of the diet is:

Alfalfa meal	40%
Barley	44.6%
SBM	14.9%
Salt, trace mineralized	0.5%
	100.0%

This diet contains 18% protein. Our next concern is to see if it contains at least 13% crude fiber. The fiber contents of the ingredients are as follows: alfalfa 25%, barley 5.6%, and soybean meal 5.8%.

Alfalfa	40×0.25	$= 10$
Barley	44.6×0.056	$= 2.50$
SBM	14.9×0.058	$= 0.86$
		13.36

Similar calculations could be performed to calculate DE, calcium, and phosphorus levels. This simple diet is in fact adequate for rabbit production. Improvements might include adding molasses for palatability and improved pellet quality and a small amount of fat for increasing ease of pelleting. No mineral or vitamin supplement, besides trace mineralized salt, is needed for growing animals if good quality alfalfa meal is used. For lactating does, the addition of 1% dicalcium phosphate and a vitamin premix would be advisable.

III. OPEN VERSUS CLOSED DIET FORMULAS

A closed formula is one that is not altered to take into account changes in feedstuff prices. The diet calculated in the above example would be a closed-formula diet if a rabbit raiser requested this exact diet, month after month, with no change, even if barley became very expensive or cottonseed meal became much cheaper than soybean meal. If it were an open-formula diet, then it would be modified to take advantage of changing ingredient prices. Many rabbit raisers want a closed-formula diet, because they believe that changes in ingredients may have such adverse consequences as causing anorexia or an enteritis outbreak in their animals. In most cases, this is an unwarranted concern, and advantage should be taken of changes that would lower the diet cost.

IV. QUALITY CONTROL OF DIETS

Large, modern feed mills have laboratories in which feed ingredients are analyzed before they are used, and each batch of feed is checked before it leaves the plant, to make sure that nutrient specifications have been reached. Some ingredients are more likely to be variable than others. Soybean meal is a very standard product, while alfalfa can be quite variable. A large Italian feed mill specializing in rabbit feed uses four types of alfalfa in the formula. Thus, if there is a change in the quality of one type (e.g., sun-cured meal), it is unlikely to alter the total diet sufficienty to be detectable.

V. SPECIFIC PROBLEMS IN RABBIT RATION FORMULATION

Compared to other types of livestock, rabbits are fastidious with respect to their feed. They will sometimes refuse to consume a new batch of feed, or will scratch large quantities of it out of the feeders for no apparent reason. Obviously the animals can detect some abnormality with the feed that humans cannot detect. This situation may lead to some serious problems between rabbit raisers and feed manufacturers. The rabbit raisers may have a legitimate concern with the quality of the feed, as assessed by how their animals perform; yet, there is no detectable problem that the feed manufacturer can correct. This is a frustrating situation that calls for understanding and goodwill on both sides.

Frank nutritional deficiencies are not normally a problem in commercial rabbit diets. Because of the nutritional contributions of cecotrophy, a simple mixture of energy and protein sources will usually provide adequate levels of required nutrients. The major problems encountered with rabbit diets are more subtle as to their cause. These problems include enterotoxemia, cecal impaction, reproductive problems, and unpalatability. These can be associated with differences between batches of ingredients in such factors as particle size and starch content. Variations in fiber content, saponins, chlorophyll, and perhaps other components between one batch of alfalfa and another, can modify their acceptability to rabbits. Variations in starch content among batches of cereal by-products (e.g., wheat mill run) might be involved in enteritis incidence. Rabbits seem to be much more sensitive to these variations than are other animals.

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17

Feeding Rabbits for Various Productive Functions

The nutritional requirements of rabbits, as is true for other animals, vary according to age and productive function. For optimal feeding efficiency, diets should be formulated to meet the needs of animals of a particular age or stage of production. In the swine industry, for example, it is common to have a sow gestation diet, lactation diet, creep diet, starter diet, grower diet, and finisher diet, with each one balanced to meet the requirements of pigs of a given age or function. Pregnant sows need a low-energy diet to prevent obesity; lactating sows need a high-energy, high-protein diet to support milk production. As the pigs grow, dietary energy and protein levels can be reduced without adversely affecting performance. The protein levels range from 20% for a starter diet to 15% for a grower diet and 13% for a finisher diet. Reducing the protein level as the pigs grow results in substantial savings in feed cost, particularly since most of the feed in a swine operation is consumed by the growing–finishing pigs, which have the lowest protein requirements. While similar relationships are true for rabbits, most rabbit farms are not large enough to justify the use of several different feeds, so it is a common practice to use just one diet for the entire herd. In this chapter, diets suitable for different production stages will be presented. As the rabbit industry becomes more intensive, it is likely that rabbit producers will use at least two diets, a grower diet for fryers and a lactation diet for does.

I. NUTRIENT REQUIREMENTS AND DIETS FOR GROWTH

A. Creep Diets

Nutrient requirements for growth are highest for the young animal and decrease with age. Creep diets are those fed to baby animals while they are still nursing. Creep feeds are commonly used with various types of livestock including pigs, calves, and lambs. Creep feeding of rabbits is not often done, but may

TABLE 17.1

Composition of a 22% Crude Protein Creep Diet[a]

Ingredient	Composition (%)
Oats, ground	19.0
Wheat, ground	10.0
Barley, ground	10.0
Wheat bran	6.4
Soybean meal	12.0
Rapeseed meal (canola meal)	2.5
Fish meal (herring)	3.2
Dehydrated alfalfa meal	23.7
Dried brewer's yeast	3.0
Dried distiller's solubles	4.0
Dried whey	4.0
Molasses	1.0
Salt, iodized	0.5
Vitamin, mineral premix	0.775
DL-Methionine	0.07
Feed flavor	0.05

[a]From Hunt and Dunkelgod (1981).

have potential as a means of increasing productivity. Hardman *et al.* (1970), in an interesting study, showed that the baby rabbit is capable of a much greater growth rate than is commonly observed. They found a greatly enhanced growth rate in kits allowed to nurse two does each day, indicating that they are genetically capable of a greater growth rate than is normally achieved. Hunt and Dunkelgod (1981) evaluated the effect of providing a creep diet, whose composition is shown in Table 17.1. The results (Table 17.2) do not show any benefit from the provision of a creep diet. In view of the additional costs required for provision of a creep feeder (to prevent the doe from having access to the feed) and the higher cost of a creep diet, creep feeding does not appear to be an economically sound practice in rabbit production at this time.

B. Weaning

Weaning is the period when an animal's diet changes from one based on milk to one based on solid feeds. In the neonatal period, when animals are entirely dependent on milk as a nutrient source, they have a high activity of digestive enzymes that function in the digestion of the major components of milk. There is a high activity of lactase, which digests lactose (milk sugar). Conversely, there is

TABLE 17.2

Effect of Creep Feeding on the Performance of Rabbits[a]

Item	No creep feed	Creep feed from days 8 to 28	Lactation diet available as creep feed
Litter size, day 1	8.7	8.7	8.8
Litter size, day 28	6.2	6.9	6.4
Weight at 28 days (g)	573	574	587
Weight at 49 days (g)	1557	1540	1521
Feed intake,[b] 1–49 days (kg)	23.20	25.28	24.18
Mortality, 1–49 days (%)	35.2	20.7	27.3

[a]From Hunt and Dunkelgod (1981).
[b]Feed consumed by both doe and litter.

a low activity of other carbohydrate-digesting enzymes such as amylase, which functions in starch digestion. It is necessary that the development of enzymes like amylase be sufficient by the time of weaning, so that the animal is capable of digesting nonmilk products such as starch and plant proteins. Apparently the development of this enzyme activity in rabbits is adequate (Alus and Edwards, 1976). McCuistion (1964) postulated that young rabbits have inadequate amylase activity, leading to an inability to utilize starch normally. He suggested that the undigested starch would cause diarrhea, presumably by carbohydrate overload of the hindgut. While this hypothesis is appealing, no data were presented by McCuistion in its support, and the study of Alus and Edwards (1976) showed that amylase activity increases very rapidly in the period of 15–30 days of age. However, weanling rabbits are very sensitive to carbohydrate overload of the hindgut and often develop enteritis when fed high-energy diets, so perhaps amylase activity is inadequate.

Grobner *et al.* (1983) evaluated the effects of the use of either high- or low-fiber diets at weaning, and the response to switching to a different diet 2 weeks after weaning. It was hypothesized that at weaning, a high-fiber, low-starch diet might be beneficial, followed by a switch 2 weeks later to a high-starch diet, at which time the capacity of the animal to digest starch might be higher. The results (Table 17.3) supported the hypothesis, as far as enteritis incidence was concerned. The authors suggested that for maximum production efficiency, a feeding system using a highly palatable, high-fiber diet at weaning with a switch to a high-carbohydrate fattening ration might be desirable.

The crude protein requirement for growth is less than for lactation, so the use of one diet for does and fryers will either be adequate for does and contain excess protein for fryers, or will be adequate in protein for fryers but less than sufficient to meet the protein needs for lactation. Several studies (see Chapter 4) indicate

TABLE 17.3

Effect of Type of Weaning Diet on Performance of Weanling Rabbits[a]

Diet	Average daily gain (g)	Average daily feed intake (g)	Feed/gain	Mortality (%)
High starch (54% corn)	39.9	102	2.54	27.8
High fiber (54% alfalfa)	36.5	124	3.41	16.7
High starch; high fiber[b]	38.0	109	2.86	27.8
High fiber; high starch[b]	38.6	117	3.02	5.6

[a]From Grobner *et al.* (1983).

[b]Fed the first diet for 2 weeks, and then switched to the second diet for 2 weeks.

TABLE 17.4

Examples of Adequate Diets for Fryers Aged 4–12 Weeks[a]

Ingredient	Composition (%)
Alfalfa meal	54
Wheat mill run	36.5
Soybean meal	6
Molasses	3
Salt (trace, mineralized)	0.5
Alfalfa meal	40
Ground oats	27.5
Ground barley	20
Soybean meal	9
Molasses	3
Salt (trace, mineralized)	0.5
Alfalfa meal	40
Ground barley	25
Wheat mill run	23.5
Cottonseed meal	8
Molasses	3
Salt (trace, mineralized)	0.5

[a]If good-quality, bright-green alfalfa meal is used, a vitamin supplement is unnecessary. If the alfalfa quality is questionable, it is advisable to add a vitamin premix (a swine or poultry vitamin premix is satisfactory).

that a level of 16% crude protein is adequate for fryer diets. This relationship is also true for energy. High-energy lactation diets are needed for maximum lactation and reproduction performance, but these diets will provoke enteritis if fed to fryers.

Examples of several diet formulas for fryer diets are given in Table 17.4. Many others can be formulated. The "best" diet depends on the prices of ingredients available.

II. GESTATION–LACTATION DIETS

Lactating does have higher requirements for protein, energy, calcium, and phosphorus than do fryers. For maximum production, at least 18% crude protein is required. Because does in commercial herds are usually simultaneously pregnant and lactating, the same diet can be used for both gestation and lactation. During periods when does are not with litters, restricted feeding should be used to prevent obesity. The quantity of feed offered will depend on the composition of the diet, breed, environmental conditions, and other factors.

TABLE 17.5

Examples of Lactation Diets[a]

Ingredient	Composition (%)
Alfalfa meal	40
Ground barley	20.25
Wheat mill run	20
Soybean meal	14
Molasses	3
Fat	1.5
Dicalcium phosphate	0.75
Salt (trace, mineralized)	0.5
Alfalfa meal	30
Ground oats	26.5
Ground barley	23
Soybean meal	16
Molasses	3
Dicalcium phosphate	1
Salt (trace, mineralized)	0.5

[a]If good-quality, bright-green alfalfa meal is used, a vitamin supplement is unnecessary. If the alfalfa quality is questionable, it is advisable to add a vitamin premix (a swine or poultry vitamin premix is satisfactory).

TABLE 17.6

Changes in Quantity and Composition of Milk during Lactation

Parameter	References	Days postkindling					
		1	7	14	21	24	30
Milk yield (g/day)	Lebas (1968)	50	160	220	240	220	160
Water (%)	Lebas (1971)	69	74	74	73	67	63
Crude protein (%)	Lebas (1971)	14	14	13	13	16	17
Fat (%)	Lebas (1971)	15	9	9	10	14	18
Lactose (%)	Lebas (1971)	1.6	0.9	1.0	0.9	0.8	0.2
Ash (%)	Lebas (1971)	1.6	2.1	2.2	2.4	2.6	2.8
Gross energy (kcal/kg)	Partridge *et al.* (1983)	—	2012	2296	2009	—	2450

Examples of diets that are satisfactory for gestation–lactation are given in Table 17.5.

Milk Production of Rabbits

Lebas (1968) measured milk production in rabbits. Peak lactation occurs about 21 days postkindling (Table 17.6). In does bred 24–48 hr postpartum, milk production declines rapidly after 21 days of lactation, and the mammary glands prepare for the initiation of a new lactation period. During the third week of lactation, does are in negative nitrogen balance if fed diets with less than 20% crude protein (Sanchez *et al.*, 1985). Maximum milk production of New Zealand White does is 250–300 g of milk per day (Sanchez *et al.*, 1985; Partridge *et al.*, 1983; Partridge and Allan, 1982).

Lebas (1971) reported changes in milk composition over the lactation curve. After peak lactation, the water and lactose contents decrease, and the protein, fat, and ash components increase, on a percentage basis (Table 17.6).

Compared to the milk of other common animals, rabbit milk is low in water, high in protein and fat, and low in lactose (Table 17.7). Thus it is a high-protein, high-energy nutrient source. This might be expected because of the nursing behavior of rabbits, which normally suckle only once per day for a brief period of 5 min or less (Venge, 1963). Not all kits suckle every day (Lang, 1981), so a concentrated food source is needed. Milk production can easily be measured by use of the weigh–suckle–weigh method (Lukefahr *et al.*, 1983). The nest-box can be removed from the cage, and returned only once per day for a brief suckling period. Milk production is measured by weighing the doe before and after nursing. It is preferable to weigh the doe rather than the kits, because the kits often urinate immediately after suckling.

Partridge *et al.* (1983) have shown that with traditional low-energy rabbit diets, does cannot consume sufficient feed to meet their energy requirements

TABLE 17.7

Approximate Milk Composition of Various Species

Species	Composition (%)				
	Water	Protein	Fat	Lactose	Ash
Rabbit	74	13	9	1	2.2
Cow	88	3	4	5	0.8
Goat	87	4	4	5	0.8
Human	87	2	4	7	0.3
Cat	82	9	3	5	0.5
Rat	68	12	15	3	1.5

during lactation and so are in negative energy balance. They evaluated the use of a high-protein, high-energy lactation diet containing 24.9% crude protein and a gross energy content of 4462 kcal/kg. The diet contained 39.9% soybean meal, 27.5% ground oats, 15.0% grass meal, 5% sucrose, 5% corn oil, 2.5% vitamin premix, and 5% mineral premix. Even with this diet, does were in negative protein and energy balance during peak lactation (Partridge *et al.*, 1983). However, feed was restricted to a maximum of 360 g/day; with *ad libitum* feeding, it is possible that the does may have been able to meet their protein and energy requirements for lactation without mobilizing body tissue.

One potential method of increasing doe productivity is to reduce the interval between kindling and rebreeding. Postpartum mating is breeding the does at 24–48 hr after kindling, at which time fertility is high. Harris *et al.* (1982) compared rebreeding at 1 and 14 days postpartum, with does fed a 54% alfalfa meal diet, with a crude protein content of 21.7% and digestible energy (DE) of 2815 kcal/kg. A commercial diet (Carnation Albers) with a crude protein content of

TABLE 17.8

Productivity of Does Mated Either 1 or 14 Days Postpartum[a]

Item	Rebreeding schedule	
	1 Day postpartum	14 Days postpartum
Fertile matings (%)	61.0	68.1
Litter interval (days)	39.3	50.9
Litter size at birth	7.95	8.62
Born alive (%)	75.1	80.9
Litter weight at 28 days (g)	3652	3748
Average number of kits weaned per doe per year	34.9	37.3

[a]From Harris *et al.* (1982).

TABLE 17.9

Reproductive Performance of Does Mated 1, 7, 14, and 21 Days Postpartum over a 1-Year Production Cycle[a]

Item	Breeding schedule (days postpartum)			
	1	7	14	21
Conception rate	86	91	93	90
Number of litters per doe per year	8.9	8.5	7.8	6.7
Kits born per doe per year	75.0	73.4	67.4	59.1
Kits born alive per doe per year	58.3	52.6	45.2	45.0
Number of kits weaned per doe per year	48.3	43.5	40.0	33.3
Weight of kits weaned per doe per year (g)	26,459	23,194	21,410	17,744

[a]From Partridge *et al.* (1984).

18.8% and DE of 2605 kcal/kg was used as the control diet. In Table 17.8, results with the two diets are combined to compare the effects of 1- and 14-day postpartum rebreeding. There was little difference in annual production of weaned fryers between the two rebreeding schedules. Mendez *et al.* (1986) fed diets containing either 2140, or 2330 kcal/kg, with remating intervals of 1, 9, and 25 days. With these energy levels, the production per doe per year was adversely affected by rebreeding at 1 day postpartum. Partridge *et al.* (1984) remated does at 1, 7, 14, or 21 days postpartum over a 1-year production cycle, using the high-protein, high-energy lactation diet (Partridge *et al.*, 1983). With this diet, rebreeding at 1 day postpartum did increase productivity (Table 17.9). Two major conclusions from these data are that intensive breeding offers a means of increasing productivity if a high-quality lactation diet is used, and another way of making a large increase in productivity would be to decrease the high mortality of kits at birth. Partridge *et al.* (1984, 1986) noted that high mortality at birth is a major factor limiting productivity of rabbits, and suggested that induction of parturition with hormones such as prostaglandins might be a means of increasing neonatal survival.

Further studies are needed to evaluate the use of high-quality lactation diets. A major concern would be the possible induction of enterotoxemia when high-energy diets are used.

III. COMPLEMENTARY DIETS

In some situations, particularly with small-scale rabbit production, it may be desirable to feed hay or greens free choice and supplement this diet with a restricted quantity of high-energy, high-protein concentrate. This can be accomplished in several ways. One is to purchase a pelleted swine, calf, or poultry diet, and use it as a supplement. In developing countries, one or more of these types of

TABLE 17.10

Examples of Complementary Diets Which Can Be Used to Supplement Roughage Offered Free Choice

Ingredient	Diet		
	1[a]	2[a]	3
Dehydrated alfalfa	50	30	15
Oats	13	25	30
Soybean meal	25	8.5	25
Yeast	6	0.9	—
Mineral–vitamin premix[b]	4.5	2	1
Methionine	1.5	0.6	—
Barley	—	3	—
Wheat bran	—	8	16
Sunflower meal	—	7	—
Wheat straw	—	15	—
Corn	—		12
Salt	—		1

[a]From Rougeot and Thebault (1985).

[b]Composition (%) as follows:

Dicalcium phosphate	70
Magnesium carbonate	13.8
Calcium carbonate	7.7
Sodium chloride	7.7
Ferric chloride	0.535
Zinc sulfate	0.100
Cobalt sulfate	0.065
Manganese sulfate	0.060
Copper sulfate	0.035
Potassium iodide	0.005
Vitamin A	1 million IU/100 kg feed
Vitamin D	100,000 IU/100 kg feed
Vitamin E	5000 mg/100 kg feed

feeds is usually available commercially, while pelleted rabbit feed generally is not available. Another alternative is to get a special diet preparation specifically formulated for use as a supplement to roughage. Several examples are shown in Table 17.10.

IV. NONPELLETED DIETS

Rabbits generally are not as productive when fed nonpelleted diets as when pellets are used (see Chapter 11). Under some circumstances, especially with small-scale rabbit production, it might be feasible to use nonpelleted diets, either

TABLE 17.11

Diet Composition and Performance of Fryer Rabbits Fed Nonpelleted Diets[a]

Item	Control (pelleted)	Nonpelleted diets		
		0% Molasses	5% Molasses	10% Molasses
Diet composition (%)				
Sun-cured alfalfa	54	40	40	40
Soybean meal	21	15	15	15
Wheat mill run	20	29	24	19
Rolled barley	—	15	15	15
Molasses	3	—	5	10
Tallow	1.25	—	—	—
Trace mineral salt	0.5	1	1	1
Dicalcium phosphate	0.25	—	—	—
Rabbit performance				
Average daily gain (g)	33.7*[b]	21.7**	31.1*	33.5*
Average daily feed intake (g)	97*	177**	151**	155**
Feed/gain	2.9	8.1	4.8	4.6

[a]From Sanchez *et al.* (1984).

[b]* Different from ** ($p < 0.05$).

commercially prepared or home-mixed. Sanchez *et al.* (1984) evaluated meal-type diets, containing various levels of molasses. Diet composition and animal performance are shown in Table 17.11. Growth rate was reduced with the nonpelleted diet with no molasses, but with the 5% and 10% molasses levels, gains were similar to those obtained with the control diet. However, feed intake was much higher with the nonpelleted diets, largely because of feed wastage. The animals sorted through the feed, preferentially seeking out the rolled grain. Perhaps more satisfactory results could be obtained by feeding the hay separately, either as loose hay or pelleted alfalfa in a separate feeder, and providing the concentrate portion as rolled grains and extruded soybeans (which are flakes, rather than the more granular soybean meal). In spite of the apparent economic attractiveness of using nonpelleted diets, they generally result in excessive feed wastage and greater expense than pelleted feed.

V. REX FUR PRODUCTION

The Rex breed originated from a mutation first observed in France in 1919. Rex rabbits have a soft, dense pelt of uniform hair length, giving a fur with luxurious qualities normally associated with expensive furs like mink and sable.

A commercial Rex fur industry may be developing in the United States. Because the physiology of hair growth is basically the same for Rex fur and Angora wool, they will both be considered in the following discussion of hair growth.

A. Hair Growth

Hair fibers grow from follicles embedded in the skin. The young mammal is born with all of the primary hair follicles it will have; the development of the hair coat is mainly dependent on nutritional and environmental conditions. The follicle is the saclike structure in the skin that anchors the hair. Growth of the hair occurs in a highly vascular layer of the follicle called the papilla, where nutrients are removed from the blood and used for synthesis of the hair and its pigments. The growth of the hair occurs from the matrix plate of the hair bulb directly above the papilla. The hair cells die shortly after their formation, so the hair fiber

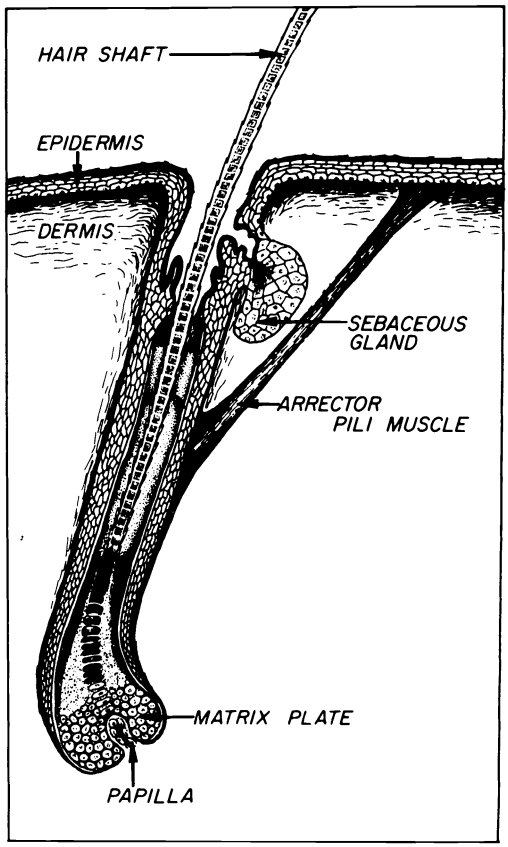


Fig. 17.1 Schematic diagram of a hair and hair follicle.

consists of dead cornified cells. The structure of the hair follicle is shown in Fig. 17.1.

There are several types of hair follicles. The primary follicles produce the longest type of hair, called guard hair, while the underfur grows from lateral primary follicles and secondary follicles. Primary follicles usually have a sebaceous gland and an arrector pili muscle, whereas secondary follicles lack the muscle. When the arrector pili muscles contract, they cause the guard hair to become erect during fright or displays of anger and under cold conditions. The erect hair traps air and increases the insulatory properties of the coat. The primary hair follicles are arranged in a trio pattern, with a central follicle and two laterals. Secondary follicles can branch to form new follicles. The number of secondary follicles can vary seasonally. In the snowshoe hare, for example, the dense winter underfur is produced from an increased number of secondary follicles (Severaid, 1945; Keogh, 1969). The underfur of the snowshoe hare is always pigmented; the white winter coat is associated with white guard hairs (Keogh, 1969). The development of the white winter coat is apparently due to the action of melatonin, a hormone produced by the pineal gland. The production and secretion of melatonin is regulated by the photoperiod. The action of

TABLE 17.12

Seasonal Effects on Angora Rabbit Wool Production[a]

Item	Summer	Autumn	Winter	Spring	Yearly mean
Total weight of wool produced (g)	172	230	237	219	859
Types of hair					
Guard hair					
Length (cm)	9.26	10.31	10.24	10.11	9.98
Diameter (μm)	58.06	60.00	58.92	60.05	59.26
Awn					
Length (cm)	7.27	8.24	8.57	8.36	8.11
Diameter (μm)	29.18	29.26	30.24	30.80	29.87
Down					
Length (cm)	6.26	7.19	7.51	7.29	7.06
Diameter (μm)	16.06	16.88	17.06	16.92	16.73
Follicle growth					
Central primary follicles in anagen phase (%)	84	95	90	92	—
$\frac{LP + SF^b}{PF}$	37.0	51.5	49.5	45.1	—

[a] Adapted from Rougeot and Thebault (1983).

[b] $\frac{\text{Number of primary lateral follicles + number of secondary follicles}}{\text{Number of central primary follicles}}$

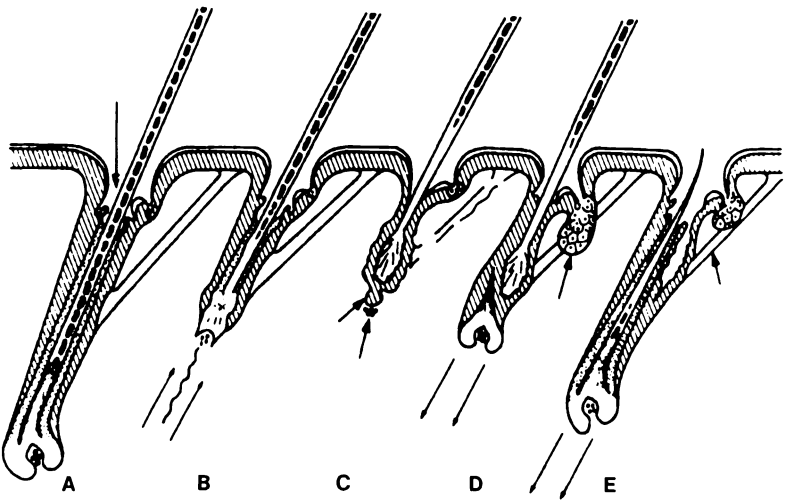


Fig. 17.2 Cycles of hair growth in the rabbit. The growth of a new hair, or anagen phase (A), is followed by the catagen phase (B) during which the lower part of the follicle atrophies. Melanin pigments move from the dermis area to the epidermis, resulting in the underskin of the pelt changing from dark to white (see Figs. 17.3 and 17.4). The catagen phase is of short duration, leading to the telogen phase (C, D), in which the hair has an epithelial sac (the bulblike structure on the end of the hair shaft). At this point, the hair is prime. Then a new hair begins growth in the same follicle, causing the previous hair to be shed, followed by a new anagen phase (E).

melatonin is mediated by its effects on prolactin synthesis and/or secretion (Rose *et al.*, 1985).

Rougeot and Thebault (1983) have studied the seasonal changes in hair follicles in the Angora rabbit. Wool production is highest in the winter (Table 17.12) and lowest in the summer. This is a result of both increased hair length and diameter of the fibers (Table 17.12), since both the lateral primary follicles and the secondary follicles produce underfur. The underfur can be subclassified into awns and down. The awn hairs grow from lateral primary follicles, while the down grows from secondary follicles.

The depth of the follicle in the skin changes throughout the hair growth cycle (Fig. 17.2). When the hair is actively growing, the base of the follicle is deep within the skin. The hair pigment cells, called melanocytes, can be seen as the dark-colored areas on the leather side of an unprime pelt (Fig. 17.3). As the priming process occurs, the hair follicle shortens until its base is located just below the sebaceous gland in the upper layer of the skin, and the papilla atrophies. The pigment cells have all been drawn up into the hair shaft. At this stage, the pelt is prime. The leather side of the prime pelt is creamy white (Fig. 17.4), because the pigment cells have moved up into the hair shaft.

A hair undergoes three distinct growth phases in which periods of active

growth alternate with resting periods. These periods are called the anagen, catagen, and telogen phases. During the anagen phase, the hair shaft is undergoing rapid growth. During the catagen phase, of very short duration, the hair changes from the growing to the resting state. The lower part of the follicle dries up. The telogen or resting phase is when the hair is prime. Following the resting stage, a new hair begins growth in the same follicle and forces out the old hair, causing a molt or shedding. In Rex rabbit production, as with other fur animals, it is necessary to harvest the pelt only when it is in prime condition. If it is not prime, the hair will shed and the pelt cannot be used for manufacture of quality garments.

The Rex rabbit goes through three basic prime cycles. The baby prime is from birth to about 10 weeks; the intermediate prime is from 10 weeks to 5 months, and the senior prime occurs from 5 months onward. Cycles of senior prime occur every 2–4 months. Priming proceeds in a definite pattern, generally commencing at the midpoint of the back and abdomen and progressing to the sides. The priming cycle is influenced by hormones and environmental conditions. In animals with a seasonal fur growth cycle, such as mink, the cycle is regulated by changes in photoperiod (day length). Decreasing day length in the summer

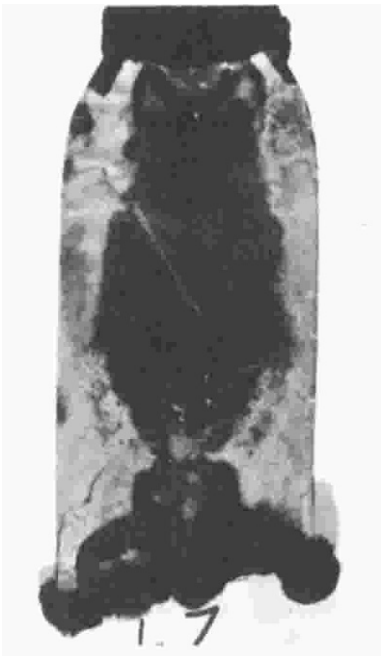


Fig. 17.3 A Rex rabbit pelt, showing lack of prime. The nonprime areas are dark, because the pigment granules have not yet migrated up the hair shaft. (Courtesy of Dr. N. P. Johnston, Brigham Young University, Provo, Utah.)



Fig. 17.4 A Rex rabbit pelt in prime condition. Compare with Fig. 17.3. (Courtesy of Dr. N. P. Johnston, Brigham Young University, Provo, Utah.)

stimulates growth of the winter pelt, while lengthening days in the spring induce molting and growth of the summer fur (Rose *et al.*, 1985). It appears that the pineal gland hormone melatonin and the pituitary hormone prolactin are involved in regulation of these effects. Rose *et al.* (1984) showed that giving mink implants of melatonin accelerated the production of the prime winter pelt. The effect of melatonin appears to be on prolactin synthesis or secretion (Rose *et al.*, 1985). These relationships have not been examined in Rex rabbits. Because the wild rabbit has seasonal changes in its pelage, producing both winter and summer coats, it is likely that similar hormonal effects exist as seen in mink. Rose *et al.* (1984) noted that a single implant of 10 mg of melatonin resulted in a prime pelt being produced 6 weeks earlier than in mink not so treated. This treatment, if effective in rabbits, could have major economic value in Rex rabbit production.

Very little research on Rex fur production has been reported. Taylor and Johnston (1984) demonstrated that feed restriction was of benefit in increasing the numbers of Rex rabbits in prime condition at 6 months of age (Table 17.13). Restriction of feed intake to a level of 75% of *ad libitum* intake resulted in an increase in the number of animals with a prime pelt, without significantly reducing pelt size. The restriction also reduced the number of abdominal fat deposits. This is desirable, because fat deposits on the underside of the pelt must be

removed or deterioration during storage occurs and the fur sheds. Further studies are necessary to determine if it is a restriction in protein or energy or both that has a favorable influence on increasing the number of animals in prime at 6 months of age.

B. Nutritional Effects on Fur

Hair is composed of keratin, a protein with a high cystine content. Keratin is a polymer of amino acids in a helical coil; cystine functions in forming sulfhydryl bonds between the coils, giving the hair elasticity. Hairs consist of a central core of cells, the medulla, surrounded by the cortex. The cortex is covered with an outer layer of cells called the cuticle. The cuticle cells overlap like shingles, providing water-repellent properties to the hair. The medulla contains air spaces. The color of hair is influenced by its structure and the presence of pigments, which are melanin (brown, black) and pheomelanin (red, yellow). These pigments are synthesized from the amino acid tyrosine. Copper and iron are cofactors for tyrosinase, the enzyme involved in pigment synthesis. White hair results from both a lack of pigment and reflection of light off the intercellular air spaces. Other factors influencing apparent hair color include whether the cuticle structure is smooth or rough, and the degree of gloss produced by sebaceous gland secretions. The glossiness can be influenced by the fat content of the diet. Feeding unsaturated fats, such as vegetable oils, tends to increase the sebaceous gland secretions and produce a glossy hair coat or sheen.

Animals with the Himalayan gene (c^H), such as the Californian and Himalyan breeds, exhibit an interesting effect of environmental temperature on coat color. The c^H gene restricts coat color pigmentation to the extremities of the body, such as nose, ears, feet, and tail. The body temperature of the extremities is slightly

TABLE 17.13

Effect of Feed Restriction on Pelt Production of Rex Rabbits at 6 Months of Age[a]

Item	Feeding level (% of *ad lib*)		
	50	75	100
Body weight (g)	2323*[b]	2680	3175†
Total pelt area (cm^2)	1305*	1409*,**	1478**
Animals with prime pelt (%)	70.4*	64.3*	48.6**
Animals with underside of pelt in prime condition (%)	75.7*	65.0*	35.6**

[a]From Taylor and Johnston (1984).

[b]*,**, † Differ ($p < 0.05$).

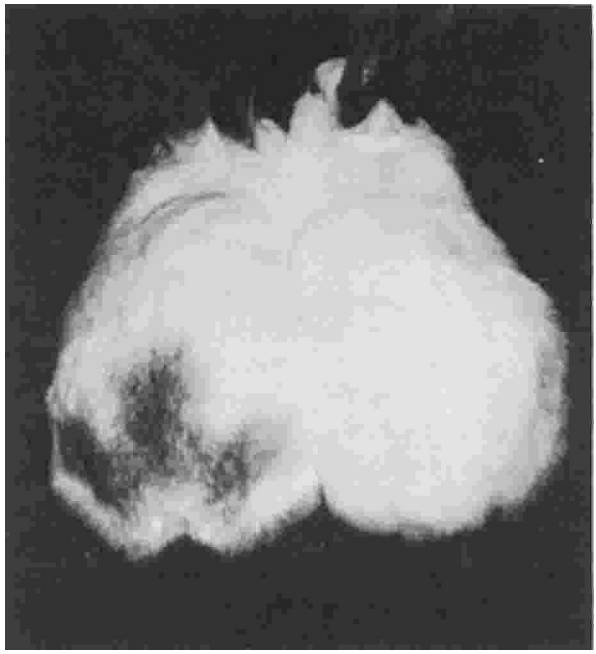


Fig. 17.5 Californian rabbits showing the temperature-dependent effect on melanin synthesis. The animal on the left had a patch of hair shaved, and then was kept in a cold environment for a few days. Melanin synthesis occurred at the lower temperature, resulting in the growth of dark hair.

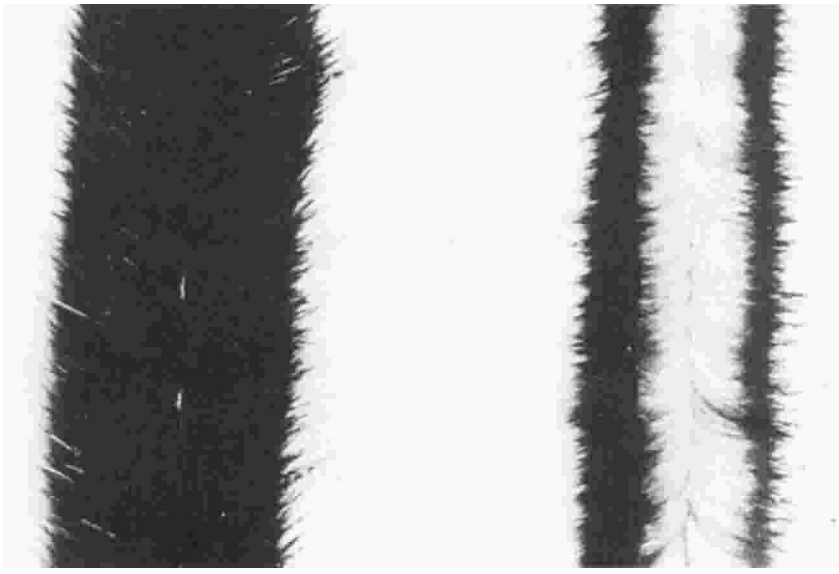


Fig. 17.6 A normal mink pelt (left) and a "cotton fur" pelt (right) resulting from iron deficiency anemia. Iron is a cofactor in melanin synthesis, so iron-deficient dark mink cannot synthesize the hair pigments. (Courtesy of Oregon State University Experimental Fur Farm, Corvallis.)

lower than for the rest of the body, allowing the temperature-dependent c^H gene to be expressed. If Californian and Himalayan kits are chilled shortly after birth, they may develop a pigmented coat. If an ice cube is held against the skin, the hair will grow in dark (Fig. 17.5). This is a result of the temperature-dependent enzyme involved in melanin synthesis.

In mink, a number of nutritional deficiencies have been shown to influence fur color (Wehr *et al.*, 1982). Iron deficiency can be induced by feeding certain types of fish that contain trimethylamine oxide and formaldehyde. These compounds inhibit iron absorption and induce an iron deficiency. Iron is essential in melanin synthesis. With iron deficiency, the fur is unpigmented, causing a

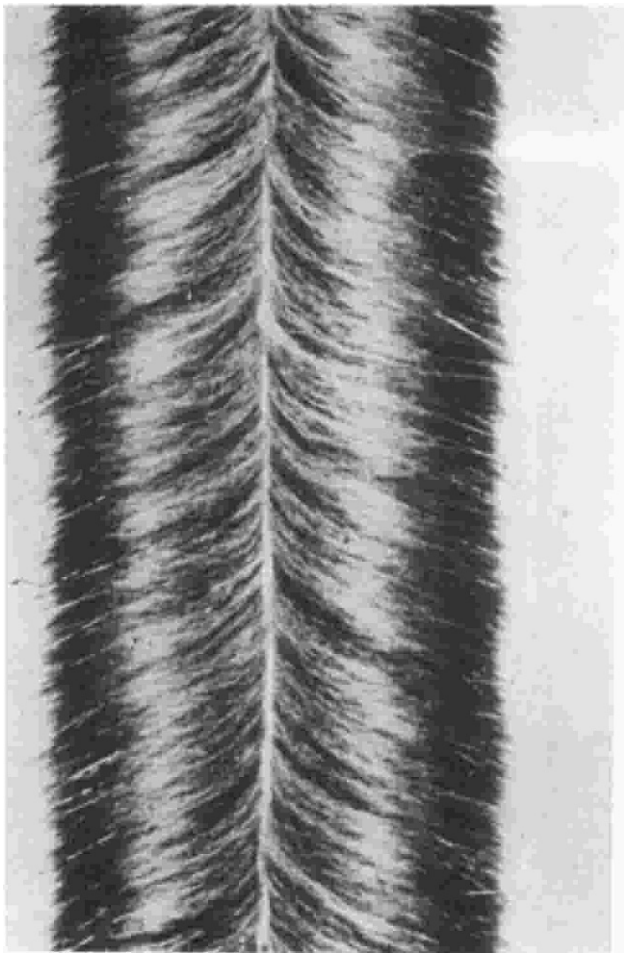


Fig. 17.7 A pelt from a biotin-deficient mink, showing graying of the fur. Biotin deficiency was induced by feeding raw eggs, which contain avidin, a protein that impairs biotin absorption. (Courtesy of Oregon State University Experimental Fur Farm, Corvallis.)

condition called "cotton fur" (Fig. 17.6). A deficiency of the B vitamin biotin causes loss of normal hair pigmentation. This can be induced by feeding raw eggs, which contain a glycoprotein called avidin. Avidin binds biotin and prevents its absorption, thus inducing a biotin deficiency (Fig. 17.7). Copper is another nutrient involved in melanin synthesis. Copper-deficient rabbits develop a graying of normally black fur (Fig. 8-4). Aulerich *et al.* (1982) found that high levels of dietary copper intensified the hair color of black mink. Other nutrients involved in hair pigmentation include pantothenic acid, folic acid, and lysine. The role of these nutrients in hair pigmentation in rabbits, with the exception of copper, has not been investigated. Wehr *et al.* (1982) have reviewed nutritional effects on fur pigmentation, while further details on the chemistry and synthesis of melanin pigments are provided in the review of Jimbow *et al.* (1986).

C. Diets for Rex Fur Production

No experimental studies have been reported on nutritional requirements for Rex fur production. In the absence of other information, it would appear sound to use normal commercial rabbit feeds. Because hair is virtually 100% protein, there is a tendency to think that fur-producing animals would have high protein requirements. However, normal rates of hair synthesis do not create any unusual demand for protein, and in fact the demand is quite low in comparison to the protein requirements for growth. The work of Taylor and Johnston (1984) on feed restriction, and observations by Rex rabbit producers, suggest that it may be advantageous to use low-protein diets for Rex pelters. High-protein diets may speed up the priming cycle, reducing the length of time during which the animal has a prime pelt. This makes it difficult to detect and harvest prime pelts. Lower protein diets may aid in keeping animals in prime longer. Research is needed to evaluate the effect of dietary protein and energy levels on Rex fur production.

VI. ANGORA WOOL PRODUCTION

Angora rabbits produce a high-quality wool that is used in the manufacture of luxury garments and therapeutic clothing for people with arthritis and other joint diseases. The medulla of the Angora wool fiber has large air chambers (Fig. 17.8), which give it excellent insulation properties and allow the fabric to absorb moisture without feeling wet.

Relatively little research on the nutritional requirements for Angora wool production has been reported. Lall *et al.* (1984) fed groups of castrated male woolers five different diets, varying in crude protein from 10.2% to 25.4%. Wool production was measured over a 3-month period, and a 5-day nitrogen balance trial was conducted. The results (Table 17.14) showed no difference in

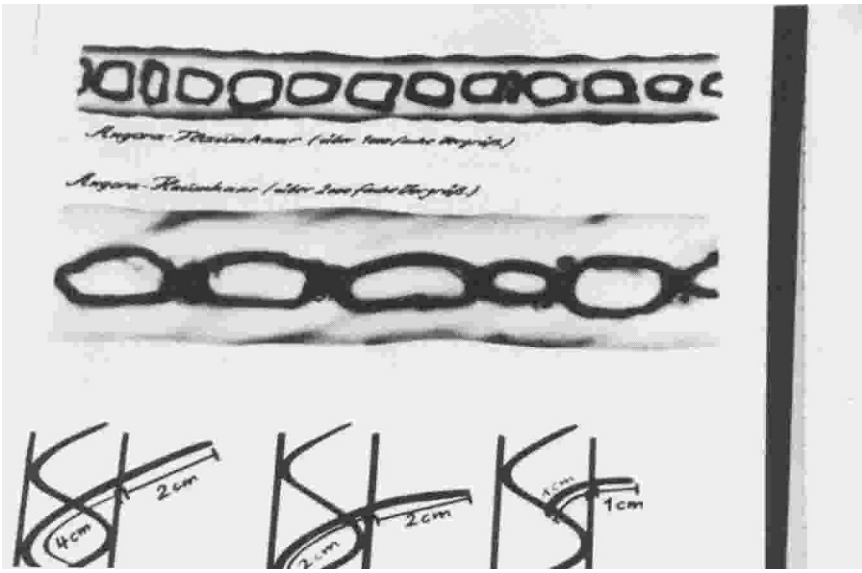


Fig. 17.8 Air chambers in Angora rabbit hair account for the insulatory properties of garments manufactured from this fiber. (Courtesy of W. Schlolaut, Neu-Ulrichstein, Federal Republic of Germany.)

TABLE 17.14

Wool Production and Nitrogen Balance of Angora Rabbits Fed Varying Levels of Dietary Protein[a]

Item	Dietary crude protein level (%)				
	25.4	21.2	19.3	13.8	10.2
Live weight (kg)					
Initial	3.02	2.93	3.10	3.13	3.06
After 3 months	3.16	3.19	3.21	3.49	3.26
Dry matter intake (g/day)	87	94	113	110	107
Digestible crude protein intake (g/day)	19.2	15.4	17.5	11.5	6.2
N Intake (g/day)	3.7	3.2	3.5	2.5	1.7
N Balance (g/day)	1.0	0.5	1.5	0.0	−4.9
Wool production (g 13 months)	73	76	88	82	78

[a]From Lall *et al.* (1984).

wool production. Animals on the lowest protein level were in negative nitrogen balance, indicating that they were mobilizing body tissue to maintain wool production. Nitrogen balance was maintained with the other protein levels. Singh *et al.* (1984, 1985) reported on Angora wool production and N balance with rabbits fed concentrate diets supplemented with tree leaves (Table 17.15). In these three studies, there appeared to be no relationship between N intake and wool production. The level of wool production in these studies was low (200–300 g wool per year). In Germany, maximum wool production levels of 874 g for males and 1159 g for females have been achieved (Schololaut, 1982). Using the higher figure, this represents a wool production of 3.18 g/day as a maximum. Assuming the wool to be pure protein, a daily intake of 3.18 g of protein or 0.51 g N would be required for wool synthesis. The maintenance protein requirement is 12% of the diet (National Research Council, 1977). With a feed intake of 120 g/day for an Angora wooler, the protein requirement for maintenance (14.4 g) and the requirement for maximum wool production (3.2 g) would give a protein requirement of 15% of the diet. In most cases, the feed intake would probably exceed 120g/day. It thus appears that the protein requirement of Angora woolers could be met with a dietary level of about 15% crude protein. The results of Lall *et al.* (1984) support this suggestion. Contrary to what might be assumed, the protein requirements for Angora wool production seem to be quite low in comparison to the requirements of growth and lactation.

Requirements for other nutrients by Angora rabbits have not been well stud-

TABLE 17.15

Nitrogen Balance and Wool Production of Angora Rabbits Fed Pelleted Diets Supplemented with Forage

	Dietary treatment					
	Pelleted diet plus tree leaves[a]			Pelleted diet plus tree leaves[b]		
Item	I	II	III	IV	V	VI
Dry matter (DM) intake (g/day)	78.1	64.9	79.0	50.9	104.7	125.3
Trees leaves (as % DM intake)	37	29	38	0	19.8	33.0
Digestible crude protein intake (g/day)	8.72	8.05	9.83	7.31	15.38	16.56
N Intake (g/day)	2.15	1.85	2.18	1.74	3.40	3.70
N Balance (g/day)	0.87	0.55	1.00	0.52	1.22	1.54
Average wool production (g/year)	223	264	258	223	315	251

[a]Singh *et al.* (1984). Three different pelleted diets were used, each supplemented with mulberry leaves (*Morus alba*) free choice.

[b]Singh *et al.* (1985). Treatment IV was pellets alone; V was pellets plus *Dendrocalamus hamiltonii* leaves; VI was pellets plus *Celtis australis* leaves. Leaves were offered free choice.

ied. Because the nutrient requirements for maintenance are low, and the nutrient needs for hair growth also appear to be low, Angora rabbits for wool production can probably be adequately fed on commercial diets containing 15% crude protein. Because wool block is a major problem with Angoras (see Chapter 12), a dietary level of at least 15% crude fiber is desirable.

In sheep, the rate of wool growth is very sensitive to energy intake, while dietary protein level, unless markedly deficient, has little effect on wool production (Ryder and Stephenson, 1968). The effect of energy on Angora rabbit wool production has not been studied, but should be, in view of the importance of energy level in sheep wool production. The book by Ryder and Stephenson (1968) is an exceptionally good compilation of information relating to all aspects of wool production and utilization. While oriented toward sheep wool, much of the information is applicable to other wool-producing animals.

Chemical shearing by administration of a substance that causes loss of the hair has been examined in both sheep and Angora rabbits, using cyclophosphamide. Rougeot and Thebault (1970) found that oral administration of 60–80 mg cyclophosphamide to Angora rabbits in a single dose resulted in wool loosening in 5–6 days, so that the animals could be plucked rapidly. The amino acid mimosine in leucaena causes a similar effect. It might be useful to evaluate this substance as a chemical shearing agent.

VII. FEEDING RABBITS FOR EXHIBITION

Raising rabbits for showing at exhibitions is a common activity. In fact, most of the rabbit raisers in North America and Europe are fanciers rather than commercial producers. The nutritional requirements for show animals are lower than for commercial rabbits. Nutrient requirements for maximum growth and lactation are much higher than for animals under maintenance conditions. Of more importance to the fancier are diet effects on longevity and disease resistance. Again, a diet that meets the needs for commercial production is likely to be more than adequate for longevity and health, in spite of common opinion to the contrary. It is more likely that a diet designed for commercial production contains excessive protein and energy for show rabbits. The result might be obesity and difficulty in maintaining the hair coat in prime condition. As Taylor and Johnston (1984) demonstrated, a high level of protein–energy intake results in a more rapid hair growth cycle, so that the fur is in prime condition for only a short time and then begins to shed.

Part of the pleasure of raising rabbits for exhibition or simply keeping them as pets is to coddle them with special feeds and "treats." Many long-time rabbit raisers have special concoctions that they use to condition show animals. In most cases, it is probably the extra attention and time spent with the animals that is helpful, rather than any special nutrient properties of the diet supplements.

TABLE 17.16

Breed Differences in Digestibility of Diets Differing in Energy Content[a]

	Low energy		Medium energy		High energy	
	ND[b]	FG[b]	ND	FG	ND	FG
DE (kcal/kg) of diet	2056	2296	2524	2702	2781	2800
Digestibility (%)						
kcal	50.4	56.3	62.9	67.4	68.3	68.7
Crude protein	59.8	67.1	66.8	72.3	65.0	65.6
Acid detergent fiber	13.9	23.1	18.0	25.2	15.5	15.1

[a]From Grobner *et al.* (1985).

[b]ND, Netherland Dwarf; average weight of animals used = 1200 g. FG, Flemish Giant; average weight of animals used = 6900 g.

Raisins, bread, pieces of fruit, carrots, and many other supplements can be given. Vegetable oils increase the glossiness or sheen of the hair coat. Supplements like sunflower seeds or other oilseeds, or a teaspoon of corn oil added to the pellets twice a week will help to maintain an attractive hair coat.

There is evidence that there are breed differences in nutritional requirements. It is reasonable to speculate that dwarf animals that have a mature weight of less than 2 lb might have less ability to utilize low-energy fibrous feeds than large breeds, because of the limitations of a small gut size. Grobner *et al.* (1985) compared the responses of dwarf, intermediate, and giant breeds to diets of low, intermediate, and high energy content. Dwarfs were unable to consume a sufficient quantity of a low-energy diet to maintain body weight. The low-, medium-, and high-energy diets contained 0, 28, and 58% corn, and 80, 34, and 15% alfalfa, respectively. Comparative digestibility data with the dwarf and giant animals are shown in Table 17.16. While there was little difference between the two breeds in digestibility of the high-energy diet, the Flemish Giants had higher digestibility of protein, energy, and fiber of the medium- and low-energy diets. As a result, the DE content of these diets was higher in Flemish Giants than for Netherland Dwarfs. These results indicate that small breeds may require a higher quality diet than large breeds, particularly under conditions that increase the energy requirement. These would include cold environmental temperatures and lactation.

VIII. FEEDING LABORATORY RABBITS

Rabbits produced for sale as laboratory animals are raised in a similar manner as commercial rabbits for meat production. Often, laboratory rabbits are kept for

extended periods on long-term studies. They are usually not mated, so are kept under maintenance conditions. They should be fed a low-energy maintenance diet to prevent obesity. A satisfactory formula of simple composition is as follows: 44.5% alfalfa meal, 40% ground barley, 12.5% soybean meal, 2.5% molasses, and 0.5% salt. A popular diet in Britain is the SG1 laboratory diet (Short and Gammage, 1959). Its composition is as follows: fish meal 10%, grass meal 20%, wheat bran 40%, ground oats 12%, and wheat middlings 18%. Sebesteny *et al.* (1985) reported an outbreak of corneal opacity and atherosclerosis with elevated serum cholesterol in rabbits fed the SG1 diet; replacement of the fish meal with grass meal overcame the problem.

For certain types of nutritional studies, it is desirable to use purified diets so that the content of particular nutrients can be carefully controlled. An example of a suitable purified diet (Gaman *et al.*, 1970) is shown in Table 17.17.

TABLE 17.17

An Adequate Purified Diet for Rabbits[a]

Ingredient	Diet level (%)
Isolated soy protein	20.0
Purified cellulose	16.0
Corn oil	5.0
Mineral mixture[b]	6.6
Vitamin mixture[c]	0.2
Choline chloride (70%)	0.1
Ethoxyquin (antioxidant)	0.025
DL-Methionine	0.2
α-Tocopherol acetate	50 IU/kg
Glucose monohydrate	15.0
Corn dextrin	5.0
Corn starch	27.4
Water (for pelleting)	5.0

[a]From Gaman *et al.* (1970).

[b]Composition (in mg/kg): $CoCl_2 \cdot 6H_2O$, 3.5; $CuSO_4 \cdot 5H_2O$, 34.6; $MnSO_4 \cdot H_2O$, 81.1; $ZnSO_4$, 169; $FeC_6H_5O_4 \cdot 14H_2O$, 706.3; $(NH_4)_6Mo_7O_{24} \cdot 4H_2O$, 22.7. Composition (in g/kg): KH_2PO_4, 10; $KHCO_3$, 10; $NaHCO_3$, 8; NaCl, 5; $CaCO_3$, 12.5; $CaHPO_4$, 10.

[c]Composition (in mg/kg): thiamin-HCl, 25; riboflavin, 16; Ca pantothenate, 20; pyridoxine-HCl, 6; biotin, 0.6; folic acid, 4; menadione, 5; vitamin B_{12}, 0.02; ascorbic acid, 250; niacin, 150; vitamin A, 10,000 IU; vitamin D_3, 600 IU; α-tocopherol acetate, 10 IU.

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18

Nutrition of Wild Rabbits and Hares

Rabbits and hares are members of the order Lagomorpha, which contains two families and 12 genera (Dawson, 1982). The modern lagomorphs are listed in Table 18.1. In North America, the principal wild lagomorphs include the cottontail rabbits (*Sylvilagus* spp.), the hares such as the jackrabbit, arctic hare, and snowshoe hare (*Lepus* spp.), and the pikas or rock rabbits (*Ochotona* spp.). While there are substantial anatomical and behavioral differences among rabbits, hares, and pikas, they seem to share similar digestive and nutritional characteristics, at least in so far as can be determined from the limited amount of information available. Very few nutritional studies have been conducted with the wild lagomorphs in comparison to the information available on the domestic rabbit.

There are several reasons why the nutrition of wild lagomorphs should be studied. The first is that of simple scientific inquiry and intellectual curiosity. How do digestive processes and nutrient metabolism in cottontails, hares, and pikas compare with each other and to the domestic rabbit? There are other reasons of a more prosaic nature for developing knowledge on wild lagomorph nutrition. In game management, such as with cottontails, it is desirable to know the types of feeds preferred and how well they meet the nutrient requirements, and if other plants could be introduced into the habitat that would better meet the animals' requirements. Knowledge of the requirements and the composition of available feed can allow predictions of carrying capacity and level of permissible harvest. Some lagomorphs are endangered species, and knowledge of their nutritional requirements could be of critical importance, particularly in terms of habitat needs and captive breeding programs. Estimates of protein and energy requirements can be useful in assessing potential damage to crops and livestock production from jackrabbits and other "pest" lagomorphs. In some cases, wild lagomorphs are raised for release for hunting. The European hare is raised on game farms in France for release into the wild for hunting purposes. Knowledge of nutritional requirements is of obvious importance when animals are produced in this manner, as they will require feeding when raised in captivity.

An excellent compilation of information on the biology of wild lagomorphs is contained in the proceedings of the World Lagomorph Conference (Myers and MacInnes, 1981).

TABLE 18.1

Classification and Distribution of Lagomorphs[a]

Families and genera	Number of species	Examples	Common name	Distribution
Family Leporidae				
Lepus	26	*L. americanus*	Snowshoe (varying) hare	North America
		L. arcticus	Arctic hare	North America
		L. californicus	Black-tailed jackrabbit	North America
		L. europaeus	European brown hare	Europe
		L. timidus	Mountain hare	Europe
Sylvilagus	13	*S. bachmani*	Brush rabbit	North America
		S. floridanus	Eastern cottontail	North America
Oryctolagus	1	*O. cuniculus*	European rabbit (domestic and wild)	Worldwide
Caprolagus	1	*C. hispidus*	Hispid hare	India
Bunolagus	1	*B. monticularis*	Bushman hare	South Africa
Poelagus	1	*P. marjorita*	Bunyoro rabbit	Africa
Pronolagus	2	*P. randensis*	Red rockhare	Africa
Pentalagus	1	*P. furnessi*	Amami rabbit	Japan
Romerolagus	1	*R. diazi*	Volcano rabbit	Mexico
Nesolagus	1	*N. netscheri*	Sumatran hare	Indonesia
Brachylagus	1	*B. idahoensis*	Pygmy rabbit	North America
Family Ochotonidae				
Ochotona	14	*O. princeps*	Pica, rock rabbit	North America

[a]Adapted from Dawson (1981).

I. DIGESTIVE PHYSIOLOGY

Wild lagomorphs appear to have similar digestive physiology as domestic rabbits. Coprophagy occurs in jackrabbits (Lechleitner, 1957), the European wild rabbits (Myers, 1955), the European hare (Flux, 1981), snowshoe hares (Sinclair *et al.*, 1982), cottontails (Heinsinger, 1962), and pikas (Haga, 1960; Johnson, 1967). Rabbits and hares have similar cecotrophic behavior, producing soft fecal pellets enveloped in a mucous covering. These are consumed once or twice every 24 hr, and are consumed directly from the anus without mastication. Fermentation within the cecotropes continues for several hours in the stomach. In contrast, pikas have no distinct periods of cecotrophy, but produce small amounts of soft feces at random periods through the day and night. The soft feces are an amorphous paste without a mucous envelope. Part is consumed directly from the anus, while the remainder is pasted on stones and other objects and consumed later in a semidry state (Hornicke and Bjorhag, 1980). The soft feces are often deposited on hay piles, presumably to be consumed at a later date. Pikas in a captive colony have been observed to consume soft feces that were

covered with mold (A. T. Smith, Arizona State University, Tempe, personal communication). The digestive strategy of all lagomorphs appears to be based on the efficient use of nonstructural carbohydrates and soluble proteins of plants, through cecal fermentation and reingestion of cecal contents, with the selective and rapid excretion of indigestible fiber. Arctic lagomorphs such as the snowshoe hare consume a winter diet of twigs and browse with a very high content of structural carbohydrate. The cecal-colonic separation of large fiber particles and the selective retention of small particles and solubles is an efficient digestive strategy for subsisting on a low-energy herbage diet. It should be emphasized that this is a process of selective excretion and retention, and not "eating soft pellets direct from the anus to pass the food through the gut a second time before producing the final hard pellets" (Sinclair *et al.*, 1982). The hard fecal pellets are in fact primarily fiber that has been selectively removed on the "first passage," while the soft feces (cecotropes) consist of cecal contents that have been retained by antiperistaltic movement of proximal colon contents into the cecum (see Chapter 3).

Wild lagomorphs raised in captivity seem to be susceptible to the same enteric diseases that afflict domestic rabbits. Ducluzeau *et al.* (1975) observed neonatal diarrhea in captive European hares, with the peak incidence at about 1 week of age. Mortality reached 50% of young born. *Clostridium difficile* was implicated as a causative organism (Dabard *et al.*, 1979). The occurrence of enteric diseases in animals in the wild is difficult to assess. Affected animals no doubt quickly succumb to predators. Because of the fibrous nature of the diet and the lack of high-starch feeds (e.g., grains) in most situations, it is probable that there is a much lower incidence of enteric disease in wild lagomorphs than in domestic rabbits.

II. FEEDING BEHAVIOR AND FOOD SELECTION

Diet selection by wild lagomorphs can be assessed by examination of stomach contents, observation of feeding behavior, monitoring plants to assess browsing, and examination of fecal pellets microscopically for the identification of plant cells or cell structures. A problem with the last approach is that plant tissues of highly digestible species may not be identifiable in the fecal pellets, so as Chapman *et al.* (1982) point out, this approach may overestimate the importance of grass in the diet and underestimate the importance of highly digestible succulent weedy forbs. Cheeke *et al.* (1985), with microscopic examination of fecal pellets from domestic rabbits fed a variety of legume and grass forages, found that the high digestibility of clovers and alfalfa resulted in an absence of characteristic cell structures in the feces, whereas for grass there was much less degradation of the plant structure.

Food habits of cottontail rabbits have been reviewed by Chapman *et al.* (1982). Preferred feeds include grasses, forbs, and young woody plants. The seasonal availability of plant species is a major determinant of the diet. Spring diets consist mainly of herbaceous plants, such as clovers, grass, and alfalfa. Agricultural crops such as corn, soybeans, and wheat are a major portion of the diet where available. In the fall, there is a transition to woody plants. The winter diet consists of tree twigs (birch, maple, aspen, apple, wild cherry) and shrubs (blackberry vines, willow, alder).

The pygmy rabbit (*Brachylagus idahoensis*) of Idaho has a near-obligate relationship with sagebrush (*Artemisia*), which constitutes about 99% of its winter diet (White *et al.*, 1982). Sagebrush contains monoterpenes (Cheeke and Shull, 1985), which may have adverse effects on gut microflora. White *et al.* (1982) determined that 77% of the monoterpenoids consumed by pygmy rabbits was volatilized during mastication, and postulated that this reduction allows the animals to consume sagebrush without ill effects.

Jackrabbits prefer green succulent plant material. Grasses are most important in the spring and summer, forbs later in the year, and shrubs are the dominant feed in the winter (French and Heasley, 1981). Cultivated crops such as alfalfa, wheat, and crested wheatgrass are heavily used during the winter (Dunn *et al.*, 1982). Green vegetation is the major source of water for jackrabbits in desert areas. Additionally, the poor nutritional quality of most desert plants late in the year indicates that when the natural vegetation dehydrates, jackrabbits must migrate to sites with succulent vegetation or die (Nagy *et al.*, 1976).

The snowshoe hare and mountain hare are browsers, feeding primarily on woody species, preferring mature twigs over juvenile plant growth (Sinclair and Smith, 1984b). Forage preferences of these hares are willow > aspen > larch > dwarf birch > tree birch > jack, lodgepole, and Scotch pine > white pine > red pine > fir > white spruce > black spruce > alder (Bryant and Kuropat, 1980). The snowshoe hare undergoes regular population fluctuations of 8- to 11-year cycles (Keith, 1981) in northern environments. One theory to explain this cyclic pattern relates to the interaction of hares with woody plant species. Bryant (1981b) reviewed the evidence suggesting that browsing by hares on arctic trees and shrubs results in a marked increase in the content of secondary plant substances that reduce palatability and may have negative metabolic effects such as inhibition of microbial fermentation in the gut. In other words, with increasing feeding pressure by hares (and other herbivores) on these plants, the plants respond by synthesizing increased levels of toxic substances ("toxic" encompasses feeding deterrents—substances that are unpalatable). Bryant (1981b) proposed that the 10-year hare cycle can be explained as follows. The early-peak phase of the expanding hare population depletes the supply of small-diameter, mature-growth twigs of browse species that constitute the hares' winter diet. The mature crown twigs are readily available to snowshoe hares in winter because

snow bends the trees down to the ground (Clausen *et al.*, 1986). This browsing causes the plants to sprout adventitious shoots, which have a high content of resins, tannins, or other constitutents that are unpalatable to hares. Because of the depletion of the mature small twigs and the production of unpalatable adventitious shoots, the hares are forced to feed on low-preference browse species and on unpalatable adventitious shoots, and to girdle and kill preferred browse species. Consequently the hare population "crashes" because of the lack of suitable feed. With the drop in hare population, the browse plants begin to recover, but retain a high level of secondary compounds for 2–3 years following the decline in hare populations. These interactions would explain a 10-year hare cycle. The elevated levels of secondary compounds are apparently the result of the higher concentrations of protective compounds in juvenile plant tissues (suckers from root or stump sprouts) rather than an increase in these compounds in mature vegetation (Chapin *et al.*, 1985). The specific secondary substances involved vary with different plant species. Reichardt *et al.* (1984) isolated a triterpene called papyriferic acid from paper birch (*Betula resinifera*); it appears to be the feeding deterrent in birch. They showed that juvenile birch twigs contained 25 times the papyriferic acid concentration as mature twigs. Feed preference tests showed that this compound is a strong feeding deterrent to snowshoe hares, providing good evidence to support its role in protection of juvenile birch sprouts from hare predation. Adventitious shoots of birch, quaking aspen, balsam poplar, and green alder contain high levels of terpene and phenolic resins, which

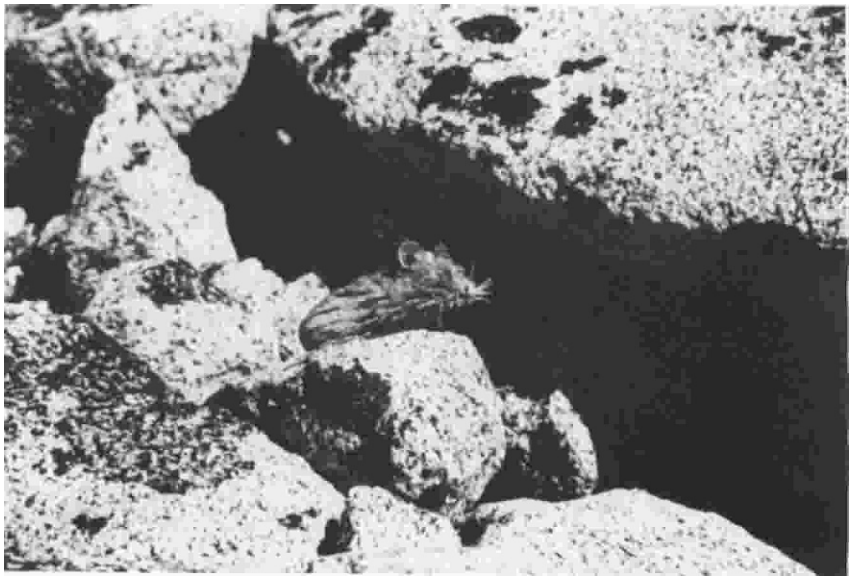


Fig. 18.1 A pika in its typical rock pile (talus) habitat, carrying forage harvested for addition to its hay pile. (Courtesy of A. T. Smith, Arizona State University, Tempe.)

are repellent to hares (Bryant, 1981a,b). Bryant *et al.* (1983) and Clausen *et al.* (1986) reported that pinosylvin methyl ester, a phenolic compound, protects green alder from hare browsing. Tahvanainen *et al.* (1985) demonstrated that phenolic compounds in twigs of northern willow (*Salix* spp.) provide chemical deterrence to hare feeding. Risenhoover *et al.* (1985) determined that a number of these secondary metabolites, including papyriferic acid, are inhibitory to cellulose digestion. Thus there is abundant evidence to support the hypothesis that cycles of hare populations in subarctic environments may be related to chemical defenses of plant tissues. Browsing by herbivores is a major threat to the survival of trees and shrubs in the subarctic (Bryant, 1981a,b). Coevolution of herbivores and arctic vegetation to ensure the survival of both would require that at least some of the time the vegetation must be protected against a high degree of herbivory, or it would cease to exist. This is apparently accomplished by a high level of chemical defense in juvenile tissues, with a relaxation of defense in more mature tissue. This in turn provides the herbivores with a food supply until their numbers exceed the availability of mature vegetation. At this point, the plants respond by regrowth of juvenile tissue with a high content of feeding deterrents, causing a food crisis for the herbivores and a population



Fig. 18.2 Pikas construct large hay piles, which are used throughout the winter months. (Courtesy of H. E. Broadbooks, Southern Illinois University, Edwardsville, and the American Midland Naturalist.)

crash. It should be recognized that other factors, such as cyclic fluctuations in predator numbers (Wagner, 1981) and climatic factors (Jonasson *et al.*, 1986), may also influence cycles of hare numbers.

There is essentially no research on the nutrition of pikas. These animals harvest forage during the summer, and build large hay piles (Figs. 18.1, 18.2). The forage cures into hay in the pile. Foraging behavior of pikas has been described by Huntley *et al.* (1986). Broadbooks (1965) noted that legume forage (lupine, vetch), grasses, forbs, and tree leaves were harvested. The pikas also collected marmot feces, which were added to the hay piles, and presumably were consumed. The haystacks are built up on rock piles (talus) inhabited by pikas, and are consumed during the winter. Johnson (1967) noted that forb and shrub leaves and stems made up about 80% of the diet, during all seasons. Plants consumed by pikas include some poisonous ones, such as *Senecio* spp. and *Veratrum californicum* (Johnson, 1967), although A. T. Smith (Arizona State University, Tempe, personal communication) noted that plants of the Ranunculaceae family, which contain toxicants, were not consumed until they began to dry up and the toxicants were translocated to the roots.

III. NUTRIENT REQUIREMENTS

A. Protein

Snyder *et al.* (1976) conducted a feeding trial with growing cottontails fed semipurified diets to evaluate protein requirements. The results (Table 18.2) indicate that the protein requirement for growth can be met with a level of about 12% digestible protein. Casein, a highly digestible substance, was used as the source of dietary protein. Holter *et al.* (1974), in a trial with snowshoe hares, used diets containing red maple browse, commercial rabbit feed, soybean meal, and corn to study protein and energy requirements. From the results (Table 18.3) they estimated the digestible protein requirement to be 2.6 g/kg $W^{0.75}$. Sinclair *et al.* (1982, 1984a) found that 11% dietary crude protein was the threshold level for maintenance of body weight in snowshoe hares. Pehrson (1983b,c, 1984) suggested that hares can maintain nitrogen balance on low-protein winter browse because of cecotrophy. The selective excretion of fiber and cecal retention of nonfiber components in lagomorphs (see Chapter 3) allows a high feed intake of low-quality material. As Pehrson (1984) points out, this process gives a mixture of large particles of low protein content and small particles of high protein content and nutritive value. The wood and outermost bark layer of twigs are mechanically resistant and of low nutritive value, while the inner bark cells are of high nutritional value and easily degraded into small particles. This appears an adequate explanation for the ability of wild lagomorphs to survive on low-quality twigs during the winter. Nagy *et al.* (1976) estimated the minimum digestible

TABLE 18.2

Responses of Juvenile Cottontails Fed Diets Differing in Protein Content[a]

Treatment	Average daily gain (g)	Average daily feed intake (g)	Feed/gain
Trial I			
Commercial rabbit pellets	8.21	74.3	9.05
20% Crude protein	6.02	45.9	7.63
15% Crude protein	7.39	47.7	6.46
10% Crude protein	4.91	38.4	7.83
Trial II			
16% Crude protein	6.35	33.9	5.34
14% Crude protein	5.46	33.4	6.12
12% Crude protein	6.30	34.7	5.50
10% Crude protein	3.77	27.3	7.24

[a]From Snyder *et al.* (1976).

nitrogen requirement of jackrabbits to be between 330 and 450 mg/kg body weight per day, compared to a value of 375 mg for snowshoe hares (Holter *et al.*, 1974).

B. Energy

French and Heasley (1981) summarized energy requirements of grassland lagomorphs. For jackrabbits and desert cottontails, the daily energy requirement

TABLE 18.3

Responses of Snowshoe Hares to Diets Differing in Protein Content[a]

Item	Dietary crude protein (%)					
	10.2	13.3	16.5	19.7	22.8	26.0
Daily dry matter intake (g)	96	93	95	96	97	95
Daily crude protein balance (g)	−0.2	0.1	−0.8	1.4	0.8	1.1
Apparent digestibility (%)						
Crude protein	37.6	49.4	48.8	63.8	66.6	68.2
Ether extract	80.0	73.0	77.1	79.8	71.5	71.8
NFE	61.2	60.7	61.8	60.9	56.8	54.2
ADF	2.0	4.2	6.9	9.2	12.1	11.6
Gross energy	47.1	48.7	49.5	50.3	50.4	51.6
Dry matter	47.4	48.8	50.1	51.0	50.0	51.1

[a]From Holter *et al.* (1974).

for nonproducing animals is about 150 kcal/kg body weight. Holter *et al.* (1974) estimated daily requirements of 112, 116, and 91 kcal DE, ME, and net energy per $W^{0.75}$ for snowshoe hares. The arctic hare has a lower basal metabolic rate than would be predicted from its body weight (Wang *et al.*, 1973). The effectiveness of its fur as insulation and the reduction of surface area/volume ratio (the animals when resting achieve a near-spherical shape, with their ears depressed against the body) compensate for the lower metabolic rate, allowing the animal to maintain normal body temperature. MacArthur and Wang (1973) observed that resting metabolic rate in the pika is reduced at low environmental temperatures below the critical temperature.

C. Feed Digestibility in Wild Lagomorphs

A number of digestibility trials with wild lagomorphs have been conducted. Walski and Mautz (1977) evaluated three winter browse species with snowshoe hares. The dry matter digestibilities for diets containing 40% quaking aspen, white cedar, and red maple were 43, 35, and 23%, respectively, indicating a low digestibility of the browse. Digestibility of the crude protein in white cedar and red maple samples was extremely low, varying from mostly negative values to a high of 20.8% (Mautz *et al.*, 1976). Pehrson (1981), working with mountain hares, observed dry matter digestibilities of twigs of various browse plants to range from 18.0% to 41.0%. As noted earlier, mature twigs of browse species are preferred by hares over juvenile shoots. Reichardt *et al.* (1984) compared digestibility of mature versus less mature birch twigs in snowshoe hares. The dry matter digestibility was 38.14% for mature twigs versus 18.15% for less mature browse. Nitrogen digestibilities were 39.65 and −3.06%, respectively. It is apparent that wild lagomorphs survive during the winter on forage of extremely low nutritional value. Presumably they survive because of a high feed intake and the ability of the hindgut to separate out and selectively retain the plant parts with higher nutritive value and to excrete rapidly the indigestible, nonnutritive fiber.

D. Minerals and Vitamins

There have been even fewer studies on mineral and vitamin nutrition of wild lagomorphs than with protein and energy. It appears that all lagomorphs are very efficient absorbers of calcium, and excrete excess calcium in the urine. Nagy *et al.* (1976) observed that the urine was the major route of calcium excretion in jackrabbits, and the urine was loaded with precipitated calcium carbonate, as noted by Cheeke and Amberg (1973) for domestic rabbits. Broadbooks (1965), in an ecological study of pikas, noted that conspicuous white urine splotches accumulated on rocks where the animals urinated, indicating a high content of calcium carbonate in the urine (Fig. 18.3). Pehrson (1983b) noted that the urine

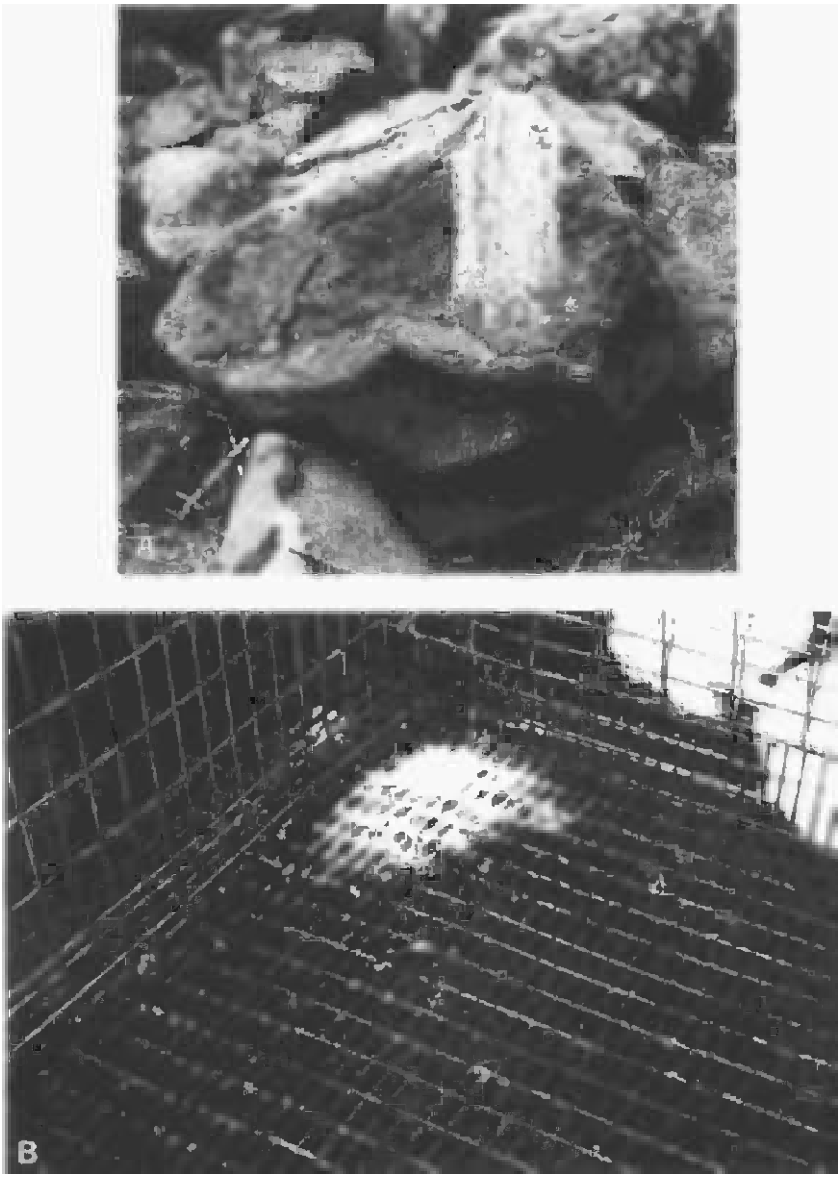


Fig. 18.3 Lagomorphs typically excrete urine with a high calcium content, resulting in white deposits of insoluble calcium carbonate where they urinate. (A) Pika urine splotches on rocks, illustrating the high urinary calcium levels of this species. (Courtesy of H. E. Broadbooks, Southern Illinois University, Edwardsville, and the American Midland Naturalist.) (B) Similar urinary deposits are seen on and beneath the cages of domestic rabbits.

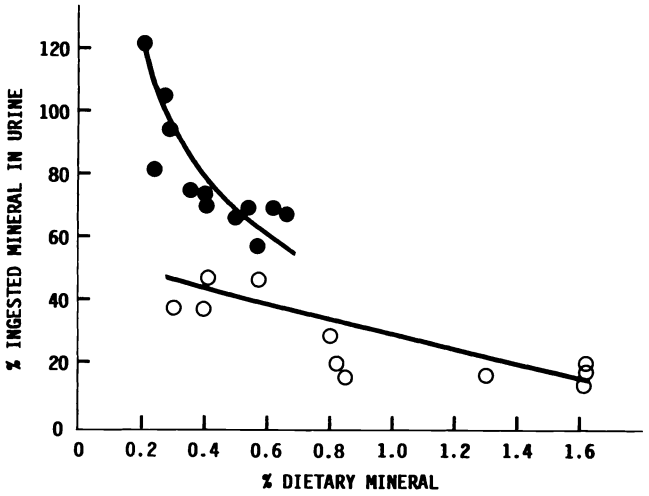


Fig. 18.4. Relationships between dietary intakes and urinary excretion of calcium (○) and potassium (●) in the mountain hare. (Data from Pehrson, 1983a.)

was a major route of excretion of calcium, potassium, and magnesium in the mountain hare. Surprisingly, the relative urinary excretion of calcium and potassium was increased at lower dietary mineral levels (Fig. 18-4).

Myers *et al.* (1981) proposed that attempts by the kidney of the rabbit to conserve sodium in areas of sodium-deficient vegetation cause enlargement of the adrenal glands and impair the animals' ability to cope with metabolic stress. Rabbits with enlarged adrenals due to salt deficiency are unable to survive a challenge of administered ACTH. This hormone is involved in the regulation of salt appetite in rabbits (Blaine *et al.*, 1975). Adrenal enlargement has been noted in snowshoe hares inhabiting a sodium-deficient area (Smith *et al.*, 1978). As noted previously (Chapter 8), the rabbit has an unusually low ability to conserve sodium. Cizek (1961) noted that evolutionarily the rabbit seems adapted to a diet of continuous salt intake. When feed is withheld from rabbits, water intake increases, causing a high urinary loss of sodium and a sodium deficiency. Providing a saline solution in place of water prevents the rise in fluid intake. Palo *et al.* (1983) and Pehrson (1983a) noted that mountain hares consuming birch and willow twigs were in negative sodium balance. The urinary sodium excretion was highest in animals consuming fine-diameter twigs that were highest in phenolic content, suggesting a possible interrelationship. For example, excretion of phenolics might involve an increase in urine volume, which could lead to increased sodium losses. Pehrson (1983b) noted a very high urinary excretion of sodium (27.88% of ingested sodium) when pine needles (which are high in phenolics) were fed to a mountain hare.

The only information available on vitamin requirements of wild lagomorphs concerns vitamin C. Jenness *et al.* (1978) studied the activity of L-gulonolactone oxidase, the enzyme lacking in animals unable to synthesize vitamin C, in cottontails, jackrabbits, and snowshoe hares. Cottontails showed a seasonal change in activity, with about a 10-fold greater level in winter than in summer. In contrast, the activity in snowshoe hares was low throughout the year. Depletion studies on a low-ascorbate diet indicated that liver vitamin C was depleted in snowshoe hares to levels comparable to those in ascorbate-depleted guinea pigs. Jenness *et al.* (1978) hypothesized that snowshoe hares, like guinea pigs, are dependent on dietary sources of vitamin C because they are unable to synthesize it in adequate quantities.

IV. NUTRITIONAL EFFECTS ON REPRODUCTION

Wild lagomorphs are seasonally breeding animals in most environments. Winter is a period of food shortage, and reproduction at this time would be evolutionarily disadvantageous, because of lack of sufficient nutrients and an unsatisfactory environment for neonatal animals. There are several possible physiological mechanisms to account for seasonal breeding. In many seasonally breeding animals, photoperiod has an important role, mediated through the pineal gland. The pineal functions as a neuroendocrine transducer, converting cyclic neural activity generated by light into hormonal output. Light impulses are transmitted from the eye to the pineal by at least two neural pathways. The principal hormone synthesized in the pineal is melatonin; the concentration of melatonin is elevated during the dark portion of the daily light–dark cycle. Light inhibits the rate-limiting enzyme in melatonin synthesis. Melatonin seems to be involved in the regulation of hair coat cycles (e.g., brown summer coat and white winter coat in snowshoe hares), as well as influencing reproductive activity. The effect of melatonin on both functions may be mediated through another hormone, prolactin. A short photoperiod reduces serum prolactin levels (Rose *et al.*, 1985). Changes in serum prolactin throughout the year are synchronized with changes in photoperiod.

There is evidence that dietary factors may also play a role in seasonality of reproduction. Onset of breeding in many small animals coincides with the appearance of green succulent vegetation in the spring (Negus *et al.*, 1977). The onset of breeding in European wild rabbits begins abruptly when succulent plant species begin to grow (Poole, 1960). Wallage-Drees (1983), in Holland, noted that successful conceptions in wild rabbits coincide with the spring growth of grasses, while the onset of lactation for these first litters generally coincides with the growth of forbs. Wallage-Drees (1983) postulated that the growth of grasses is a trigger for the first successful conceptions. This suggestion is supported by

the reports of Berger *et al.* (1977, 1981) and Sanders *et al.* (1981) that grasses contain phenolic substances that are dietary cues for the initiation of reproduction in small herbivores such as meadow voles. They isolated 6-methoxybenzoxazolinone (6-MBOA) as the active component of spring grass forage. 6-MBOA is structurally similar to melatonin, so its activity might be mediated through this hormone.

The apparent stimulatory effect of spring grass on reproduction of seasonally breeding small herbivores might be simply an effect of energy intake. Domestic rabbits are quite responsive to dietary energy intake, and may fail to conceive or resorb the fetuses if energy intake is inadequate. The increased availability of feed (and thus energy) associated with grass growth in the spring might be the factor that triggers reproductive activity.

Pehrson and Lindlof (1984) evaluated the impact of plane of nutrition during the winter on subsequent reproductive performance of mountain hares. Does on the high plane of nutrition received 150 g of pelleted feed as a supplement to twigs and hay, whereas those on the lower plane of nutrition received only twigs and hay. Does on the higher plane of nutrition had higher birthweights of the leverets in the first litter (150 g versus 108 g), while for the second litters the leverets were similar in size to those from the unsupplemented group.

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19

Nutrition of Guinea Pigs

The guinea pig or cavy (*Cavia porcellus*) is one of the few species of American wildlife that has been domesticated. Others include the llama and alpaca domesticated by the Incas of the Andean region of South America, the turkey of the Aztecs, and the capybara of South America, which is in the process of domestication in Colombia, Venezuela, and Brazil. When the Spanish conquistadores arrived in the Andes they found that guinea pigs were widely raised as food animals. The Spanish introduced them to Europe, where they found favor as pets. The name "guinea pig" probably has its origin in the fact that the Europe-bound ships stopped in West Africa, or "guinea," for water and supplies.

Guinea pigs are an important meat source in Bolivia, Colombia, Ecuador, and Peru (Gade, 1967; Huss, 1982; Loetz and Novoa, 1983; Vietmeyer, 1985; and see Fig. 19.1). In Peru, it is estimated that 70 million guinea pigs are produced annually for food (Vietmeyer, 1985). A major research program on guinea pigs as "microlivestock" has been established at the National Agrarian University in La Molina, Peru. A strain of "giant" guinea pig has been developed.

There are numerous advantages of guinea pigs as meat animals in developing countries. In Peru, guinea pigs are raised by many families in their houses. A small stone is placed across the doorway of the house to prevent their escape, and the animals are allowed free run of the house. They are provided with a hideaway in a corner where they can hide and bear their young. They are cared for by the women and children. In the large cities such as Lima, guinea pigs are even raised in high-rise apartments, and are often kept in cardboard boxes under the owner's bed (Vietmeyer, 1985). Guinea pigs for meat production have been introduced into Central America and West Africa. Among the advantages of guinea pig production are the ease of raising the animals, their simple diet of greens and table scraps, and their tractable nature. Their small size and high reproductive rate make them available even to the most poverty-stricken people. They are hardy, and diseases are not a major problem. The young are physiologically quite mature at birth, and begin eating grass and other food almost immediately. Guinea pigs are likely to become increasingly important as food animals in many countries.

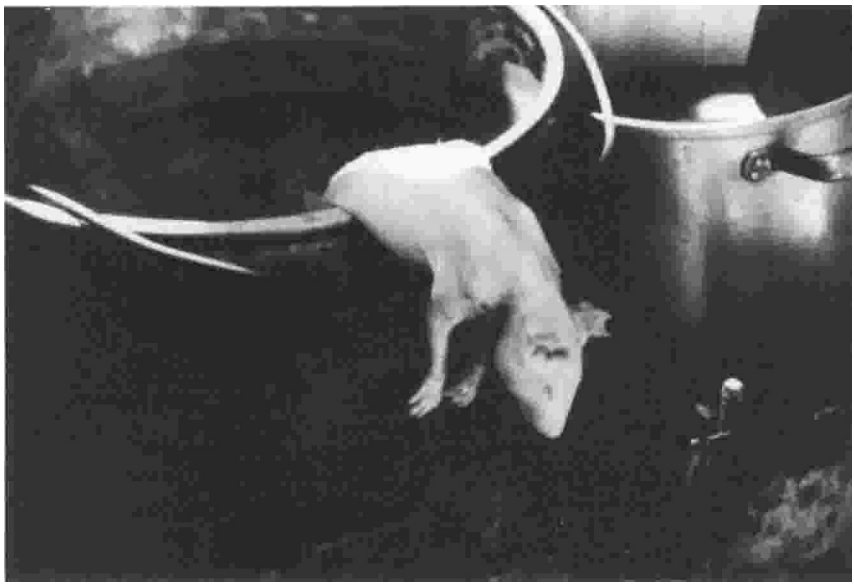


Fig. 19.1 In the Andean countries of Bolivia, Ecuador, and Peru, guinea pigs are important food animals. This is a typical method of preparation of a guinea pig for cooking. (Courtesy of Dr. N. P. Johnston, Brigham Young University, Provo, Utah.)

In the United States, guinea pigs are widely raised as pets and for exhibition purposes. They are commonly referred to as cavies, and are shown at exhibitions such as the annual American Rabbit Breeders Association convention. A national organization, the American Cavy Breeders Association, establishes Standards of Perfection for the various recognized breeds of guinea pigs.

Guinea pigs are widely used laboratory animals. They are the only common animal (besides the monkey) that has a dietary requirement for vitamin C, so they have been extensively used in studies of the metabolism of this vitamin, and in research on collagen synthesis, wound healing, and bone growth.

I. NUTRIENT REQUIREMENTS

A. Protein and Energy

No specific experiments to determine energy requirements of guinea pigs have been conducted. These animals are nonruminant herbivores, with an enlarged cecum in which fermentation occurs. Henning and Hird (1970) demonstrated that volatile fatty acid (VFA) production occurs in the cecum. In contrast to what is

TABLE 19.1

Comparison of Digestibility Coefficients in Guinea Pigs, Rabbits, and Equines Fed a Pelleted Alfalfa Diet[a]

Species	Organic matter	Crude protein	Ether extract	Crude fiber	NFE	Energy
Horse	60.4	74.0	−6.4	34.7	71.5	56.9
Pony	62.5	76.2	−19.0	38.1	73.9	58.3
Rabbit	54.3[b]	73.7	23.6	16.2[b]	68.7	51.8[b]
Guinea pig	62.8	69.0[b]	14.7	38.2	76.0	59.4

[a]Adapted from Slade and Hintz (1969).
[b]Significantly lower than other values ($p < 0.05$).

observed with rabbits, in which butyrate is more important than propionate, butyrate is a minor VFA in guinea pig cecal fermentation. Guinea pigs are more efficient than rabbits in fiber digestion (Table 19.1). Diets commonly contain 9–18% crude fiber. As in rabbits, coprophagy or cecotrophy occurs (Sharkey, 1971), which results in more efficient utilization of protein and provides a source of B vitamins. Holtenius and Bjornhag (1985) have studied coprophagy in the guinea pig. Two types of fecal pellets are produced. The feces that are consumed have a high content of bacterial protein. The proximal part of the colon has a longitudinal furrow between two mucosal folds. It acts as a separation mechanism by which bacteria-rich fluid is concentrated in the cecum. This ensures a

TABLE 19.2

Effect of Coprophagy on Nutrient Utilization by Guinea Pigs[a]

Item	Apparent digestibility (%)	
	Coprophagy allowed	Coprophagy prevented
Alfalfa diet		
Dry matter	53.5	45.4
Crude protein	59.1	44.9
Acid detergent fiber	32.6	22.3
Semipurified diet		
Dry matter	94.4	85.4
Crude protein	91.1	78.4
Acid detergent fiber	88.2	63.2

[a]Adapted from Hintz (1969).

high population of organisms to maintain fermentation, as well as providing the animal with a source of bacterial protein when the cecal contents are consumed.

Hintz (1969) studied the effect of coprophagy on nutrient utilization (Table 19.2). Prevention of coprophagy, by taping wooden tongue depressors lengthwise to the body to prevent bending of the spine, resulted in reduced digestibility of protein and acid detergent fiber (ADF). The fecal excretion of minerals was elevated in animals in which coprophagy was prevented, indicating that recycling of cecal contents is important in mineral utilization. Slade and Robinson (1970) found that dietary urea did not appear to contribute to the nitrogen economy of guinea pigs fed a low-protein diet, suggesting an inability to utilize nonprotein nitrogen.

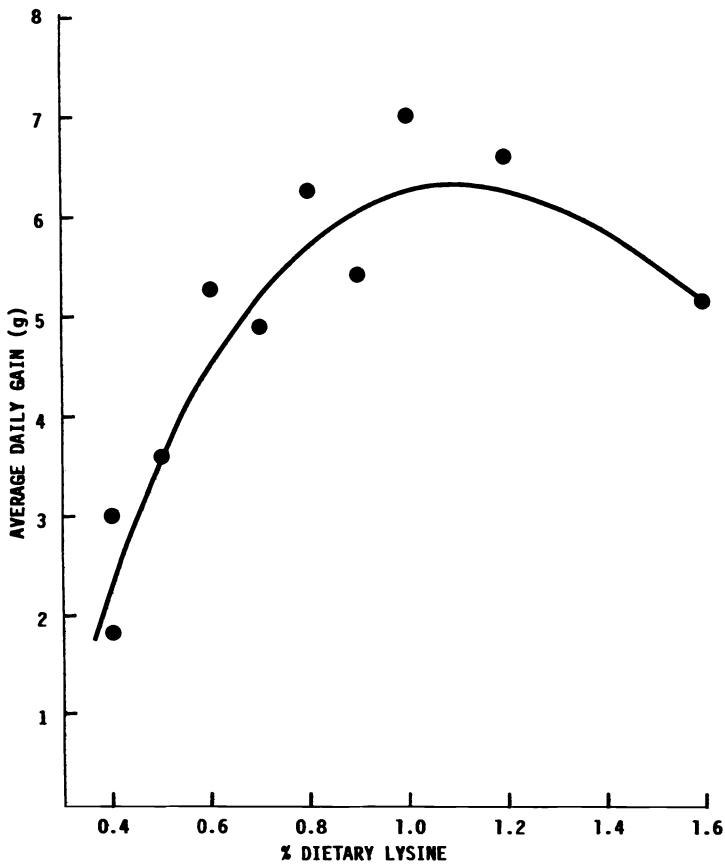


Fig. 19.2 Growth response of guinea pigs to various levels of dietary lysine supplementation. (Data from Typpo *et al.* 1985.)

The predominant hindgut bacteria in guinea pigs are anaerobic lactobacilli; coprophagy is necessary for the maintenance of this population (Smith, 1965). Dehority (1977) isolated several cellulolytic cocci of the *Ruminococcus* genus from guinea pig cecal contents.

Guinea pigs are susceptible to enterotoxemia (Borriello and Carman, 1985), and if given clindamycin (see Chapter 12), may succumb to *Clostridium spiroforme*.

A few studies have been conducted on protein and amino acid requirements. Jeffrey and Typpo (1982) developed a crystalline amino acid diet for use in studying amino acid requirements. Using this diet, they determined that the lysine requirement for growth is about 0.7% of the diet (Fig. 19.2). Other amino acid requirements for growth are 0.71% sulfur amino acids (methionine plus cystine) and 0.16–0.20% tryptophan. Arginine has been shown to be essential [National Research Council (NRC), 1978]. A level of 18–20% crude protein seems to be adequate for growth and lactation.

Johnston and Berrio (1985) compared several types of oilseeds as protein sources for guinea pigs. Soybeans (extruded) and soybean meal were superior in supporting growth to cotton, safflower, and flax seeds (Table 19.3), whereas rabbits fed the same diets performed equally well on all of them. A feed preference test showed that 90% of the total intake of the guinea pigs was of the soybean-containing diets, when all were offered simultaneously free choice (Table 19.3).

In contrast to rabbits and most other animals, guinea pigs do not increase their feed intake when the diet is diluted with cellulose or other sources of fiber

TABLE 19.3

Comparative Performance of Guinea Pigs and Rabbits Fed Extruded Oilseeds as Protein Sources[a]

	Guinea pigs		Rabbits
Seed source	Body weight at 9 weeks of age (g)	Feed preference[b]	Body weight at 8 weeks of age (g)
Soybean meal	837*[c]	48	1560
Soybeans	820*	42	1550
Cotton	542**	1	1390
Safflower	644**,†	2	1520
Flax	670†	7	1490

[a]From Johnston and Berrio (1985).

[b]Percentage intake of each diet over a 30-day period when guinea pigs were offered the five diets free choice in a feed preference test.

[c]*, **, †, Different ($p < 0.05$).

(Hirsch, 1973). Apparently they regulate feed intake on the basis of gastrointestinal fill rather than on metabolic energy need basis.

B. Mineral and Vitamins

Mineral and vitamin studies with guinea pigs have been summarized by the NRC (1978). The most notable specific requirement of guinea pigs is their need for a dietary source of vitamin C (ascorbic acid). They lack the enzyme, L-gulonolactone, required for ascorbate synthesis (Chatterjee, 1973). Vitamin C is needed for hydroxylase reactions, which function in the hydroxylation of proline to form hydroxyproline, and of lysine to form hydroxylysine. These hydroxylated amino acids function in crosslinking of collagen fibers in connective tissue. In vitamin C deficiency, abnormal collagen formation results in disturbed bone growth, hemorrhages, and defective gums, leading to the classical signs of scurvy.

The mineral and vitamin requirements of guinea pigs are summarized in Table 19.4.

C. Unidentified Growth Factors

Over a long period of years, numerous studies have shown that the addition of alfalfa meal or other plant products stimulates the growth of guinea pigs fed purified diets. These studies have been summarized in the NRC report (1978).

TABLE 19.4

Recommended Nutrient Allowances for Growing Guinea Pigs[a]

Nutrient	Amount in diet	Nutrient	Amount in diet
Crude protein	18%	Vitamin A	7 mg/kg
Digestible energy	3000 kcal/kg	Vitamin D	1000 IU/kg
Crude fiber	10%	Vitamin E	50 mg/kg
Calcium	0.8–1.0%	Vitamin K	5 mg/kg
Phosphorus	0.4–0.7%	Vitamin C	200 mg/kg
Magnesium	0.1–0.3%	Thiamin	2 mg/kg
Potassium	0.5–1.4%	Riboflavin	3 mg/kg
Zinc	20 mg/kg	Niacin	10 mg/kg
Manganese	40 mg/kg	Pyridoxine	3 mg/kg
Copper	6 mg/kg	Pantothenic acid	20 mg/kg
Iron	59 mg/kg	Choline	1000 mg/kg
Iodine	1 mg/kg	Folic acid	4 mg/kg
Selenium	0.1 mg/kg	Biotin	0.3 mg/kg
Chromium	0.6 mg/kg	Vitamin B_{12}	0.010 mg/kg

[a]Adapted from NRC (1978).

Knehans *et al.* (1979) examined various extracts of alfalfa and cabbage for their growth-stimulating properties. They suggest that the holocellulose fraction contains a growth-stimulating factor. (Holocellulose is the residue after hot-water extraction followed by sodium chlorite bleaching of the plant material.) The suggested "growth factor" activity is not entirely convincing. The average daily gains reported in their study were in the order of 6–8 g, which is lower than values of up to 20 g/day reported by Typpo *et al.* (1985). Herbivorous animals such as rabbits and guinea pigs tend to find purified diets less palatable than those based on natural ingredients. The "growth factor" activity may be, at least in part, simply a preference for a diet containing a natural plant product such as alfalfa meal. Huang *et al.* (1986) reported evidence that phenolic acids, such as caffeic acid, may be the "growth factors" in fibrous feeds.

II. RESPONSES TO DIETARY TOXINS

As is the case for rabbits, guinea pigs are resistant to the toxic effects of pyrrolizidine alkaloids (Cheeke and Shull, 1985). They have a low activity of liver enzymes that convert the alkaloids to their active metabolites (Chesney and

TABLE 19.5

Composition of a Nutritionally Adequate Diet for Guinea Pig Production[a]

Ingredient	Dietary level (%)
Alfalfa meal	38.15
Ground wheat	28.90
Ground oats	17.75
Soybean meal	13.25
Ground limestone	1.10
Iodized salt	0.50
Dicalcium phosphate	0.25
Minerals[b]	0.05
Vitamins[c]	0.05

[a]From NRC (1978).

[b]Contains 12% manganese from manganous oxide, 10% zinc from zinc oxide, 8% iron from iron sulfate, 0.8% copper from copper sulfate, 0.2% iodine, 0.1% cobalt, made up to 100% with bentonite.

[c]Ascorbic acid is added at 0.62 g/kg diet, vitamins A and D at 2000 IU/kg, and vitamin E at 18 mg/kg.

Allen, 1973). They are particularly resistant to the toxic effects of monocrotaline (Carlton, 1967; Chesney and Allen, 1973; Swick *et al.*, 1982; White *et al.*, 1973), an alkaloid in *Crotalaria* species. They are also resistant to the alkaloids in *Senecio* species such as tansy ragwort (Swick *et al.*, 1982). Other small herbivores such as rabbits, hamsters, and gerbils share this resistance to the toxic effects of pyrrolizidine alkaloids (Cheeke and Pierson-Goeger, 1983).

Jacobs and Labows (1979) presented evidence that wild guinea pigs could distinguish toxic from nontoxic plants. For example, the animals developed an aversion for toxic plants such as common nightshade, or consumed only those parts of the plant with a low alkaloid content. Jacobs (1978) reported that guinea pigs are very tolerant of bitter substances in the diet, such as quinine sulfate. He hypothesized that herbivores may be tolerant of bitter compounds because most of the plants found in their habitats contain bitter secondary compounds. An a priori rejection of bitterness might simply mean that the animal would not eat.

III. EXAMPLES OF ADEQUATE DIETS

Examples of adequate diets based on natural ingredients are shown in Tables 19.5 and 19.6. Several purified diets suitable for laboratory experimentation

TABLE 19.6

A High-Alfalfa Diet Suitable for Growing and Lactating Guinea Pigs[a]

Ingredient	Dietary level (%)
Alfalfa meal	50.0
Ground wheat	32.72
Soybean meal	15.0
Vitamin–mineral premix[b]	1.0
Iodized salt	0.3
DL-Methionine	0.02
Monosodium phosphate	0.86
Ascorbic acid	0.10

[a]From Johnston and Berrio (1985).

[b]Contributes the following per kilogram of diet: vitamin A, 7128 IU; vitamin D, 1979 IU; niacin, 41.58 mg; riboflavin, 7.128 mg; menadione sodium bisulfite, 4.752 mg; folic acid, 0.594 mg; thiamin, 1.188 mg; pyridoxine hydrochloride, 1.188 mg; BHT, 47.52 mg; choline chloride, 1.278 g; manganese, 5.49 mg; zinc, 5.27 mg; iron, 1.83 mg; copper, 0.229 mg.

purposes are available (NRC, 1978). They are usually based on casein, corn starch, and purified cellulose.

Guinea pigs are susceptible to ketosis (Ganaway and Allen, 1971). Pregnant animals that are obese are likely to develop ketosis (pregnancy toxemia) if subjected to some type of stress. The amount of feed offered should be regulated to prevent obesity.

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20

Nutrition of the Capybara

The capybara (*Hydrochoerus hydrochaerus*), a native of South America, is the world's largest rodent, with the adults weighing from 30 to 50 kg. Its habitat is the flood plains and inundated savannah of Venezuela, Colombia, and Brazil. Wild capybara have been hunted for many years as a source of meat, and the hides are in demand for leather production. The animals can be farmed as domestic animals, and in Venezuela, semiwild capybara are "ranched" and rounded-up periodically by gauchos on horseback (Sunquist, 1986). Although there have been sporadic attempts to domesticate the animal, a serious effort began in the 1970s. Projects include those of Dr. E. Gonzalez-Jimenez and Dr. R. Parra at the Central University of Venezuela, and of Dr. Abel Lavorenti at the University of Sao Paulo, Piracicaba, Brazil (Fig. 20.1).

The capybara is a nonruminant herbivore, with an enlarged hindgut where fermentation occurs. Comparison of different segments of the gut with those of ruminants shows that the cecum has a capacity comparable to the reticulorumen (Table 20.1) in terms of the percentage of total gut capacity. Forage is efficiently masticated to small particle size by the grinding action of the molars, while the incisors are capable of harvesting short, prostrate forages that are inaccessible to cattle (Gonzalez-Jimenez, 1977). Capybara do not compete with cattle for feed, but rather use forage unavailable to cattle, including submerged aquatic vegetation. They are proficient swimmers, and spend much of their time in the water. Aquatic weeds, such as water hyacinth, are consumed along with a variety of grasses and sedges.

Few studies on feed utilization or nutrient requirements have been conducted. Gonzalez-Jimenez (1977) reported that the digestibility of forage-based diets by capybara was similar to values obtained with sheep, and with high-concentrate diets, capybara were superior (Table 20.2). Baldizan *et al.* (1984) studied digestion and fermentation in capybara fed either high-forage or high-concentrate diets. The forage diet was fresh-chopped *Pennisetum purpureum* (Napier grass); the concentrate was a commercial pelleted diet. The results for weights of digesta in different gut segments, and contents of dry matter, ammonia–nitrogen, and pH taken at 4 hr after feeding are shown in Table 20.3. The importance of the cecum is evident; about 80% of the forage and 70% of the concentrate diet were

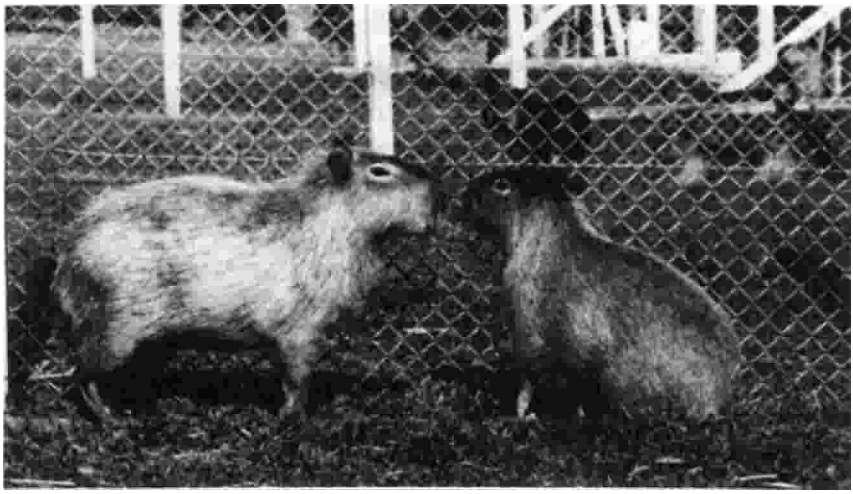


Fig. 20.1 Capybara in a breeding program in Brazil, where the animals are being evaluated for domestication as meat animals.

TABLE 20.1

Gastrointestinal Volume of Various Species[a]

Species	Total contents	Proportion of total contents (%)			
		Stomach	Small intestine	Cecum	Colon
Ruminants					
Cattle	13–18	10.6–16.3	0.9–2.3	0.8	0.8–1.5
Sheep	12–19	9.8–14.9	1.0–1.6	0.9–1.6	0.5–0.7
Nonruminants					
Swine	10	3.6	1.9	1.6	3.4
Nonruminant herbivores					
(a) Cecal fermentors					
Capybara	16.5	1.8	1.0	11.7	1.3
Rabbit	7–18	2–7	0.6–1.8	2.5–7.8	0.7–1.3
Guinea pig	8	1.9	0.9	3.7	1.6
(b) Colonic fermenter					
Horse	16	1.3	2.6	2.4	8.8

[a]Adapted from Van Soest (1982).

[b]Includes rumen, reticulum, omasum, and abomasum in ruminants.

TABLE 20.2

Comparison of Percentage Digestibility of Dry Matter in Concentrate or Roughage Diets in Various Species[a]

Diet	Diet composition (%)				
Concentrate	0	25	50	75	100
Forage	100	75	50	25	0
Species	**Digestibility of dry matter (%)**				
Capybara	50.5	59.0	65.6	76.0	84.7
Rabbit	39.5	49.4	95.5	61.1	79.8
Sheep	49.1	54.5	59.8	65.2	70.5

[a]Adapted from Gonzalez-Jimenez (1977).

in the cecal contents (not including the contents of the small intestine, which were not reported). The pH of the cecum is in a range optimal for microbial fermentation. The production of VFA is shown in Table 20.4. As would be expected, the highest VFA concentrations are in the cecum. Acetate was the major VFA; the proportion tended to be highest with the high-forage diet. As is true with most herbivores (except rabbits), butyrate was a minor VFA. These studies, while limited, indicate that the capybara is a hindgut fermenter, with dietary habits and adaptation to a semiaquatic environment that suggest it has considerable potential as a new livestock species in many tropical countries.

TABLE 20.3

Gut Measurements of Digesta Weight, Percentage Dry Matter, pH, and NH_3–N Concentration in Capybara Slaughtered 4 Hr after Feeding Either a Forage or Concentrate Diet[a]

	Gut section	Weight wet digesta (g)	Dry matter (%)	pH	NH_3–N (mg N/liter)
Forage (*Pennisetum purpureum*)	Stomach	545	12.4	2.5	183
	Cecum	3657	8.8	6.6	78
	Colon	371	13.7	7.0	120
Concentrate	Stomach	917	10.0	3.4	305
	Cecum	2726	8.4	6.3	146
	Colon	244	13.8	6.5	246

[a]Adapted from Baldizan *et al.* (1984).

TABLE 20.4

Concentrations of Volatile Fatty Acids (VFA) in Gut Segments of Capybara Fed Forage or Concentrate Diets[a]

Diet	Gut section	Total VFA (n*M*)	Proportions (%)		
			Acetate	Propionate	Butyrate
Forage	Stomach	6	73	21	6
	Cecum	44	83	15	2
	Colon	26	80	17	3
Concentrate	Stomach	6	65	28	7
	Cecum	41	81	14	4
	Colon	21	77	16	7

[a]Adapted from Baldizan *et al.* (1984).

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APPENDIX 1

Table of Feed Composition

On a practical basis, only a few nutrients need to be considered when formulating rabbit diets. Only those nutrients that are normally of concern are presented here. The data have been taken from various tables of feed composition, or in some cases where data are scanty, have been estimated using the author's best judgment. The list of feedstuffs is comprehensive, and should cover most rabbit diet ingredients encountered throughout the world. Two values are presented for each ingredient: first, dry weight basis; and second, as-fed basis. The digestible energy (DE) values are specific for rabbits, being experimentally derived or, in some cases, estimated from values obtained with other species. The sulfur amino acid content is the sum of cystine and methionine. Common names have been listed first, followed by botanical names if appropriate. In a few cases, where there are numerous common names, the botanical name only has been used.

Individual ingredients may vary widely in composition because of the variation in species or variety (cultivar), storage conditions, climate, soil moisture, and soil fertility. Variations in analytical procedures also have an influence. Therefore, the listed values are averages and are subject to interpretation and modification as necessary, as is true of all "book values."

Table of Feed Composition follows.

Feedstuff	Dry matter (%)	DE (kcal/kg)	Crude protein (%)	Crude fiber (%)	Neutral detergent fiber (%)	Acid detergent fiber (%)	Lysine (%)	Sulfur amino acids (%)	Ca (%)	P (%)
Alfalfa, hay	90	1800	15.3	27	42.3	33	0.63	0.54	1.35	0.27
	100	2000	17	30	47	37	0.7	0.6	1.50	0.30
Alfalfa meal, dehydrated	92	2024	17.5	23.9	40.5	30	0.64	0.55	1.38	0.29
	100	2200	19	26	44	33	0.7	0.6	1.50	0.31
Alfalfa meal, sun-cured	92	2024	16	23.9	41	31	0.8	0.55	1.38	0.28
	100	2200	17	26	45	34	0.9	0.6	1.50	0.30
Amaranthus, grain	92	3220	14.7	4.1	—	—	0.81	0.63	0.18	0.18
	100	3500	16	4.5	—	—	0.88	0.68	0.19	0.20
Amaranthus, leaves	15	285	4.1	—	4.1	1.9	—	—	0.32	0.08
	100	1900	27	—	27	12.5	—	—	2.1	0.52
Apples, fresh	21	693	0.5	1.2	—	—	—	—	0.01	0.01
	100	3300	2.3	5.8	—	—	—	—	0.06	0.06
Apple pomace	90	3294	4.6	16.5	—	—	—	—	0.12	0.11
	100	3660	5.1	18.3	—	—	—	—	0.13	0.12
Artichoke, Jerusalem, tubers	19	608	1.7	0.8	—	—	—	—	—	0.06
	100	3200	9.0	4.3	—	—	—	—	—	0.29
Banana, fruit	24	840	1.1	0.5	—	—	—	—	0.01	0.03
	100	3500	4.5	2.1	—	—	—	—	0.03	0.11
Banana, leaves	16	254	1.0	3.8	—	—	—	—	—	—
	100	1590	6.4	23.7	—	—	—	—	—	—
Barley, grain	89	3115	10.7	5.5	14.9	7.7	0.41	0.37	0.06	0.35
	100	3500	12	6.2	16.7	8.7	0.46	0.42	0.07	0.39
Beans, fava	89	3300	27	8.2	—	—	1.7	0.4	0.14	0.54
	100	3700	30	9.2	—	—	1.9	0.45	0.16	0.61
Beans, kidney, navy, pinto, etc.	90	2565	21.6	4.1	13.0	—	1.58	0.48	0.14	0.46
	100	2850	24	4.6	14.4	—	1.75	0.53	0.15	0.51
Beet, mangel, root	11	374	1.3	0.8	—	—	—	—	0.02	0.02
	100	3400	11.6	8.4	—	—	—	—	0.22	0.22

Beet pulp, dried	91	2675	8.8	19.0	53.7	25.9	0.59	0.06	0.68	0.09
	100	2940	9.7	20.9	59.0	28.8	0.65	0.07	0.75	0.10
Beet, sugar, root	20	780	1.5	1.5	—	—	—	—	0.05	0.05
	100	3900	7.7	7.4	—	—	—	—	0.24	0.24
Bermuda grass, hay	92	1656	11	27.6	68	32	0.74	0.18	0.38	0.56
	100	1800	12	30	74	35	0.80	0.20	0.41	0.61
Black locust, leaves (*Robinia pseudoacacia*)	20	400	4.6	2.7	10.8	5.6	—	—	0.54	0.04
	100	2000	23	13.5	54	28	—	—	2.70	0.20
Bread, white	64	2700	8.5	0.3	—	—	—	—	0.06	0.10
	100	4200	13.3	0.5	—	—	—	—	0.09	0.16
Brewer's grains, dried	91	1820	25.8	14.7	—	—	1.0	0.75	0.27	0.48
	100	2000	28.3	16.1	—	—	1.1	0.82	0.30	0.53
Buckwheat, grain	88	2970	11.4	10.6	—	15	0.62	0.36	0.10	0.33
	100	3375	13	12	—	17	0.71	0.41	0.11	0.37
Cabbage, leaves	12	284	2.2	2.0	2.8	2.8	—	—	0.08	0.04
	100	2370	18	17	23	23	—	—	0.64	0.35
Canola meal (see Rapeseed meal)										
Carob, pods	84	—	4.8	8.0	—	—	—	—	—	—
	100	—	5.7	9.5	—	—	—	—	—	—
Carob, seeds	88	—	11.4	8.2	—	—	—	—	0.34	0.08
	100	—	13.0	9.3	—	—	—	—	0.39	0.09
Carrot, leaves	17	—	2.7	1.9	—	—	0.15	0.07	0.32	0.03
	100	—	16	11	—	—	0.90	0.40	1.94	0.19
Carrot, root	12	480	1.2	1.1	—	1.6	0.15	0.07	0.04	0.04
	100	4000	9.8	9.4	—	13.4	1.27	0.59	0.37	0.32
Cassava, leaves	21	475	5.0	2.0	4	3.8	—	—	0.08	0.08
	100	2260	23.7	9.6	20	18	—	—	0.38	0.38
Cassava, root	32	1088	1.2	1.0	—	—	—	—	—	—
	100	3400	3.6	4.6	—	—	—	—	—	0.03
Celery, stalks	6	156	0.9	0.6	—	—	0.04	0.04	0.04	0.03
	100	2600	15.3	10.2	—	—	0.60	0.60	0.66	0.47

(*continued*)

Appendix 1 (*Continued*)

Feedstuff	Dry matter (%)	DE (kcal/kg)	Crude protein (%)	Crude fiber (%)	Neutral detergent fiber (%)	Acid detergent fiber (%)	Lysine (%)	Sulfur amino acids (%)	Ca (%)	P (%)
Citrus pulp, dehydrated	90	3420	6.4	11.6	—	—	0.20	0.18	2.0	0.14
	100	3800	7.1	12.9	—	—	0.22	0.20	2.22	0.15
Clover, red, fresh	20	440	3.8	4.6	—	—	—	—	0.36	0.01
	100	2200	19.0	23.0	—	—	—	—	1.80	0.40
Clover, red, hay	88	1760	17.3	21.8	49	36	—	—	1.28	0.20
	100	2000	19.7	24.8	56.0	41.0	—	—	1.45	0.23
Clover, white, fresh	19	437	3.8	3.2	—	—	—	—	0.27	0.09
	100	2300	20.0	16.9	—	—	—	—	1.40	0.51
Clover, white, hay	92	2024	21.4	20.9	—	—	—	—	1.75	0.28
	100	2200	23.3	22.7	—	—	—	—	1.90	1.30
Comfrey, leaves	11	235	2.2	1.5	3.2	2.4	—	—	—	0.06
	100	2200	21	13.8	29.8	22.6	—	—	—	0.55
Copra meal (coconut meal)	88	2800	22.6	12.3	—	—	0.48	0.32	0.18	0.59
	100	3180	25.7	14	—	—	0.55	0.36	0.20	0.67
Corn, cobs	90	—	2.8	31.1	—	—	—	—	—	—
	100	—	3.1	34.6	—	—	—	—	—	—
Corn, grain, yellow	88	3500	9.2	2.3	9.9	3.3	0.30	0.29	0.04	0.28
	100	3980	10.4	2.6	11.2	3.7	0.34	0.33	0.05	0.32
Corn, leaves	25	—	4.3	6.7	—	—	—	—	—	—
	100	—	17.2	26.8	—	—	—	—	—	—
Cottonseed meal	92	3220	41.1	12.1	30.1	19.1	1.71	1.36	0.19	1.03
	100	3500	44.7	13.1	32.7	20.8	1.86	1.48	0.21	1.12
Cowpea, leaves (*Vigna sinensis*)	21	420	3.7	4.9	—	—	0.25	0.12	0.32	0.07
	100	2000	17.8	23.1	—	—	1.20	0.57	1.53	0.31
Dandelion, leaves	15	285	2.8	1.7	—	—	—	—	0.20	0.07
	100	1900	18.8	11.1	—	—	—	—	1.30	0.46

Desmodium spp., leaves	16	288	3.3	4.1	7.8	5.9	—	—	0.23	0.08
	100	1800	20.6	25.6	49	37	—	—	1.44	0.50
Dicalcium phosphate	96	—	—	—	—	—	—	—	22.35	18.21
	100	—	—	—	—	—	—	—	23.28	18.97
Distiller's grains, dried	93	3600	27.4	12.8	—	—	0.81	0.70	0.16	1.06
	100	3900	29.6	13.8	—	—	0.87	0.74	0.17	1.15
Fat	100	8000	—	—	—	—	—	—	—	—
	100	8000	—	—	—	—	—	—	—	—
Fat, vegetable oil	100	8500	—	—	—	—	—	—	—	—
	100	8500	—	—	—	—	—	—	—	—
Fat, tallow	100	6500	—	—	—	—	—	—	—	—
	100	6500	—	—	—	—	—	—	—	—
Fish meal, anchovy	93	3720	65	0.8	—	—	5.1	2.6	3.7	2.6
	100	4000	69.8	0.9	—	—	5.50	2.79	3.95	2.82
Fish meal, herring	92	3680	70	—	—	—	5.6	2.8	2.2	1.7
	100	4000	75.4	—	—	—	6.07	3.00	2.41	1.83
Fish meal, menhaden	92	3533	61.5	0.9	—	—	4.8	2.3	5.4	3.1
	100	3840	66.8	1.0	—	—	5.17	2.54	5.83	3.35
Grape pomace (grape marc)	90	666	12.0	23.2	48	49	0.50	0.36	0.52	0.05
	100	740	13.3	25.8	53.2	54.4	0.55	0.40	0.58	0.05
Guatemala grass, leaves (*Tripsacum*	23	—	3.1	6.7	15.2	—	—	—	0.11	0.09
dactyloides)	100	—	13.6	29.2	66.4	—	—	—	0.49	0.39
Guinea grass, leaves (*Panicum maximum*)	24	96	2.6	8.4	17	11	—	—	0.13	0.06
	100	400	11	35	70	45	—	—	0.56	0.23
Jackfruit, leaves (*Artocarpus heterophyllus*)	16	—	2	3.2	—	—	—	—	—	—
	100	—	12.5	20.0	—	—	—	—	—	—
Kale, leaves	15	330	3.1	2.0	—	—	0.12	0.03	0.24	0.08
	100	2200	20.8	13.6	—	—	0.80	0.20	1.60	0.50
Kikuyu grass, leaves (*Pennisetum*	20	—	3	5.1	—	7.2	—	—	0.09	0.05
clandestinum)	100	—	14.8	25.6	—	36	—	—	0.43	0.25

(*continued*)

Appendix 1 (*Continued*)

Feedstuff	Dry matter (%)	DE (kcal/kg)	Crude protein (%)	Crude fiber (%)	Neutral detergent fiber (%)	Acid detergent fiber (%)	Lysine (%)	Sulfur amino acids (%)	Ca (%)	P (%)
Kudzu, leaves	26	390	4.6	7.9	—	—	—	—	0.6	0.09
	100	1500	17.6	30.5	—	—	—	—	2.35	0.35
Lespedeza, hay	92	1290	12.7	28.1	—	—	0.92	0.09	0.92	0.23
	100	1400	13.8	30.5	—	—	1.0	0.10	1.00	0.25
Lettuce, leaves	5	120	1.2	0.6	—	—	—	—	0.05	0.02
	100	2200	22.0	11.2	—	—	—	—	0.86	0.46
Limestone, ground	99	—	—	—	—	—	—	—	36.6	0.04
	100	—	—	—	—	—	—	—	36.6	0.04
Linseed meal	91	3370	36.5	9.0	22.1	9.3	1.17	1.41	0.40	0.83
	100	3700	40.1	9.9	24.3	10.2	1.29	1.55	0.44	0.91
Lupine, seed	94	3480	31.7	13	—	—	1.9	0.75	0.24	0.43
	100	3700	33.7	14	—	—	2.0	0.8	0.25	0.46
Meat and bone meal	94	3100	51	2.3	—	—	2.9	1.2	9.1	4.5
	100	3300	54	2.5	—	—	3.05	1.23	9.73	4.76
Molasses, beet	78	2575	8.0	—	—	—	—	—	0.12	0.02
	100	3300	10.3	—	—	—	—	—	0.16	0.03
Molasses, cane	74	2440	4.2	—	—	—	—	—	0.78	0.08
	100	3300	5.7	—	—	—	—	—	1.05	0.11
Molasses grass, leaves (*Melinis minutiflora*)	22	—	2.0	7.3	—	—	—	—	—	—
	100	—	9.0	33.2	—	—	—	—	—	—
Mulberry leaves (*Morus* spp).	—	—	—	—	—	—	—	—	—	—
	100	—	18	11.2	—	—	—	—	—	—
Napier grass, fresh (*Pennisetum purpureum*)	21	363	2.0	6.4	12.9	8.0	—	—	0.10	0.08
	100	1730	9.7	30.6	61.4	38.2	—	—	0.48	0.37
Oats, grain	90	2700	11.1	11.3	24.6	14.3	0.40	0.36	0.03	0.03
	100	3000	12.3	12.6	27.3	15.9	0.44	0.40	0.03	0.33

Olive pulp, with pits	92	368	5.9	36.5	—	—	—	—	—	—
	100	400	6.4	39.7	—	—	—	—	—	—
Olive pulp, without pits	95	760	14.0	19.3	—	—	—	—	—	—
	100	800	14.7	20.3	—	—	—	—	—	—
Orchard grass, fresh	27	513	3.8	6.9	14.2	—	—	—	0.07	0.11
	100	1900	14.0	25.7	52.6	—	—	—	0.25	0.39
Pangola grass, fresh (*Digitaria decumbens*)	21	—	2.4	6.3	—	7.8	—	—	0.10	0.07
	100	—	11.6	30.1	—	36.9	—	—	0.45	0.35
Panicum maximum, fresh (see Guinea grass)										
Papaya, fruit (*Carica papaya*)	10	—	0.63	0.84	—	—	—	—	0.02	0.02
	100	—	6.3	8.4	—	—	—	—	0.21	0.21
Papaya, leaf	24	382	6.2	—	7.4	3.9	—	—	0.72	0.09
	100	1592	25.8	—	30.8	16.3	—	—	3.00	0.38
Paspalum spp., fresh	27	385	1.9	9.0	—	—	—	—	0.16	0.05
	100	1425	6.9	33.4	—	—	—	—	0.59	0.17
Peanut, hulls	92	—	6.6	59.8	—	—	—	—	0.25	0.06
	100	—	7.2	65.0	—	—	—	—	0.27	0.07
Peanut, leaves	19	380	4.0	4.5	—	—	—	—	0.32	0.06
	100	2000	20.9	23.6	—	—	—	—	1.71	0.29
Peanut, meal	92	2850	48	8.0	12.9	5.5	1.7	1.06	0.20	0.58
	100	3100	53	8.7	14.0	6.0	1.84	1.15	0.22	0.63
Peas, seed	89	2930	23	1.4	17.4	—	0.32	0.48	0.12	0.41
	100	3300	26	6.0	19.5	—	1.71	0.54	0.14	0.46
Pigeon pea, leaves (*Cajanus cajan*)	34	680	5.3	11.3	—	—	—	—	0.35	0.15
	100	2000	15.5	33.2	—	—	—	—	1.02	0.43
Pineapple, fruit, fresh	15	—	0.41	0.41	—	—	—	—	0.02	0.01
	100	—	2.7	2.7	—	—	—	—	0.14	0.07
Potato, tubers	23	830	2.5	0.4	—	—	—	—	0.01	0.06
	100	3600	10.8	1.8	—	—	—	—	0.05	0.24
Raisins, fresh	85	—	3.4	4.4	—	—	—	—	—	—
	100	—	4.0	5.2	—	—	—	—	—	—

(*continued*)

Appendix 1 (*Continued*)

Feedstuff	Dry matter (%)	DE (kcal/kg)	Crude protein (%)	Crude fiber (%)	Neutral detergent fiber (%)	Acid detergent fiber (%)	Lysine (%)	Sulfur amino acids (%)	Ca (%)	P (%)
Ramie (*Boehmeria nivea*)	15	330	2.9	3.2	—	—	—	—	0.7	0.04
	100	2200	19.2	21.1	—	—	—	—	4.60	0.24
Rape, forage	16	350	2.8	2.4	—	—	—	—	0.24	0.07
	100	2200	17.7	15.1	—	—	—	—	1.47	0.43
Rapeseed meal	91	2700	36.9	11.9	—	—	2.0	1.1	0.67	1.16
	100	3000	40.5	13.1	—	—	2.21	1.21	0.74	1.27
Rhodes grass, fresh (*Chloris gayana*)	29	—	3.0	9.7	19	9.3	—	—	0.18	0.12
	100	—	10.3	33.4	65.2	32.2	—	—	0.63	0.40
Rice bran	90	2970	11.5	14.1	22.8	25.6	0.51	0.42	0.14	1.31
	100	3300	12.8	15.7	25.3	28.4	0.57	0.47	0.15	1.46
Rice hulls	91	—	3.2	38.9	73.4	60	0.06	0.09	0.13	0.01
	100	—	3.5	42.7	80.7	65.9	0.07	0.10	0.14	0.08
Ryegrass, fresh	20	—	3.1	4.8	—	—	0.07	0.01	0.10	0.07
	100	—	15.6	24.1	—	—	0.36	0.07	0.50	0.37
Safflower meal	92	—	21.5	32.1	—	—	0.75	0.61	0.25	0.73
	100	—	23.4	34.9	—	—	0.82	0.66	0.27	0.79
Sesame meal	91	—	44.5	6.7	—	—	1.23	1.90	2.02	1.26
	100	—	48.9	7.4	—	—	1.36	2.09	2.22	1.39
Sesbania spp., leaves	20	660	3.8	—	7	5	—	—	0.15	0.07
	100	3300	19	—	35	25	—	—	0.75	0.37
Sorghum, fresh	4	—	2.0	7.4	14.3	9.4	—	—	0.10	0.04
	100	—	8.2	30.7	59.5	39.0	—	—	0.43	0.18
Sorghum, grain (milo)	89	3100	10.6	3.0	18.1	8.3	0.26	0.33	0.05	0.30
	100	3480	11.9	3.4	20.3	9.3	0.29	0.37	0.06	0.34
Soybean, hulls	92	—	11.3	33.1	—	—	—	—	0.54	0.16
	100	—	12.3	36.0	—	—	—	—	0.59	0.17

Soybean, leaves	20	—	3.2	5.9	—	—	—	—	0.29	0.05
	100	—	16	29.5	—	—	—	—	1.45	0.26
Soybean meal	89	3160	44	6.2	12.5	8.9	2.8	1.26	0.32	0.61
	100	3550	49.7	7.0	14.0	10.0	3.19	1.42	0.36	0.69
Soybean, seeds	89	4480	33.7	5.8	—	—	2.27	0.86	0.22	0.62
	100	5035	37.9	6.5	—	—	2.55	0.97	0.25	0.70
Stylosanthes spp., fresh	23	390	2.9	7.9	9.7	7.6	—	—	0.29	0.05
	100	1700	12.8	34.4	42	33	—	—	1.24	0.22
Sudan grass, fresh	21	—	2.5	6.5	11.8	7.8	—	—	0.10	0.04
	100	—	12.0	31	56	37	—	—	0.48	0.18
Sugarcane, bagasse	93	—	2.0	39.7	79	53	—	—	—	—
	100	—	2.1	42.7	85	57	—	—	—	—
Sugarcane, leaves	28	—	1.9	10	11.5	—	—	—	0.13	0.05
	100	—	6.8	36	41	—	—	—	0.47	0.17
Sugarcane, stems	30	—	1.7	9.5	—	—	—	—	—	—
	100	—	5.5	31.6	—	—	—	—	—	—
Sunflower, meal	89	2100	30.2	23.2	—	—	1.18	0.85	0.34	0.95
	100	2400	33.9	26.1	—	—	1.33	0.96	0.38	1.07
Sunflower, seeds	92	3300	17.1	22.3	—	—	0.63	0.56	0.20	0.63
	100	3600	18.6	24.2	—	—	0.68	0.61	0.22	0.68
Sweet potato, leaves	22	—	2.8	5.9	—	—	—	—	—	—
	100	—	12.8	26.9	—	—	—	—	—	—
Turnip, root	8	—	1.6	0.9	—	1.2	—	—	0.04	0.02
	100	—	20.2	11.5	—	15.0	—	—	0.56	0.28
Water hyacinth, leaves (*Eichhornia crassipes*)	6	97	0.8	0.9	—	—	—	—	0.15	0.05
	100	1620	14	15	—	—	—	—	2.5	0.77
Wheat, bran	89	3200	15.5	10.0	41.9	11.2	0.56	0.44	0.14	1.01
	100	3600	17.4	11.2	47.1	12.6	0.63	0.49	0.16	1.14
Wheat, grain	89	3200	12.6	2.7	9.3	3.3	0.39	0.4	0.06	0.35
	100	3600	14.2	3.2	10.4	3.7	0.44	0.45	0.07	0.39

(*continued*)

Appendix 1 (*Continued*)

Feedstuff	Dry matter (%)	DE (kcal/kg)	Crude protein (%)	Crude fiber (%)	Neutral detergent fiber (%)	Acid detergent fiber (%)	Lysine (%)	Sulfur amino acids (%)	Ca (%)	P (%)
Wheat, middlings	89	3200	17.4	6.5	—	—	0.7	0.33	0.10	0.89
	100	3600	19.6	7.3	—	—	0.79	0.37	0.11	1.00
Wheat, mill run	89	3200	15.8	8.8	—	9.8	0.57	0.56	0.10	1.05
	100	3600	17.7	9.9	—	11	0.64	0.63	0.11	1.18
Wheat, shorts	89	2580	13.9	6.8	—	—	0.83	0.64	0.09	0.83
	100	2900	15.6	7.6	—	—	0.93	0.72	0.10	0.93
Whey, dried	93	3400	13.6	—	—	—	0.97	0.50	0.97	0.76
	100	3656	14.6	—	—	—	1.0	0.53	1.0	0.8
Winged bean, leaves (*Psophocarpus tetragonolobus*)	24	—	5.8	—	—	—	0.21	0.10	0.18	0.07
	100	—	24.0	—	—	—	0.87	0.47	0.76	0.30
Winged bean, tubers (*Psophocarpus tetragonolobus*)	39	—	8	3.5	—	—	0.6	0.33	0.04	0.06
	100	—	20.4	9.0	—	—	1.53	0.84	0.09	0.15
Yeast, brewer's	93	—	43.7	3.1	—	3.7	2.9	1.2	0.21	1.06
	100	—	47	3.3	—	4	3.09	1.24	0.22	1.14

APPENDIX 2

Organ Weight in Relation to Body Weight

Organ	Organ weight[a] (g)	Organ weight[a] (as % of body weight)
Body	3352	100
Head	178	5.3
Trunk	1855	55.3
Forelimbs	122	3.64
Hindlimbs	481	14.3
Integument	517	15.4
Musculature	1501	44.8
Digestive tract	128	3.8
Liver	103	3.1
Pancreas	6.47	0.19
Lungs	16.9	0.50
Heart	9.0	0.27
Spleen	1.52	0.045
Thyroid	0.296	0.0088
Adrenals	0.598	0.0178
Kidneys	22.7	0.67
Brain	11.7	0.35
Spinal cord	5.8	0.17

[a]Data adapted from Latimer and Sawin (1955, 1957).

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Index

A

Acid–base balance, of feed, 117
Acid detergent fiber, 204
Acidifier, 269
Acidity, of gut, 21, 81, 85, 183
Adrenocortical hormone, 115
Aflatoxin, 290
Alfalfa, 218
  bitterness of, 283
  intake of, 161
  saponin in, 282
Alkali treatment, of roughage, 89
Alkaloid, 279
Amaranthus spp., 240
Amino acid
  as feed additive, 264
  structure of, 34–37
Ammonia, in cecum, 183
Ampulla coli, 24
Amylase, 80
Angora wool
  production of, 320
  protein requirement for, 50
  seasonal effect on growth, 313
Animal fat, 97
Animal protein, 263
Antibiotic, 265
  effect on enteritis, 187
Antioxidant, 104
Appendix, 24, 86
Appetite, control of, 164
Arctic hare, 336
Arginine requirement, 40
Arrowroot, 243
Ascorbic acid, *see* Vitamin C
Ash, determination of, 206

B

Bacillus piliformis, 191
Bacteroides spp., 30, 182, 184
Banana leaf, 243
Barley, 79, 247
Basal metabolic rate, 70
Bean, 262
Beet pulp, 251
Bentonite, 269
Bile, 21
Bile acid, 21
Bile pigment, 22
Bilirubin, 22
Biliverdin, 22
Biuret, 57
Black locust, 227, 286
Brassica spp., 236, 281
Brassica anemia factor, 287
Breed difference
  in fiber digestibility, 91
  in nutrient requirement, 324
Brewers grain, 250
Buffer, 266
Burn out, 75
Butyric acid
  effect on *Clostridia*, 183
  metabolism of, 83

C

Cabbage, 216
Calcitonin, 109
Calcium
  absorption, 107
  availability, 110
  blood level, 108, 109

Calcium (*cont.*)
excretion, 109, 336
in urine, 107, 108
Calorie, definition of, 63
Canola meal, 256
Capybara
as livestock, 7
digestion in, 354, 356
Carbohydrate, 11
digestion of, 79
in grain, 79
Carbohydrate overload, 81, 182
Carcass fat, 100
Carob meal, 268
β-Carotene, 137
Cassava, 247, 281
Cecal fermentation, 82, 190
Cecal impaction, 188
Cecal paresis, pulmonary edema, 190
Cecotrope, 26, 27, 84, 148
Cecotrophy, 26
and fiber digestibility, 90
in guinea pigs, 346
prevention of, 53, 347
protein digestibility, 51, 52, 54
urea utilization, 56
vitamin synthesis, 147, 148
in wild rabbits and hares, 329
Cecum, 24
Cellular metabolism, 66, 67
Cellulase, 78
Chemical defense, of plant, 332
Chlorine requirement, 116
Cholesterol
in blood, 186, 283
in meat, 100, 101, 103
Chromium, 130
Citrinin, 291
Citrus pulp, 250
Clostridium spp., 30, 186
Clostridium cocleatum, 190
Clostridium difficile, 183, 330
Clostridium perfringens, 178
Clostridium piliformis, 192
Clostridium spiroforme, 122, 178, 348
Clover, 222
Coastal bermuda grass, 230
Cobalt, 129
Coccidiosis, 114, 181, 192, 193
Coconut oil meal, 260
Coevolution, 277
Colon, 25
Comfort zone, 73
Comfrey, 124, 215, 234, 279
Complementary diet, 309
Complex carbohydrate, 77
Copper
alkaloid, 279
deficiency, 120
as growth promotant, 121
in manure, 123
metabolic function, 120
toxicity, 123, 193
Copper sulfate, 122
Copra, 260
Coprophagy, *see* Cecotrophy
Corn, 79, 246
Cottonseed meal, 256, 289
Cottonseed oil, 100
Cottontail rabbit, 328, 329, 331, 334, 335, 339
Creep diet, 302
Crop residue, 215
Crown vetch, 222
Crude fiber, 88, 202
Crude protein, 34, 202
Cyanide, 281
Cyclopropenoid fatty acid, 100

D

Dehydrated forage, 216
Diarrhea, *see* Enteritis
Diet
for guinea pig, 350
quality control, 300
for rabbit, 303, 305, 306, 310, 311, 325
Diet formula, open versus closed, 300
Digestibility
in capybara, 356
determination of, 209
of grass, 90, 91
in guinea pig, 346
of protein, 52
of tropical forage, 228
in wild rabbit and hare, 336
Digestible energy, 64, 207
Digestive strategy, 17, 19
Disaccharide, 77
Distillers grain, 250

E

Eimeria spp., 192
Electrolyte metabolism, 186
Energy requirement
  of guinea pig, 345
  of rabbit, 68
  of wild rabbit and hare, 335
Energy toxicity, 74
Enteritis, 176–192
Enterotoxemia, 177–184, 187, 188
Ergot, 279
Escherichia coli, 30, 179, 184
Essential amino acid, 39, 40, 41
Essential fatty acid, 104
Estrogen, in plant, 284
Ether extract, 96, 205
European hare, 328, 329, 330
European wild rabbit, 329
Extruded seed, for guinea pig, 348
Extruded soybean, 255

F

Fat
  digestibility of, 98, 99
  digestion of, 93, 193
  in rabbit diet, 99
  in rabbit meat, 100
Fatty acid, 96, 102
Fatty liver, 194
Fava bean, 262
Feather meal, 263
Feed composition table, 359–368
Feed conversion, 170
Feed intake, factors affecting, 160, 164
Feed restriction, 172
Feeding, for exhibition, 323
Feeding behavior, 15, 330
Fermentation, in cecum, 82
Fiber
  definition of, 87
  digestibility, 88
  effect on enteritis, 181
  effect on protein utilization, 58
Fishmeal, 263
Flavor, in feed, 267
Forage conservation, 216
Forage, 213–245
Forbs, 214
Foxglove toxicity, 282
Fructose, 77
Fruit pomace, 252
Full-fat oilseed, 261
Fur chewing, 113, 196
Fusus coli, 27

G

Gelatinization, 79
Gestation diet, 306
Ginseng, 270
Glucose, 77
Glucosinolate, 281
Glutathione peroxidase, 126, 127
Glycocalyx, 24
Glycoside, 281
Goblet cell, 190
Goiter, 128
Goitrogen, 128
Gossypol, 289
Grain, cereal, 246
Grain legume, 262
Grain screening, 250
Grape pomace, 252
Grass, 214, 229
Grass tetany, 113
Greens, 238
Guar gum, 189
Guar meal, 261
Guatemala grass, 218
Guinea pig, as meat animal, 7, 344
Guinea pig nutrient requirement, 345

H

Hair, structure of, 312
Hard feces, 26
Hay feeding, 216
Heat stress, 73
Hemicellulose, 78
Herb, 270
Hominy feed, 249
Hot feed, 75
Hydrocephalus, 140, 142
Hypomotility, of gut, 181

I

International Unit
  of vitamin A, 138

International Unit (*cont.*)
of vitamin D, 144
of vitamin E, 146
Inulin, 244
Iodine, 128
Iodine number, 97
Iodine toxicity, 129
Iron, 119

J

Jackrabbit, 74, 331
Jerusalem artichoke, 244
Jojoba meal, 260

K

Kale, 236, 287
Ketosis, 194, 352
Kudzu, 223

L

Laboratory rabbit, diet for, 325
Lactose, 79, 80
Lactation diet, 306
Lactic acid, 84
Lactobacilli spp., 30
Lactulose, 182
Lagomorph, taxonomy of, 329
Lectin, 286
Legume, 213
Lepus spp., 328–340
Lespedeza, 223, 288
Leucaena leucocephala, 224, 286
Linseed meal, 260
Lipid, 11
Lupine, 262, 280
Lysine requirement, 42, 347

M

Magnesium, 113
Maintenance requirement, 70
Maize, *see* Corn
Manganese, 117, 118
Manure, as feed, 245
6-MBOA, 288, 340
Meadowfoam meal, 260
Meat and bone meal, 263
Melanin, 317
Melatonin, 313, 316, 339
Metabolic body size, 69
Metabolizable energy, 64
Methionine hydroxy analog, 45
Microbe, of gut, 30
Microlivestock, 7
Microvilli, 22, 23
Milk composition, 79
Milk enterotoxemia, 188
Milk fever, 110
Milk production, 307
Milkweed toxicity, 282
Millet, 247
Milo, 79, 247
Mimosine, 286, 323
Mineral, 11
Molasses, 250
Molybdenum, 125
Monosaccharide, 77
Motility of gut, 24
Mountain hare, 331, 334, 336, 338, 340
Mucoid enteritis, 188
Mucopolysaccharide, 78, 85
Mucus, 78, 182
Mycotoxin, 290

N

Net energy, 65
Neutral detergent fiber, 204
Night feces, *see* Cecotrope
Nitrate, 159, 291
Nitrogen balance, 321
Nitrogen-free extract, 207
Nonpelleted diet, 310
Nonprotein nitrogen, 54, 55
Nutrient, role of, 12
Nutrient requirement
breed difference, 324
table of, 296

O

Oats, 79, 247
Oat hull, 247
Ochotona, *see* Pika
Ochratoxin, 291
Oil, vegetable, 97
Olive pulp, 254

Organ weight, 369
Organic feed, 216
Osteoporosis, 113

P

Palatability, 160
Palm kernel meal, 260
Pancreas, enlargement of, 285
Papyriferic acid, 332
Parathyroid hormone, 107
Particle size, 168
Pasteurellosis, 8, 196
Peanut meal, 260
Pea, 263
Pectin, 78
Pellet, preference for, 167
Pellet binder, 269
Peristalsis, 24
Pesticide, 159
pH, of gut, 30
Phenolic, 287
Pheomelanin, 317
Phosphorus
  availability, 111, 112
  blood level, 112
Photosynthesis, 11
Phytate, 111, 119, 121
Phytoestrogen, 284
Pika, 328, 329, 332, 333, 336, 337
Pigeon pea, 229
Pinosylvin methyl ester, 333
Pinto bean, 262
Polysaccharide, 77
Population cycle of hares, 331, 332, 333
Potassium, 114, 115, 188
Pregnancy toxemia, 194
Prime, of Rex rabbit, 314
Probiotic, 266
Prolactin, 339
Protein
  digestion of, 50
  excess, 59
  quality, 43
  requirement of cottontail, 334
  requirement of guinea pig, 345
  requirement of rabbit, 46
  structure of, 34
  synthesis, 38, 39
Protozoa, of gut, 31
Proximate analysis, 201
Psyllium, 189
Pygmy rabbit, 331
Pyrrolizidine alkaloid, 124

Q

Quinine, effect on palatability, 161

R

Radish seed, 262
Ramie, 243
Rancidity, 104
Rapeseed, toxin in, 281
Rapeseed meal, 256
Raw soybean, toxicity of, 284
Red clover, toxin in, 280
Red urine, 22, 109, 156
Restricted feeding, 316
Rex rabbit
  diet for, 320
  production of, 311
Ribose, 77
Rice bran, 249
Rice hull, 237
Rickets, 113
Robinia pseudoacacia, 227
Rotavirus, 179
Roughage, 213

S

Sacculus rotundus, 24
Safflower meal, 259
Salt, 116
Saponin, 101, 160, 282
Sarsaponin, 283
Saturated fatty acid, 96
Sawdust, as feed, 244
Screening, 250
Selenium, 126, 146
Senecio spp., 277, 279, 334
Sesame meal, 260
Show rabbit, feeding of, 323
Silage, 217
Snowshoe hare, 313, 329, 331, 335, 336, 339
Soap, in feces, 205
Sodium excretion
  in diarrhea, 114
  of wild rabbit, 338

Soft feces, *see* Cecotrope
Soilage, 217
Sorghum, 247
Soghum tannins, 287
Soybean, 255
Soybean meal, 255
Starch, 78, 79, 182
Starch digestibility, 81
Starch granule, 79
Stomach, 20
Straw, 237
Stress, 151, 187
Sucrose, 77, 79
Sugar, 77, 79
Sulfur amino acid, 41
Sunflower meal, 257
Swelling capacity of feed, 89, 156
Sylvilagus spp., 328–335

T

T-2 toxin, 291
Tall fescue, toxins in, 281
Tannin, 287
TDN, *see* Total digestible nutrient
Thyme, 268
Total digestible nutrient, 65
Toxin, 276, 278, 350
Transit time, 211
Tree leaf, 214
Trefoil, 222
Trichothecenes, 290
Triglyceride, 96
Tropical forages, 217, 227
Tropical grass, 232–234
Tropical legume, 223–229
Trypanosoma, 125
Trypsin inhibitor, 284
Tyzzer's disease, 191

U

Unidentified growth factor, 349
Unsaturated fatty acid, 96
Urea, 55

V

VFA, *see* Volatile fatty acid
Villi, 22, 23
Vitamin, 12, 136
Vitamin A
  blood level, 138, 139
  chemical form, 138
  in coccidiosis, 193
  deficiency of, 140
  liver level, 139
  metabolic function, 139
  toxicity, 141
Vitamin B_{12}, 129
Vitamin C, 150
  effect on enteritis, 150
  requirement of guinea pig, 349
  and stress, 188
  synthesis in wild rabbit, 339
Vitamin D
  and calcium absorption, 107
  metabolism of, 144
  toxicity, 144, 145
Vitamin E, 145, 146, 193
Vitamin K, 147
Volatile fatty acid, 67, 82, 357
Vomitoxin, 291

W

Water
  function of, 154
  intake, 156, 157
Water hyacinth, 241
Water lettuce, 243
Water peanut, 243
Wheat, 79, 247
Wheat mill run, 249
Wheat milling by-product, 248
White muscle disease, 126
Winged bean, 228
Wood, as feed, 244
Wool block, 196

X

Xanthophyll, 137

Y

Yellow fat, 137

Z

Zearalenone, 290
Zeolite, 267
Zinc, 118, 119