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The Gastrointestinal Tract and Nutrient Utilization

The gastrointestinal tract (GI tract) is vitally important to the animal because it is made up of a number of organs that are responsible for utilization of foods and nutrients. Furthermore, some knowledge of its anatomy and function is helpful in evaluating feedstuffs and in formulation of diets (rations) and thus it is of some concern to those readers interested in the nutrition and feeding of animals.

Some knowledge in how the GI tract digests feeds and factors that affect feed utilization is important because losses in digestibility have a marked affect on efficiency of feed utilization. In addition, many feed-related factors may alter normal functioning of the GI tract. Consequently, some degree of familiarity with its anatomy and function are important for a reasonable understanding of practices and problems in feeding livestock. Information presented in this chapter will be very brief. Additional information is available from many other sources; some that the author would recommend are listed at the end of the chapter (1, 2, 3).

The GI tract of simple-stomached mammalian species includes the mouth and

associated structures and salivary glands, esophagus, stomach, small and large intestines, pancreas, and liver. These various organs, glands, and other structures are concerned with procuring, chewing, and swallowing food, and with the digestion and absorption of nutrients as well as with some excretory functions.

Digestion and absorption are terms that will be referred to frequently in this and other chapters. **Digestion** has been defined simply as the preparation of food for absorption. It may include mechanical forces such as chewing (or mastication) or muscular contractions of the GI tract, chemical action of hydrogen chloride (HCl) in the stomach or physiochemical action of bile (from the liver) in the small intestine, or activity from enzymes produced in the GI tract or from microorganisms in various sites in the tract. The overall function of the various digestive processes is to reduce food particles to a size or solubility that will allow for absorption. **Absorption** includes various processes that allow small molecules to pass through the membranes of the GI tract into the blood or lymph systems.

MAJOR ANATOMICAL FEATURES OF THE STOMACH AND INTESTINES

As might be imagined, the GI tract of different types of domestic animals varies considerably. Generally, animal species are divided into groups based on what the main ingredient in their diet is. **Herbivores** are primarily vegetarians, **carnivores** eat other animals, and **omnivores** eat a combination of vegetable and animal matter. If we wanted to include all animal species, there are many other subgroupings that could be included; for example, with birds we have those which are fish eaters, insect eaters, fruit eaters, and so forth.

When discussing digestive physiology of domestic species, it is also common to describe animals as having a simple stomach, often referred to as **monogastric** (or **nonruminant**), or as **ruminant** animals. Ruminant animals are herbivorous and include cattle, sheep, goats, deer, and many other wild species. Horses and mules are herbivorous animals, but they have a simple stomach and a rather large, complex large intestine. Rabbits are herbivores with a simple stomach with a relatively complex large gut. Swine are omnivorous simple-stomached species. Poultry are omnivorous with a complex foregut (three organs replacing the normal stomach) and a relatively simple intestinal tract.

A picture of the partially dissected stomach and intestines of a pig is shown in Fig. 2-1; it will serve as our model for a simple-stomached (nonruminant) or monogastric species.

The shape of the stomach of different animal species varies, as does the relative size within species as well as among species. In swine, for example, the stomach is relatively large, with a capacity in the adult on the order of 6-8 liters. The weight of the stomach and its contents is about 4 percent of body weight as compared to 1 percent in humans.

Most of the stomach is lined with mucosal cells which produce mucus that serves to protect the stomach lining from gastric secretions. In the central part of the stomach there are gastric glands which produce mixed secretions of HCl, enzymes, and mucus. These gastric juices are effective in initiating digestion in the stomach.

In the pig the small intestine is relatively long (15-20 m). The small intestine is generally much shorter in carnivores. The first short section, the duodenum, is the site of production of various digestive juices, and other juices enter the duodenum from the bile duct. These latter

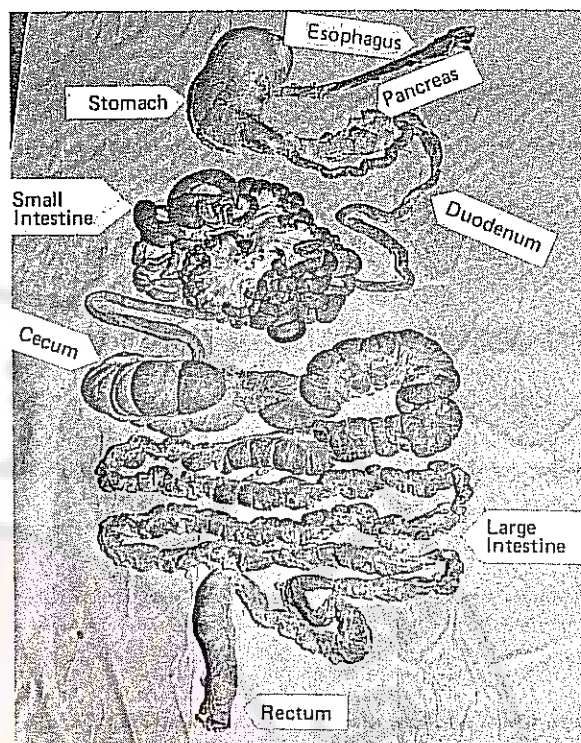


Figure 2-1. The esophagus, stomach, pancreas, and intestines of the pig. Photo by D. C. Church.

juices are derived either from the liver (bile) or the pancreas. The small intestine is lined with small, fingerlike projections, the villi, which serve to increase surface area for absorption (Fig. 2-2).

The large intestine is made up of the cecum, colon, and rectum. The relative length, diameter, and sacculations differ considerably in different species of animals. These organs tend to be much larger (relatively) in herbivorous species.

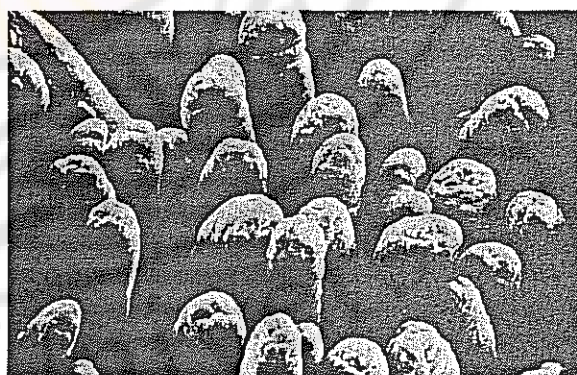


Figure 2-2. A scanning electron micrograph showing the intestinal villi of the baby pig. Courtesy of H. Moon, USDA, ARS, National Animal Disease Center, Ames, IA.

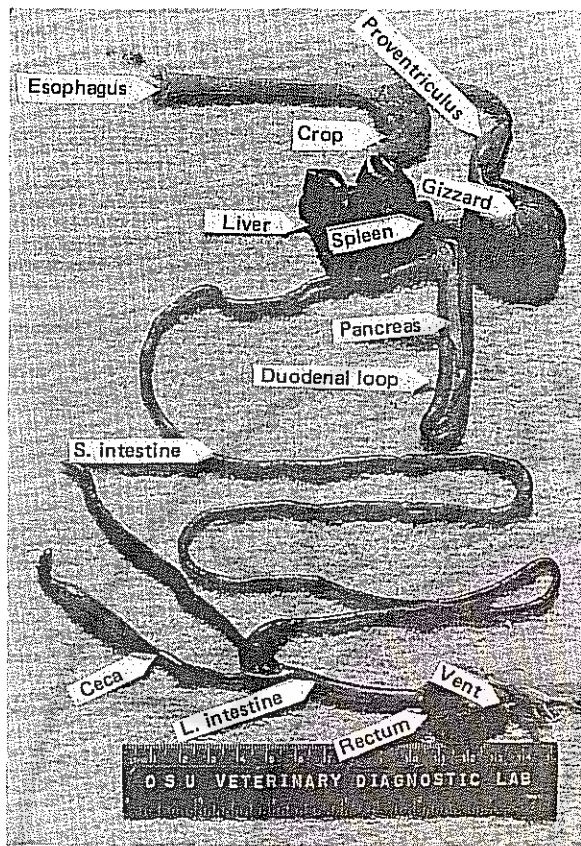


Figure 2-3. The digestive tract of the chicken. Photo by Don Helfer, Oregon State University Diagnostic Laboratory.

In avian species, the crop, proventriculus, and gizzard replace the simple stomach found in monogastric species (Fig. 2-3). Even here there are variations between different types of birds, because most insect-eating or fish-eating species have no crops.

Where a crop is present, ingested food goes directly to it and the crop serves as a temporary storage site; it is an organ which in many species has great capacity for expansion. The proventriculus of birds is the site of production of gastric juices. The gizzard is a very muscular organ with a tough lining. It normally contains grit—small stones and other hard materials. The gizzard serves some of the same functions of teeth in mammalian species, acting to physically reduce particle size of food. With regard to the intestinal tract, birds have a relatively long small intestine, two rather large ceca, and a very short section of large intestine. Birds also differ from mammals in that urine is excreted in semisolid form along with the feces.

In ruminant species the major modification of the GI tract is in the stomach, an organ which has a very complex pattern of motility and physical structure. In most ruminant species the stomach is divided into four compartments, the reticulum, rumen, omasum, and abomasum (Fig. 2-4). In a few species—the camel and related species (pseudoruminants)—the stomach has only three compartments.

The stomach of the ruminant is quite large when measured on the basis of the total GI tract or on the basis of body weight. Whereas the stomach (and its contents) of the pig is about 4 percent of body weight, the stomach of sheep and cattle will be more on the order of 25–28 percent of body weight. If expressed as a percentage of the total GI tract, the pig stomach is about 14 percent of the total, while the stomach of sheep and cattle are about 37 and 45 percent, respectively.

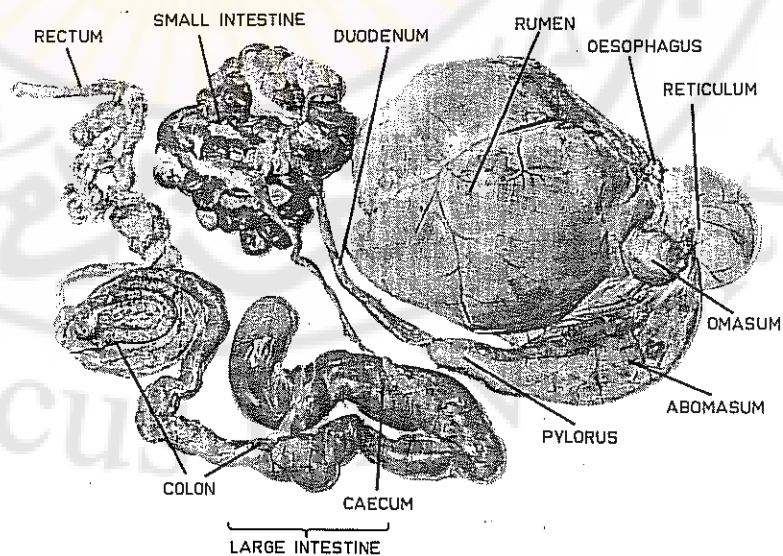


Figure 2-4. The stomach and intestines of the sheep. Courtesy of CSIRO, Canberra, Australia.

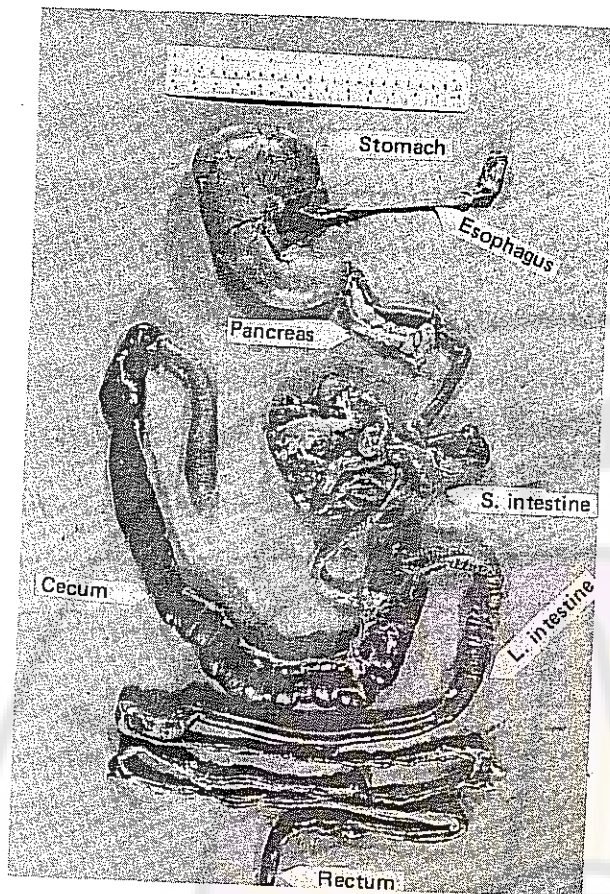


Figure 2-5. The digestive tract of the rabbit. Photo by D. C. Church.

The first three compartments of the ruminant stomach are lined with cell types (stratified *squamous epithelium*) not normally associated with organs that have absorptive surfaces. Yet research evidence indicates that substantial amounts of some materials may be absorbed here.

The reticulum gets its name from a lining of cells arranged in a network resembling the cell shape of a honeycomb, thus its common name of honeycomb. The rumen, or paunch, is lined with papillae, which cover most of the surface but are more dense in the ventral parts of the rumen of most species. It is partially divided into different sacs by pillars which function to control contractions of the organs. The omasum is a spherical-shaped organ containing leaves of different sizes, and it is normally tightly packed with fine particulate matter. The omasum empties into the abomasum, which is comparable in function to the gastric stomach of simple-stomached species in that it produces the usual gastric juices. It differs physically in that there are spiral folds, about 12 in number, extending around the interior of the organ; these

apparently act to provide more surface area for proliferation of the gastric glands.

As with other herbivorous species, the intestinal tract of ruminants is relatively long and moderately complex. The cecum is large, but relatively smaller than that of other herbivorous species such as the rabbit or horse. The large intestine is also relatively large as compared to omnivorous species, although relatively smaller than in the horse.

The rabbit is one example of a herbivorous species that has a simple stomach (Fig. 2-5) accompanied by a very voluminous cecum. Both the cecum and colon are sacculated. The horse is another example of a herbivore with a relatively large sacculated cecum and an extremely large sacculated colon. Both species are examples of animals in which extensive microbial fermentation occurs in the large gut (cecum and/or colon).

FUNCTIONS OF THE GASTROINTESTINAL TRACT

Monogastric and Avian Species

In mammalian animal species, the mouth and associated structures—tongue, lips, teeth—are used for grasping and masticating food. The degree of use of any organ depends on the species of animal and the nature of its food. In omnivorous species, such as humans or swine, the incisor teeth are used primarily to bite off pieces of the food and the molar teeth are adapted to mastication of nonfibrous materials. The tongue is used relatively little. In carnivorous species the canine teeth are adapted to tearing and rending of muscle and bone, while the molars are pointed and adapted to only partial mastication and the crushing of bones. Herbivorous species, such as the horse, have incisor teeth adapted to nipping off plant material, and the molars have relatively flat surfaces that are used to grind plant fibers. The jaws are used in both vertical and lateral movements which shred plant fibers efficiently. Ruminants, on the other hand, have no upper incisors and depend on an upper dental pad and lower incisors for biting off plant material. With regard to avian species, they have no teeth, thus the beak and/or claws serve to reduce food to a size that may be swallowed.

In the process of mastication (chewing), saliva is added, primarily from three bilateral pairs of glands. Saliva aids in forming food into a bolus that may be swallowed easily, and it has

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other functions such as keeping the mouth moist, aiding in the taste mechanisms, and providing a source of some enzymes that contribute to the digestive process.

In the stomach, gastric juices continue the digestive processes initiated by mastication and ensalivation in the mouth. Hydrochloric acid provides for an acidic pH, and the enzymes initiate digestion of protein and, in young mammals, of fats. The partially digested food, now called chyme, passes into the duodenum, where it is subjected to the action of intestinal juices and bile, which gradually raises the pH into the alkaline range. Bile also aids in emulsification of fats, a necessary step in their solubilization and absorption. Enzymes from the pancreas continue enzymic digestion of proteins, fats, and carbohydrates, and these are complemented by additional enzymes produced by glands in the wall of the duodenum. Enzymic activity continues as the food passes into the jejunum and ileum, the other segments of the small intestine. These sections are also the site of most of the absorption of nutrients that occurs in the intestinal tract. Most of the organic nutrients that are absorbed have been absorbed by the time the digesta passes into the cecum. The cecum, although a blind sac, appears to empty and refill itself by means of rhythmic contractions.

Bacterial growth develops in the ileum, cecum, and colon. By the time the digesta reaches the cecum there is a high population of many different organisms, the amount and type depending upon the species of animal and its diet. Absorption of some organic acids and other organic compounds such as ammonia occurs in the cecum and large intestine. Large amounts of water are absorbed by the large intestine, also. This may be one of the major functions of the cecum and of large (or long) and sacculated colons (3).

In addition to the digestion and absorption that occurs, the GI tract is the major route of excretion of many compounds. This statement applies particularly to bile, which is produced by the liver. The liver is a very active site of detoxification of many toxins found in plants or microbes or drugs that may be administered to the animal. The liver also excretes many metallic elements, and it is the site of degradation and excretion of many body compounds such as most of the hormones. These different compounds or detoxified chemicals are excreted via the bile. In the large intestine some net excretion of mineral elements occurs, particularly calcium, magnesium, and phosphorus.

One other important activity that occurs in the GI tract is that of nutrient synthesis. Many different research studies have shown that the microbial population in the cecum and large gut are capable of extensive synthesis of a number of water-soluble vitamins and other organic components of microbial tissues—amino acids and proteins, different carbohydrates, and some lipids. Intestinal synthesis, particularly of some of the vitamins, reduces or eliminates the dependence of the animal on a dietary supply of vitamins that may be produced there.

The amount of absorption of vital nutrients, such as vitamins, that occurs in the lower gut is not clear, although it is usually assumed that relatively little absorption of organic molecules takes place past the ileum. In some animals, particularly rodents such as rabbits and rats, this potential lack of absorption is circumvented by the practice of coprophagy (feces eating). These species typically produce night feces with a different physical character; night feces are believed to originate mainly from the cecum. This material is high in vitamin content and, perhaps, in essential amino acids. The consequence of this is that the animal may survive on diets which would otherwise not have sufficient vitamins and essential amino acids to support life.

Ruminant Species

In the GI tract of the ruminant, ingested food is exposed to very extensive pregastric fermentation. Most of the ingesta is fermented by microbes before it is exposed to typical gastric and intestinal digestive chemicals and enzymes; thus this is quite a different system than that of typical monogastric animal species.

The reticulo-rumen provides a very favorable environment for microbial activity and survival. It is moist and warm, and there is an irregular introduction of new digesta and a more or less continual removal of fermented digesta and end products of digestion. A wide variety of bacterial types may be found in the rumen and typical bacterial counts range from 25 to 80 billion/ml. In addition to bacteria, some 35+ species of ciliate protozoa have been identified from the rumen of animals in different situations, although the variety that may be found in any one animal is considerably less. Protozoal numbers vary widely, but typical counts are on the order of 20,000 to 500,000/ml. These organisms are much larger than bacteria and, although the numbers are less, they repre-

sent about the same amount of microbial protoplasm as from the bacteria.

In addition, flagellated protozoa are often present in the rumen, particularly in young animals, and very high numbers of phages (bacterial viruses) have been observed, although little is known of their importance. Yeast sometimes occur in appreciable numbers, as do other types of organisms, but the bacteria and protozoa are believed to be the most important microbes. The fate of rumen microorganisms is that eventually they pass into the abomasum and intestine and are then digested by the host animal.

The net effect of this thriving microbial population is that it has a marked effect on nutrient requirements and metabolism of the host animal. Fibrous feeds are digested more efficiently in the rumen than in the large intestine or cecum. Cellulose and hemicellulose, in particular, can be digested by microbes, whereas animals do not produce the necessary enzymes. In addition, bacteria can utilize simple forms of nitrogen, such as ammonia or urea, to synthesize their cellular proteins. This reduces the dependence of the animal on high-quality dietary proteins and allows the use of compounds such as urea as protein replacements in their diets. A further benefit is that rumen synthesis is extensive for all vitamins except vitamins A, D, and E and, as a result, the animal is not dependent upon a dietary source of these vitamins with rare exceptions.

One of the chief disadvantages of rumen fermentation is that most dietary proteins are partially degraded and the ammonia produced is resynthesized into microbial protein. This is a wasteful process. In addition, readily available carbohydrates such as sugars and starches are rapidly and completely degraded, the major end products being the volatile fatty acids—acetic, propionic, and butyric. While these acids are used readily by the animal's tissues, they are used less efficiently for energy than the original carbohydrates. Furthermore, in the fermentation process as much as 8–10 percent of the energy consumed is converted to methane, a gas which the animal cannot utilize and which is wasted as a result of microbial fermentation.

These different factors illustrate in a simplified manner why feed conversion of ruminants is low as compared to that of monogastric species. Feed conversion (units of feed consumed/unit of product produced) for ruminants is often twice or more that of monogastric species.

The overall effect of rumen fermentation is that these animals can survive and do well on less complex and lower-quality diets than monogastric species can, but, on the other hand, they use good-quality dietary ingredients less efficiently than do monogastric species.

Associated with rumen fermentation in ruminants is the production of vast amounts of saliva, perhaps as much as 150+ liters/day in mature cows. Saliva contains large amounts of sodium bicarbonate which is vital in maintaining an appropriate pH in the rumen by buffering the acids produced. Saliva is also important in maintaining an optimum moisture content.

In the young ruminant the reticulum, rumen, and omasum are relatively underdeveloped at birth because the suckling animal depends primarily on the abomasum and intestine for digestive functions. As soon as the animal starts to consume solid food, the other compartments develop rapidly, and they attain relative mature proportions by about 8 weeks in lambs and kids, 3–4 months in deer, and 6–9 months in domestic bovines.

An anatomical peculiarity of ruminant species is that they have a structure called the reticular (or esophageal) groove. This structure begins at the lower end of the esophagus and, when closed, forms a tube from the esophagus into the omasum. Its function is to allow milk consumed by the suckling animal to bypass the rumen and thus escape bacterial fermentation. The groove does not appear to remain functional in older animals unless they continue to suckle liquid diets.

In the ruminant stomach there is a well-developed pattern of rhythmic contractions of the various stomach compartments which act to circulate ingesta into and throughout the rumen, into and through the omasum, and on to the abomasum. Of importance also are contractions that aid in regurgitation during rumination. This is a phenomenon peculiar to ruminants. In effect, rumination is a controlled form of vomiting, allowing semiliquid material to be regurgitated up the esophagus, followed by swallowing of the liquids and a deliberate remastication of and reswallowing of the solids. Ruminants may spend 8 hours per day or more in rumination, the amount of time depending upon the nature of their diet. Course, fibrous diets result in more rumination time.

Eructation (belching of gas) is another mechanism that is quite important to

ruminants. Microbial fermentation in the rumen results in the production of large amounts of gases (primarily carbon dioxide and methane) which must be eliminated. This is accomplished by contractions of the upper sacs of the rumen which force the gas forward and down; the esophagus then dilates and allows the gas to escape. During this process much of the gas penetrates into the trachea and lungs, after which it is exhaled through the nostrils.

A common problem in ruminants is bloat, a condition which results, for the most part, from formation of froth in the rumen, particularly after consumption of some legume species or in some feedlot situations. Froth, if found in the area where the esophagus enters the rumen, inhibits eructation. This is a safety mechanism which prevents inhalation of froth into the lungs. Bloat may be a very severe problem in cattle, resulting in many deaths or reduced production in affected animals.

RELATION OF THE TYPE OF GI TRACT AND TYPE OF DIET REQUIRED

The information that has been presented on the anatomy and function of the GI tract of different animals gives some indication of the type of diet (physical nature, chemical composition) which may be optimal for different animals. For example, the GI tract of avian species is relatively short and simple and does not provide for extensive fermentation in the intestines. Some fermentation does occur in the ceca but relatively much less than in most other species. Consequently, avian species do not have the ability to eat fibrous plant material to any degree. In order for most birds to consume their needed nutrients, they must have a diet relatively low in fiber and one that is moderately to highly digestible. This rules out the use of large amounts of feed ingredients such as ground alfalfa hay or of the fibrous grains such as barley and oats if we wish to have maximal consumption and productivity.

In omnivorous species such as swine, the GI tract is capable of utilizing relatively more fiber than avian species but much less than herbivorous species. Some ground legumes can be used in dry rations or adult pigs can be grazed on pastures for a portion of their sustenance, but if the pig must depend entirely on pasture, it must be excellent pasture indeed if productivity is not to suffer greatly. Hogs that run wild

depend on other food items such as nuts, roots, and similar plant material in addition to herbage, but their productivity on this type of diet is much too low to be feasible commercially.

Horses, as an example of nonruminant herbivorous species, can survive and do well on plant material of much lower quality than that required by swine. Data of a recent nature are insufficient to clearly quantitate needs of nutrients, such as the amino acids and vitamins. Hard-working horses clearly require more than roughage in order to maintain body weight and performance, but a substantial amount of roughage is conducive to optimal functioning of their GI tract.

The ruminant GI tract is adapted primarily to a diet of mainly fibrous plant materials. Although cattle can be fed high- or all-concentrate diets, if this practice is carried on for any great length of time (several months), digestive disturbances are likely and much better management of the cattle and care in formulation and milling of their rations is required to obtain maximal performance. Except for recent times when there have been grain surpluses, cattle and other domestic ruminants have traditionally been fed on pasture, hay, or coarse fodders which are of little use to chickens, swine, or humans as food. Present trends suggest a return to these practices to some degree. Although a greater dependence on roughages will reduce productivity, it will probably result in fewer problems with the animals and, perhaps, a more efficient overall utilization of our total agricultural resources.

SUMMARY

The gastrointestinal tract of our common domestic animals varies considerably in anatomy from species to species. In those animals which consume large amounts of coarse herbage, there are adaptations in either the stomach or the intestine. These various modifications allow for either pregastric microbial fermentation of the food consumed (as in ruminants) or in postgastric fermentation in the large intestine (as in the horse) or cecum (as in the rabbit). Omnivorous species such as the pig (or human) have less complex digestive tracts. Thus the type of digestive tract has a major effect on what kind of food can be consumed (over an extended period) and on how efficiently the food will be utilized. Animals with simple stomachs and intestines (for example pigs

and poultry) cannot utilize large amounts of coarse, fibrous herbage. Those with more complex anatomies can utilize the fibrous herbage, and they are apt to have many problems if they are restricted to a diet containing very little fibrous material.

The gastrointestinal tract serves the

animal well by providing the means of digesting the food it eats, absorbing the digested nutrients in the food, as well as recycling water (and thereby reducing water requirements). The GI tract is also the site of excretion of various chemicals by way of bile from the liver or through the walls of the intestines.

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2. Church, D. C., and W. G. Pond. 1988. *Basic animal nutrition and feeding*. 3d ed. New York: Wiley.
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3

The Nutrients, Their Metabolism, and Feeding Standards

INTRODUCTION

Nutrition, of both plants and animals, is one of the major biological sciences. A very considerable volume of scientific literature is available on the topic. The coverage of this topic in this book is intended to provide the reader with some familiarity with the names of the various nutrients, to give a brief amount of information on nutrient function and deficiencies of problem nutrients, and to discuss feeding standards briefly. Further details on these topics can be found in a variety of reference books listed at the end of the chapter (1, 2, 3, 4).

The nutrients required by animals are water, protein, energy, lipids, minerals, and vitamins. In most instances there are differences in requirements among different species of animals, but in practical situations the livestock feeder need not be concerned with a very long list of problem (critical) nutrients in any given situation because the usual feeds consumed will provide an adequate supply of most nutrients.

WATER

Water is an extremely important compound (nutrient) for livestock because it makes up 71-73 percent of the fat-free animal body weight. It has numerous functions of vital importance and, in general, is the most vital material ingested by animals, since a lack of water will have more immediate and drastic effects on animal physiology than the lack of any other nutrient.

Water Functions and Metabolism

Water has many functions. It acts as a solvent for many different compounds. It serves to transport fluids and semisolid ingesta through the GI tract. It transports materials in the blood and other body tissues so that nutrients are moved to the cells and wastes away from the cells. It serves in the elimination of body wastes via urine and, last but not least, is used for evaporative cooling of the animal body when temperatures are elevated.

Water available to an animal's tissues comes from drinking water, water contained in or on feed, and metabolic water produced by chemical reactions (primarily oxidation) of organic compounds in the animal's tissues. The importance of these different sources of water varies from animal species to species. Animals adapted to an arid climate get a higher percentage of their total water from sources other than drinking water than do animals adapted to more humid climates. ●

Water is lost from the body by way of the kidneys as urine, from the GI tract in the feces, from the lungs and skin as water vapor, and from the sweat glands as sweat. Water losses are increased greatly in a warm environment because the animal must increase evaporative losses from the lungs and body surface to maintain body temperatures within a range that allows the animal to survive. Water losses will be increased by greater consumption of high-protein diets (more water is required for urinary excretions), diets high in salts of various kinds, high-fiber diets, and by greater consumption of food, in general. Consequently, if a limited amount of water is available, it would be better to cut down on food consumption before water became restrictive. Certainly, a reduced supply of water will reduce feed consumption and animal productivity, especially for high-producing animals.

Further details on water requirements are given in Ch. 13–25. It is important to remember that water is more critical in warm and hot periods of the year and when productivity is high. Given a chance, animals can reduce somewhat the amount of water required, but this is not a desirable situation unless reduced water intake is a matter of animal survival during a long-term drought.

Water Quality

Water quality, as well as quantity, may affect feed consumption and animal health, because low-quality water will normally result in reduced water and feed consumption. As generally defined, good-quality water should contain less than 2,500 mg/l of total solids; even though 15,000 mg/l (1.5 percent) may be tolerated, production will likely be decreased at this level. Substances which may reduce palatability of water include various saline salts. At high rates of consumption these salts may be toxic, of

course. Substances which may be toxic without much affect, if any, on palatability include nitrates and fluorine as well as salts of various heavy metals. Other materials which may affect palatability or be toxic include pathogenic microorganisms of a wide variety, algae and/or protozoa, hydrocarbons and other oily substances, pesticides of various types, and many industrial chemicals which sometimes pollute water supplies.

The various salts likely to be found in water include chlorides, sulfates and bicarbonates of sodium (Na), calcium (Ca), magnesium (Mg), and potassium (K). The tolerance of animals to salts in water depends on factors such as water requirements, species, age, physiological condition, season of the year, and salt content of the total diet as well as the type and quantity of salts present in the water. Animals will not normally choose to drink saline water if given a choice of good-quality (low salt) water, but within limits they can adjust and will drink saline waters that will be refused at first. However, sudden changes in water quality may cause acute salt poisoning and rapid death. Generally, water containing more than 1 percent NaCl (common salt) is generally not considered good quality because cattle and sheep can tolerate only about 1 percent NaCl without decreasing production in warm climates, and some animals, such as chickens and swine, will not tolerate even this much salt. Levels of 100–200 parts per million (ppm) nitrates are potentially toxic, and 1 g of sulfate/l may result in diarrhea. Thus if there is a question of water quality, the water should be tested, especially in dairy, broiler, layer, or swine water supplies.

Water as a Source of Mineral Nutrients

Water is normally overlooked as a source of nutrients that may be dissolved in it. Granted, the dissolved materials in water vary greatly depending on the source (ground water, surface water, open lakes, closed lakes, and so on) and the mineral content of the soils. If average values are used for mineral content, computations suggest that cattle might receive from 20 to 40 percent of their NaCl requirements, 7 to 28 percent of Ca needs, 6 to 9 percent of Mg needs, and 20 to 45 percent of sulfur requirements (5). In areas where mineral imbalances might be a problem, water supplies should not be overlooked as a source of excess mineral elements.

PROTEIN

Proteins are essential constituents of the tissues of all biological organisms and, in animals, are found in higher concentration in organ and muscular tissue than any other constituent except water. All cells synthesize proteins for part or all of their life cycle, and without protein synthesis life could not exist. Thousands of different proteins are found in the various tissues. They may range from very insoluble types such as feather, hair, wool, and hooves to liquid and highly soluble proteins such as plasma globulins. Proteins are large molecules with molecular weights ranging from 35,000 to several hundred thousand. Each protein has a distinctive function in the animal body (or other biological organisms), ranging from protection of the body surface (hair, skin) to defense against invading organisms. Structurally, proteins have important functions as components of muscle, cell membranes, skin, hair, and hooves. Metabolically important proteins are the blood serum proteins, enzymes, hormones, and immune antibodies, which all have important specialized functions in the body (1). Proteins are synthesized in plant and animal cells where the cell nucleus contains genetic material that determines the nature of the newly synthesized protein. The genetic material, commonly referred to as DNA (deoxyribonucleic acid), is transferred from one generation to another. The nuclear DNA controls the synthesis of all proteins regardless of their function. Thus proteins are vital to animals and must be provided in the diet in one form or other.

Composition

A characteristic of all proteins is that they are composed of long chains of amino acids. An amino acid is an organic acid, such as acetic, which also contains one or more amino groups ($-\text{NH}_2$) attached to the basic molecule. The physical and chemical characteristics of proteins are altered by the different proportions of amino acids, the sequence in which they are bound together, any cross-linking which may occur, and by the presence of other nonamino acid groups or compounds. For example, some proteins may contain metals (for example, hemoglobin, which contains iron); others may contain carbohydrates (glycoproteins) or lipids (lipoproteins). Some, such as casein, an important protein in milk, contain rather large amounts of P (phosphorus).

Although there are more than two hundred naturally occurring compounds that have been classified as amino acids, most proteins contain about twenty different amino acids, regardless of whether the protein is of plant or animal origin. Plants are capable of synthesizing all of these amino acids from inorganic nitrogen (N) sources such as ammonia or nitrate and organic compounds of various types. Many microorganisms also have this capability, but higher animals are not capable of synthesizing all amino acids required by the various tissues, the result being that some amino acids are required in the diet of most animals. The liver is the principal site of synthesis for amino acids.

Essential Amino Acids

The amino acids required in the diets of animals are referred to as essential (or nondispensable) amino acids. Those not specifically required in the diet are called nonessential (or dispensable). Both groups are listed below:

<i>Essential</i>	<i>Nonessential</i>
Arginine	Alanine
Histidine	Aspartic acid
Isoleucine	Citrulline
Leucine	Cystine
Lysine	Glutamic acid*
Methionine	Glycine*
Phenylalanine	Hydroxyproline
Threonine	Proline*
Tryptophan	Serine
Valine	Tyrosine

* Amino acids required in addition to the essential amino acids by the chick for optimal growth.

Extensive studies with rats, mice, dogs, pigs, chicks, and humans have been carried out to evaluate the requirements of these different species. Such studies have been done using purified diets that contain such components as starch, sugar(s), lard or corn oil, purified vitamin and mineral sources, and various combinations of individual amino acids.

These studies have indicated that arginine is required in the diet of some species for maximum growth but not for maintenance; neither is it required by young calves. Asparagine (a derivative of aspartic acid) is required for maximum growth during the first few days of consumption of a crystalline amino acid diet.

Because there are situations in which one or more amino acids may be essential or give an

added response (in growth or other production) when included in the diet, some authors prefer to list the amino acids as essential, semiessential, and nonessential. If divided up in this manner, the lists would be as follows:

<i>Essential</i>	<i>Semiessential</i>	<i>Nonessential</i>
Isoleucine	Arginine	Alanine
Leucine	Cystine	Aspartic acid
Lysine	Glycine	Citrulline
Methionine	Histidine	Glutamic acid
Phenylalanine	Proline	Hydroxyproline
Threonine	Tyrosine	Serine
Tryptophan		
Valine		

In practical animal nutrition, the amino acids most likely to be deficient are lysine, methionine (which contains sulfur), and tryptophan. Primary energy feeds such as corn and milo are quite low in these amino acids, and diets based on high percentages of these grains usually require supplementation with proteins which contain higher levels of these amino acids. Data on the amino acid content of some feed-stuffs are presented in Ch. 9 and in the Appendix.

Ruminants (and some other herbivores) do not require dietary amino acids to the same extent as monogastric species. This is so because the rumen and intestinal microorganisms are capable of synthesizing the essential (and nonessential) amino acids from simple compounds such as urea (or ammonia) and organic acids produced from carbohydrate metabolism. Although ruminants can survive and produce at moderate levels on N sources such as urea, optimum productivity cannot be obtained with such diets. Evidence with high-producing animals, particularly with dairy cows, suggests that they may not necessarily receive optimal amounts of lysine or methionine (2).

Biological Availability of Proteins

The biological availability of dietary proteins is affected by the ability of an animal to digest proteins to amino acids, to absorb these amino acids, and to utilize them in the body to synthesize new proteins. In simple-stomached species of animals, dietary proteins are digested in the stomach with the aid of HCl and pepsin. Further digestion of protein occurs in the lower GI tract as enzymes from the pancreas (trypsin, chymotrypsin) and duodenum (various peptidases) complete the digestion process. Proteins must be

hydrolyzed into smaller particles (amino acids) before they can be absorbed. An exception to this statement is the case of very young mammals. They are capable of absorbing some milk proteins in the early hours of life in order to pick up passive immunity to various diseases.

Protein metabolism in body tissues is a very active process with constant synthesis of new proteins and constant degradation of dead cells. During this process the amino group will be removed from the amino acid (deamination). It may be used in the synthesis of nonessential amino acids or, if in excess, will be further metabolized for excretion. In mammalian species the end product of protein catabolism (degradation) is urea, which is excreted via the urine. In avian species, uric acid is the primary form in which N is excreted from the kidneys.

The digestibility of proteins from different sources is quite different and varies among animal species. As a rule of thumb, we might say that most protein sources used as animal feed will be digested to the extent of 75-80 percent. However, many things may affect this value. For instance, many plant sources contain inhibitors of one type or another (see Ch. 8), and proper processing of animal proteins is generally critical in order to ensure high digestibility.

Efficient utilization of absorbed amino acids for resynthesis of body proteins is primarily related to the distribution of essential amino acids. Dietary proteins vary greatly in the extent to which they may be digested by animals (see Ch. 8). Those that contain essential amino acids at levels needed by the animal are referred to as high-quality proteins. Such proteins are normally highly digestible, but there are many exceptions to such a statement.

There are various means of ranking dietary proteins in addition to the content of amino acids which, by itself, does not provide information on animal utilization. The amount (concentration) of protein is one method. Digestibility of dietary protein is a second method, one often used in selection of dietary protein sources when formulating diets. Biological value (BV) is another way. BV is defined as the percentage of digested and absorbed N (protein) that is retained in the body for productive functions; it is an indirect means of evaluating how well a specific protein supplies the essential amino acids. Whole egg protein has a BV of about 100; meat proteins, 72-79; cereal proteins, 50-65; and gelatin, 12-16. Of course, in practice an animal would normally consume proteins from several sources in any given meal. Thus the in-

adequacies of a poor-quality protein are apt to be balanced out by others of higher quality. When this does not occur, then the animal's tissues are limited in the amount of new protein that can be synthesized. For example, if absorbed lysine is in short supply but is required for the proteins being synthesized, the amount of synthesis will be governed by the available lysine. Other essential amino acids present over and above the amount that can be used with the lysine will then be used primarily as an energy source and will not function as amino acids. This situation leads to poor performance and low feed efficiency if continued for any length of time.

Other measures of protein adequacy are the protein efficiency ratio (PER) and net protein value (NPV). PER is by definition the number of grams of body weight gain of an animal per unit of protein consumed. NPV measures efficiency of growth by comparing body N resulting from feeding a test protein with that resulting from feeding a comparable group of animals a protein-free diet for the same period of time. NPV can also be computed by multiplying the digestibility of a protein by the BV. Further details on this topic can be found in other sources (1).

In general, protein quality is less important to ruminant animals than to simple-stomached species. In the rumen a high proportion of dietary proteins are hydrolyzed by rumen microbes to amino acids, many of which are further degraded to organic acids, ammonia, and carbon dioxide. The free ammonia in rumen fluid is utilized by bacteria to synthesize new amino acids essential for their function. The bacteria, in turn, may be ingested by protozoa which go through the same type of cycle of degradation and resynthesis of proteins. Eventually, bacterial, protozoal, and undegraded dietary proteins pass into the intestinal tract, where they are digested to some degree and the amino acids absorbed. Bacterial and protozoal proteins are generally lower in BV than are high-quality proteins found in egg and milk, but they are of higher quality than many plant sources. Thus the tendency is to degrade the value of very high-quality proteins and upgrade that of low-quality dietary proteins. These various mechanisms allow the use of nonprotein-N compounds such as urea to be used as a feed ingredient in ruminant diets, although there are some limitations to its usage.

The value of a protein to a ruminant animal is related to how soluble the protein is in the rumen and how much of it will be de-

graded by rumen microorganisms. Some high-quality protein sources, such as fish meals, are not degraded to a great extent in the rumen. If such proteins pass into the intestinal tract and are digested rather completely, they are, therefore, able to supply the animal with a greater abundance of amino acids, such as lysine and methionine, which might otherwise be limiting. There must, of course, be an adequate supply of soluble and degradable protein to nourish the rumen microorganisms. Further information on this topic is presented in Ch. 8.

Protein Requirements

This topic is discussed to some extent in the section on feeding standards and in more detail in the chapters on feeding livestock (13-25), but some comments are in order here.

As explained earlier, the requirement for monogastric and avian species is for the essential amino acids. Although there are substantial volumes of data on the amino acid content of all major feedstuffs, chemical analyses do not tell us how much of a given amino acid will be digested and absorbed. Thus the requirements (given in various appendix tables) are usually expressed in amounts of total protein with additional information on some of the limiting amino acids.

Requirements are always highest (in terms of concentration in the diet) for young, rapidly growing animals. The needs decrease as the growth rate declines. Requirements are lowest for adult animals in a maintenance situation. They are increased during pregnancy and increased markedly during periods of peak lactation or egg production. Further details will be given in other chapters.

Protein Deficiency

Protein deficiency can be a result of one or more limiting amino acids or an inadequate protein consumption. Signs of protein deficiency include poor growth rate and reduced N retention by the body, poor utilization and lower consumption of feed, lowered birth weights often accompanied by high infant mortality, reduced milk or egg production, and infertility in both males and females. The severity of the symptoms will be highly related to the severity of the deficiency. From a practical point of view, insufficient protein will most noticeably affect young, rapidly growing animals, lactating females, or laying hens. Normally, a protein deficiency will be ac-

accompanied by deficiencies of one or more other nutrients, energy in particular for herbivore species.

Subclinical deficiencies (those which cannot be diagnosed by examination of the animal) are probably relatively common in many countries. One reason is that proteins are expensive feed ingredients to purchase, and the tendency of livestock feeders is to reduce the level or quality fed if possible. Sometimes, such mild deficiencies can be detected by lowered blood proteins, reduced growth rates, and so on, but it is usually difficult to be quite sure that the animal is deficient. Only in the case of lysine is there a specific sign of a deficiency. In black feathered turkeys, a lysine deficiency produces a white barring of the primary flight feathers.

Excess Protein

Free-ranging herbivorous animals in a natural habitat would normally encounter excess protein only during periods of lush growth of vegetation in the spring months (or early in the rainy season in the tropics). With confined domestic animals it is not a common problem because of the costs associated with protein supplements. Most of the studies that have been done do not suggest any marked adverse effects from consuming excess protein, particularly if the protein is of adequate quality and consumption is not continued for long periods of time. However, there is some information on dairy cattle indicating a decline in fertility of cows consuming high levels of protein (6).

Toxicity and death can occur in ruminant animals fed urea as a N source, particularly if fed without an adequate supply of carbohydrates such as starch or sugar. This situation arises when animals are consuming low-quality forage which results in a relatively high pH in the rumen. In this condition, urea is rapidly hydrolyzed to ammonia. The ammonia is absorbed quickly, overloading the liver system, which would normally detoxify it, resulting in a buildup in the blood and tissues and, if present in sufficient amounts, toxicity and/or death. It can also occur in other conditions if animals are not adapted to urea or if feeds have been poorly mixed, allowing the consumption of excess amounts of urea.

CARBOHYDRATES

Although plants synthesize many different carbohydrates, the basic compound is glucose, from

which more complex or different carbohydrates are synthesized. In plant tissues, carbohydrates may comprise 50 percent of the dry matter of forages and as much as 80 percent in the kernels of some cereal grains. Thus, carbohydrates are the major dietary components for all herbivorous animals. For the animal, carbohydrates serve as a source of energy or as bulk in the diet, but there is no specific requirement for any individual carbohydrate compound.

Dietary Carbohydrates

Chemically, carbohydrates are classified on the basis of the number of carbon (C) atoms each molecule contains or on the numbers of simple sugar molecules contained in more complex compounds. The various classes are shown in the following table, along with the most common carbohydrates in each class.

<i>Monosaccharides (1 sugar molecule)</i>	
Pentoses (5-C sugars)	
Arabinose	
Ribose	
Xylose	
Hexoses (6-C sugars)	
Fructose	
Galactose	
Glucose	
Mannose	
<i>Disaccharides (contain 2 sugar molecules)</i>	
Cellobiose	glucose-glucose*
Lactose	glucose-galactose*
Maltose	glucose-glucose*
Sucrose	glucose-fructose*
<i>Trisaccharides</i>	
Raffinose	glucose-fructose-galactose*
<i>Polysaccharides (contain multiple sugars)</i>	
Pentosans (contain pentose sugars)	
Araban	arabinose*
Xylan	xylose*
Hexosans	
Cellulose	glucose*
Glycogen	glucose*
Inulin	fructose*
Starch	glucose*
<i>Mixed Polysaccharides</i>	
Gums	pentoses & hexoses*
Hemicellulose	pentoses & hexoses*
Pectins	pentoses & hexoses*

*sugars contained

Glucose (also called dextrose) and fructose are the most common simple sugars in feed and food ingredients. They occur as the simple sugars in both plant and animal tissues, but only in low concentrations. Fructose is converted readily to glucose in the animal body and is, therefore, available to body metabolism as glucose. As indicated in the listing, other simple sugars are present in feeds, but in even smaller amounts than those mentioned previously.

The disaccharides (sugars containing two units of simple sugar) and polysaccharides (those containing numerous units of simple sugars) are present in plant tissues in much higher concentrations than the simple sugars. Sucrose (common table sugar) is a combination of glucose and fructose and is found in high concentrations in plants such as sugar cane or sugar beets. Lactose (milk sugar) contains glucose and galactose and is found only in milk. Maltose, which is an intermediate compound between glucose and starch, is composed of two glucose units.

Starch is the most important polysaccharide of a nonfibrous nature found in plants, particularly in grains and tubers or other root crops. It is composed of units of glucose. There are two main types of starch designated as amylose and amylopectin. The major difference between them is the amount of side chains attached to the primary chain of glucose units. Starches from different plant sources vary in the ratio of amylose and amylopectin and in their microscopic physical structure, presumably because of differences in the protein matrix within which the starch has been deposited. Even though these differences exist, starches are generally highly digestible by animals.

The fibrous plant polysaccharides provide structural support for plant tissues. In forages the most important are cellulose and hemicellulose. In woody tissues high levels of xylans are present.

Like starch, cellulose is synthesized from glucose units, but the glucose molecules are linked in a manner that makes it rather insoluble and difficult to degrade. Hemicellulose includes a broad group of plant components that are long chains of five- and six-carbon sugars, and it is also resistant to degradation, although it is more soluble in some solvents than cellulose.

↓ Absorption and Metabolism

Dietary carbohydrates must be digested to simple sugars before they can be absorbed by

simple-stomached animals. A very small amount of amylase (starch digesting enzyme) is present in the saliva of some species. The pancreas produces a potent enzyme (pancreatic amylase) which will degrade the starches and other similar polysaccharides. Other enzymes capable of hydrolyzing the disaccharides are produced by mucosal cells in the duodenum.

The simple sugars are absorbed rapidly by the small intestine (duodenum, jejunum), some studies generally indicating that glucose and galactose are absorbed most rapidly while some of the five-carbon sugars, such as xylose and arabinose, are absorbed at a slower rate. A high proportion of simple sugars will be converted to glucose in the wall of the small intestine. Those that are not will be modified by the liver or metabolized in other ways. Thus all absorbed sugars become available to the body cells for energy or other metabolic processes. The animal body stores very little energy as carbohydrate, but some glucose is converted to glycogen, a type of starch, which is stored in the liver and muscle tissues in small amounts and provides a readily available source of quick energy for the tissues. The ready availability of glycogen is one reason that animals can maintain blood glucose levels within a relatively narrow range. Because they are relatively soluble and/or easily digested, the mono- and disaccharides and starch are frequently referred to as readily available carbohydrates.

For some reason animals never developed the ability to produce enzymes capable of digesting cellulose, hemicellulose, and other fibrous carbohydrates. Although digestion of these compounds does, indeed, take place in their GI tract, it is a result of microbial action. A wide variety of microbes are capable of digesting fibrous carbohydrates, and a number of these species may be found in the large intestine (cecum and colon). Of the various domestic simple-stomached species, the horse digests the most fiber. Poultry digest very little. Swine and rabbits are intermediate.

When a young ruminant begins to eat solid food, it gradually develops a bacterial and protozoal population in its rumen. These microorganisms, in turn, can digest dietary carbohydrates. With regard to the readily available carbohydrates, they are attacked rapidly and metabolized almost completely to carbon dioxide, water, heat, and the volatile fatty acids (primarily acetic, propionic, and butyric). The volatile fatty acids are absorbed through the rumen wall or the intestine and provide a source

of energy for the animal. In the case of animals being fed high-grain diets at high levels, sometimes a substantial amount of starch may pass through the stomach into the intestine. Here, some of the starch will be digested as with monogastric species. However, the amount of amylase produced by the pancreas of ruminant animals is quite low, a factor which limits starch digestion. Consequently, if a high level of starch passes into the ruminant gut, some will be digested normally, some will be digested by microbes in the cecum and colon, and some may be excreted in the feces. In addition, other enzymes needed for digestion of disaccharides are low, with the exception of lactase in suckling animals. Ruminants do not produce sucrase, the enzyme needed for digestion of sucrose.

Ruminant animals are the most efficient of herbivorous species at digesting fibrous carbohydrates. The fibrous carbohydrates are usually retained in the rumen for some period of time—perhaps as long as 6 to 10 days by cattle fed long straw, although higher-quality forage (alfalfa hay, for example) will be retained for a much shorter period of time. At any rate, forages are retained long enough for action by the microbes. A combination of microbial action and chewing during rumination act to reduce particle size so that eventually the fibrous particles are either digested or chewed to a point where they will pass out of the rumen. The end products of rumen (or gut) digestion of fibrous carbohydrates are the same as with the readily available carbohydrates, except that higher levels of acetic acid and lower levels of propionic acid are characteristic of fibrous carbohydrates.

A comment is in order about lignin. Lignin is a long-chain polymer (similar to some plastics) which is present as a structural component in plant tissues. It is not a carbohydrate, but it is important from a nutritional point of view in that it is essentially undigestible but at the same time it interferes with the digestion of the plant tissues. Lignin content generally is found in higher concentration in forages of poor quality. In legumes, for example, much more lignin is present in the stems than in the leaves, and the overall content tends to be higher in legumes than in grasses.

LIPIDS

Lipids are organic compounds that are insoluble in water but soluble in organic solvents. Quite a variety of different types of compounds are found in both plant and animal tissues, all

of which serve some important biochemical or physiological function. Chemically, lipids range from fats and oils to complex sterols. Lipoproteins are important constituents of all cell structures. Fats serve as a concentrated form of stored energy—one gram of fat yields about 9.45 kilocalories (kcal) of heat when completely combusted compared to about 4.1 kcal for a typical carbohydrate. Phospholipids and glycolipids are compounds containing fatty acids and P or a carbohydrate, respectively. They are involved in numerous biochemical functions in biological systems. Sterols range from compounds such as cholesterol to vitamin D and, likewise, are involved in numerous functions in animal tissues.

Nutritionally, the important lipids are fats and oils, the two being differentiated on the basis of melting points. Fats are solid at room temperature, while oils will be liquid at room temperature. Fats are composed of fatty acids of varying lengths and structures and one molecule of glycerol. They are referred to as mono-, di-, and triglycerides, depending on the number of fatty acids present. Fatty acids consist of chains of C atoms ranging from 2 to 24 or more Cs in length with a carboxyl (acid) group on the end. If all of the available positions on the C atoms are taken up with hydrogen, the fatty acid is referred to as saturated. If one or more double bonds are present (in place of hydrogen), the fatty acid is unsaturated. The most common fatty acids found in fats are listed in the table following.

Fatty Acid	Abbreviated Designation*
Saturated acids	
Acetic	C2:0
Propionic	C3:0
Butyric	C4:0
Caproic	C6:0
Caprylic	C8:0
Capric	C10:0
Lauric	C12:0
Myristic	C14:0
Palmitic	C16:0
Stearic	C18:0
Arachidic	C20:0
Lignoceric	C24:0
Unsaturated acids	
Palmitoleic	C16:1
Oleic	C18:1
Linoleic	C18:2
Linolenic	C18:3
Arachidonic	C20:4

*For acetic acid, the C2 means that it contains two C atoms and :0 means that no double bonds are present.

Most fatty acids found in animal tissues are straight-chained and contain an even number of Cs. Branched-chain fatty acids and those with an odd number of Cs are often produced by microorganisms, and, in the case of ruminant animals, body fats may contain substantial amounts of such fatty acids. Other differences in structure and position of double bonds occur but are outside the scope of this discussion (1, 2). Oils found in plant seeds are generally triglycerides. However, in forage, a high percentage of the lipids are diglycerides with a molecule of galactose (simple sugar) attached to the glycerol molecule.

Metabolism

In simple-stomached animals, fats are digested in the small intestine, primarily as a result of the action of bile, which emulsifies the fat, thus greatly increasing the surface area, and by pancreatic lipase, an enzyme which hydrolyzes fatty acids from the glycerol molecule. Some diglycerides are absorbed, but the majority of absorption is as monoglycerides and fatty acids. The majority of the longer-chain fatty acids are absorbed by lacteals into the lymph system and enter the blood stream just before the *vena cava* vein enters the heart.

In ruminant animals the rumen microbes present are capable of altering dietary fatty acids. When fats are ingested in amounts typical of common feed ingredients (2-6 percent), a high proportion of the unsaturated fatty acids will be saturated by the rumen microorganisms. If abnormal amounts of fat are ingested, many of the unsaturated fatty acids will not be saturated and an abnormal rumen fermentation may result. Fats in feeds can be protected from rumen action by treating the feed with aldehydes such as formaldehyde. Such compounds inhibit rumen metabolism of proteins, which in turn protects the fats in the plant or animal feed material.

Absorption of fatty acids is usually quite high, depending on the amount in the diet. For example, in one study absorption by chicks of different fats was shown to be as follows: soybean oil, 96 percent, corn oil, 94 percent; lard, 92 percent; beef tallow, 70 percent; and menhaden oil, 88 percent. Generally, oils are absorbed more completely than are highly saturated fats. Fats in the diet also stimulate absorption of the fat-soluble vitamins (A, D, E, K) and other fat-soluble substances.

After absorption as a fatty acid or monoglyceride, triglycerides are resynthesized

in the mucosal tissues of the gut. The fats are then transported to the various tissues, particularly the liver, where they are used in synthesis of various compounds required by the body, or they are stored in the tissues (fat depots) or metabolized as a source of energy. The end products of energy metabolism are carbon dioxide, water, and heat. In instances where animals are fasting or if abnormal situations develop (diabetes, ketosis in dairy animals), intermediate products known as ketones may be present in high amounts. If present in moderate amounts, these compounds can be further metabolized for energy by most tissues, but if present in excessive amounts, they are detrimental to the animal and will normally be excreted in urine, milk, or via the lungs.

Animals may synthesize large amounts of body fat even though the dietary intake of fat is quite low. The mechanism for synthesis is relatively complex, but in simple terms it can be said that acetyl units (structure similar to acetic acid) are the basis of synthesis of most body fats. Such units can be provided by carbohydrate metabolism or metabolism of some of the amino acids.

Essential Fatty Acids

Linoleic and linolenic acids are required in the diets of monogastric species at a level of about 1 percent of the energy in the diet. A third acid, arachidonic, can be synthesized from linolenic acid, but it may be required in the diet if linolenic acid levels are marginal. The essential fatty acids are important because they are an integral part of the lipid-protein structure of cell membranes and they appear to be important in the structure of prostaglandins, hormone-like compounds that have a number of important effects on body biochemistry. Deficiencies of the essential fatty acids have been demonstrated in pigs, chickens, calves, dogs, mice, and guinea pigs. Such signs as scaly skin and necrosis of the tail, growth and reproductive failure, edema, subcutaneous hemorrhages, and poor feathering (chicks) have been observed. It is rather puzzling that deficiencies have not been shown in adult ruminants fed purified diets with no added fat, because the rumen microorganisms are capable of saturating these particular fatty acids.

Deficiencies of the fatty acids have, in most cases, been produced on purified diets or diets of natural feed ingredients quite low in fat. Thus it is not a common problem and is of no dietary significance for domestic animals except for

poultry. Fortunately, the essential fatty acids are distributed widely among most fats and feed supplements. Corn and soybean oils and animal fats are excellent sources of linoleic and linolenic acids.

Composition of Body Fat

Body (depot) fat in simple-stomached species may be influenced markedly by the type and amount of dietary fat consumed. It has been known for many years that feeding of high levels of a particular fat (± 10 percent) will alter the nature of normal body depot fat. If an oil is fed—from a source such as peanut, safflower, or fish—it will result in body fat less saturated, softer, and with a lower melting point than that typical of the species. Especially with pork, this is objectional because of the soft, oily lard and cuts of meat. If fish oil is fed, flavor associated with the oil will be present in the meat also.

Minor changes in the diet do not have a marked influence on body fat deposits of ruminant animals, primarily because of the effect of rumen microorganisms on dietary fats. However, it is possible to feed protected fats (treated with aldehydes) and substantially alter the fatty acid composition of body or milk fat. Limited research on the topic indicates that the keeping qualities of milk are reduced and at this point it is strictly of academic interest.

the form of the skeleton. Bone is formed through the deposition of Ca and P in a complex salt in a protein matrix. Small amounts of some elements such as Mg and Na are present, as are some of the trace elements such as Zn, Mo, and Mn. Another example of a structural function is the use of Ca by birds to produce egg shells.

Most of the mineral elements are also involved in complex biochemical reactions. Those involved in enzyme activity include Ca, Mg, Fe, Co, Mn, Mo, and Zn. Fe is, of course, an essential constituent of hemoglobin in the blood and myoglobin in muscle tissues. Co is a constituent of a vitamin (B_{12}). Iodine is a component of thyroid hormone. In addition, other minerals such as Ca, K, Mg, and Na are involved in activity of the nervous system. Na, K, and Cl are necessary for the regulation of osmotic pressure and pH of intestinal and systemic fluids. This short list gives only a brief description of the many activities that minerals are involved with in the body of animals.

Mineral Metabolism

Mineral elements are absorbed from the GI tract by either an active or passive method. Active absorption means that the mineral is "pumped" by the intestinal wall from the digesta in the GI tract into intestinal cells. Mineral elements that are actively absorbed include Ca, P, and Na. However, most minerals are absorbed in a passive manner. These elements simply diffuse from the digesta across the intestinal wall at a rate determined by the concentrations of the mineral in both the digesta and the mucosal intestinal cells. Thus with passive absorption the concentration of an element in the feed and in the body greatly affects the amount absorbed.

Mineral elements are absorbed primarily in the ionic form. Therefore, digesta components that bind (chelate) minerals will reduce their absorption. Phytates, oxalates, and fats are compounds that may bind some elements and reduce absorption. Ca is particularly affected in this way. On the other hand Ca as Ca-lactate is absorbed more efficiently.

Interference with absorption of some essential minerals by other elements is an important nutritional problem that must be considered in formulating livestock rations. Minerals sometimes interfere with the utilization of other essential elements. Excess Ca is particularly a problem, as it interferes with P utilization and with Zn absorption.

Other factors can alter the degree to which

MINERALS

The mineral nutrients are solid, crystalline elements which cannot be decomposed or synthesized by ordinary chemical reactions. With respect to animal nutrition, the minerals that are dietary essentials are classified as the **major** or **macrominerals** and the **trace** or **microminerals**. The major minerals are normally present in animal carcasses at levels greater than 100 ppm. Included in this group are calcium (Ca), chlorine (Cl), magnesium (Mg), phosphorus (P), potassium (K), sodium (Na), and sulfur (S). The trace minerals are usually present in the carcass at levels less than 100 ppm. Included are chromium (Cr), cobalt (Co), copper (Cu), fluorine (F), iron (Fe), iodine (I), manganese (Mn), molybdenum (Mo), nickel (Ni), selenium (Se), silicon (Si), and zinc (Zn).

Mineral Function

The most obvious function of mineral elements in the body is to provide structural support in

minerals are absorbed. Young animals are more efficient and old animals are less efficient in absorbing essential elements. The form of the element (organic versus inorganic) and the pH of the intestinal tract can also affect absorption.

The ash content (total mineral content) of the animal carcass is about 3.5 percent of carcass weight, or 17.5 kg of minerals/500 kg of carcass (cattle). Ca represents about 46 percent and P about 29 percent of the total. K, S, Na, Cl, and Mg together account for about 24 percent, while essential trace elements constitute less than 0.3 percent of the total.

The distribution of these minerals within the body's tissues is not uniform because some tissues selectively concentrate specific elements. Bone is the primary storage site for many of the essential elements, including Ca, P, Mg, K, Na, Mn, Mo, and Zn. Some organs, particularly the liver, kidney, and spleen, serve as major storage sites for Mg, Co, Cu, Fe, Mn, Mo, Ni, Se, and Zn. The thyroid gland is the most specific storage site for I, and the gland contains 70-80 percent of total body I.

Mineral Requirements and Deficiencies

Mineral requirements for the various species are listed in the appendix tables. Some information is also given in Ch. 13-25 on species or classes of farm livestock. Additional information may be obtained in other reference books (2, 6, 7).

The essential macro minerals most likely to be deficient or imbalanced in livestock rations are Ca, Mg, Na, and P. Clinical signs and symptoms vary somewhat from species to species, so only general signs will be mentioned here. A deficiency of Ca or P (or vitamin D) or an imbalance (ratios outside of about 3-5:1 of Ca:P) may result in rickets in young animals, which is manifested by inadequate mineralization of the bones, crooked legs, and enlarged joints as well as other abnormalities. In older animals the minerals are withdrawn from the bones, resulting in osteoporosis, a condition in which the mineral content is low and bones are porous and much more subject to fractures. Mild to severe P deficiencies are not uncommon, particularly in grazing species of animals. It results in a depraved appetite (pica) which is manifested by animals chewing bones, rocks, boards, and other abnormal objects. Reproduction and growth will be affected markedly. With regard to Na, it is widely recognized that livestock need added salt (NaCl). When salt is not fed and the soil or water supplies do not contain much Na,

deficiencies may result. Clinical signs are a craving for salt, emaciation, listlessness, and poor performance. A deficiency of K is not likely except in animals fed very high grain diets. Deficiency signs are similar to those of Na deficiency. Mg deficiency is not common in most livestock except for grazing ruminants. Various factors prevent normal utilization of Mg during cool, cloudy weather in the late winter and early spring or with similar light and temperature conditions in the fall, resulting in a metabolic deficiency called grass tetany (2). This condition results in irritability, convulsions, coma, and death (if not treated) in many instances. Mature animals are more likely to be affected, particularly lactating females.

With regard to the trace minerals, Fe is always deficient for very young pigs. A deficiency occurs because body reserves of newborn pigs are low, young pigs grow very rapidly, and milk is a poor source of Fe. The result will be anemia (insufficient hemoglobin in the blood) if the pig is not provided some source of Fe (see Ch. 21). With chicks and other poultry species, Mn may be deficient, the signs showing up as perosis, a condition in which the hock joint is enlarged and deformed such that the bird has great difficulty in moving about. Iodine may be deficient for most species, depending on the source of their feed. An iodine deficiency results in goiter, an enlargement of the thyroid gland. Co is deficient in some soil types. A Co deficiency results in a deficiency of vitamin B₁₂ because Co is an essential constituent of this vitamin. Animals appear listless and will develop a particular type of anemia. In some cases Cu may be deficient and in others an excess of Mo and/or sulfate may result in poor utilization of Cu and the appearance of deficiency signs. Typical signs are a light hair color, partial paralysis of the rear quarters, and other manifestations depending on the age of the affected animal. Se is deficient in many areas for domestic livestock. A clinical deficiency shows up as white muscle disease (also called nutritional muscular dystrophy), primarily in young animals. In pigs it also affects the liver. The muscles of affected animals appear lighter than normal, and they may contain high levels of Ca-P salts. High death rates are common in newly born animals with a severe deficiency. Zn deficiencies are also relatively common and can be made more severe by high levels of Ca consumption. One sign is parakeratosis, which is a dermatitis manifested by itching, skin lesions, and other changes to the skin.

All deficiencies will, sooner or later, affect animal performance (growth, lactation, egg production, and so on), even though the appearance of the animal may not, in some cases, be affected to a great degree. In some cases multiple deficiencies of nutrients may occur, such as protein-energy, energy-mineral, energy-vitamin, and the like. Mild deficiencies may be difficult to detect because the only apparent effect on the animal may be somewhat lower production than would be expected. Such situations require careful evaluation by people trained in such matters to determine what the problem may be.

Mineral Toxicity

As a general rule, mineral toxicity is much less of a problem than mineral deficiencies. Water containing high levels of some alkali salts may be toxic, but such water would not normally be consumed if better-quality water is available. Of the macro minerals, NaCl can be a problem for both poultry and swine but is not often a problem for other species.

With regard to the trace minerals, fluorine can be obtained in sufficient amounts in rock phosphates to produce toxicity over a period of months (or years). Contamination of vegetation downwind from mills processing ores high in F may also result in chronic toxicity. F toxicity results in enlarged, soft bones, teeth that wear off much more rapidly than normal, difficulty in walking, and generally poor performance. Cu toxicity can, at times, be a problem for young lambs, particularly if feed is contaminated or intake of Mo and sulfates is low. Cu toxicity affects the liver and, eventually, the blood and may result in a relatively high death rate in affected animals. Se is present in soil and vegetation in high enough levels in some areas (in the north central states in the United States) to cause chronic toxicity manifested by elongated hooves, loss of tail and mane (horses), difficulty in walking, and so on.

It should be noted that any mineral can be toxic to some degree if fed in excessive amounts. However, except for those mentioned, such conditions are not common and are usually the result of carelessness or outright mistakes in mixing feed or in animal feeding management.

VITAMINS

Vitamins are organic substances that are required by animal tissues in very small amounts. All vitamins are essential for animal tissues, but

some species of animals are able to synthesize certain vitamins in their tissues or they are able to utilize vitamins synthesized by microorganisms in their GI tract. Consequently, vitamins needed in the diet vary from animal species to species. For example, humans, guinea pigs, monkeys, and some other species require vitamin C (ascorbic acid), but most animal species do not, because they can synthesize their own vitamin C.

Vitamins are divided into water-soluble or fat-soluble compounds. The water-soluble vitamins are C (ascorbic acid) and the B-complex vitamins, namely thiamin (B_1), riboflavin (B_2), niacin, pyridoxine (B_6), pantothenic acid, folacin, cyanocobalamin (B_{12}), biotin, choline, inositol, and paraaminobenzoic acid (PABA). The fat-soluble group includes vitamin A (retinal or retinoic acid) or its precursor, carotene; vitamin D, of which there are several forms; vitamin E, α -tocopherol; and vitamin K, which has several active forms. In nutritional use, vitamins A, D, and E are frequently quantitated in international units because there are several different compounds that have vitamin activity. The other vitamins are quantitated in weight units.

Functions

The primary functions of many water-soluble vitamins are as coenzymes (a substance associated with and which activates an enzyme). Water-soluble vitamins that do not act as coenzymes include choline, ascorbic acid, inositol, and PABA. The fat-soluble vitamins do not serve as coenzymes. Vitamin A, for example, is concerned with vision and with maintenance of epithelial cells (cells which line body cavities and cover body surfaces). Vitamin D is important in absorption and metabolism of Ca and in bone metabolism. Vitamin E functions as a metabolic antioxidant, and vitamin K is concerned with the blood clotting mechanism.

Tissue Distribution

The major storage site for most vitamins is the liver, with lesser amounts in the kidney, spleen, and other tissues or organs. Most are stored bound to specific proteins. Vitamins stored in the tissues are released at a rate necessary to maintain a relatively constant level in the blood.

The presence of vitamins in milk is important because milk often provides the sole food source for newborn animals. Colostrum is especially high in all vitamins, thus ensuring

a high intake for the young mammal early in life.

Vitamin Metabolism

Vitamins are absorbed primarily from the small intestine. The B-complex vitamins and vitamin K are synthesized by microorganisms in the intestines of monogastric species and in the rumen of ruminating animals. Ruminants, with one or two exceptions, have no dietary requirements for these vitamins because sufficient quantities are produced in the rumen and absorbed from the intestinal tract.

The ability of monogastric animals to absorb vitamins synthesized in their intestinal tract varies with the vitamin and the species of animal. Vitamin K is synthesized and absorbed in such quantities that a deficiency is almost impossible to produce in animals other than poultry. Pantothenic acid and B₁₂ are synthesized in the intestine, but little of the synthesized vitamins is absorbed and, consequently, monogastric species are dependent on dietary sources of these vitamins. Swine absorb enough of the folacin from the gut to meet most of their needs, while poultry absorb none of it and are entirely dependent on dietary sources. In the upper intestine, absorption of fat-soluble vitamins is less efficient than that of the water-soluble compounds. Some dietary lipid and the presence of bile salts are required for absorption.

Vitamin D, on the basis of present knowledge, is a unique vitamin. Plants contain a precursor, ergosterol, which can be converted to vitamin D₂ (calciferol) in the animal body if exposed to some ultraviolet light. Most mammals can use this form, but birds require vitamin D₃ (7-dehydrocholesterol), which is mainly of animal origin. However, in the animal body both D₂ and D₃ are converted by the liver to a more active form, which in turn is metabolized to another compound in the kidney, and the latter compound (1,25-dihydroxycholecalciferol) has direct effect on Ca metabolism in the tissues.

With regard to vitamin A, plants produce many different carotinoid pigments, but only a few can be converted to vitamin A. This takes place in the wall of the small intestine or the liver. Plants, themselves, contain no vitamin A.

Vitamin Deficiencies

Many of the signs of the various vitamin deficiencies are similar. These include anorexia (poor appetite), reduced growth, dermatitis,

weakness, and muscular incoordination. Some vitamin deficiencies cause additional specific symptoms (1, 2). For example, vitamin A deficiency can cause various kinds of blindness, including night, color, and total blindness. Vitamin D deficiency causes rickets and related bone disorders, and vitamin K deficiency causes hemorrhaging in the tissues. If niacin is absent, lesions develop on the tongue, lips, and mouth.

Vitamins that may be deficient under practical conditions often vary among different classes of livestock and with age of the animal. With ruminants the main concern is with vitamin A, possibly with vitamin E, and probably with vitamin D in specialized circumstances, although recent evidence indicates that carotene is required for normal ovarian function in cattle. Swine feeders must be concerned about dietary requirements of riboflavin, niacin, pantothenic acid, B₁₂, and choline of the B-complex and with vitamins A, D, and possibly E of the fat-soluble group. Poultry raisers must monitor the intake of all vitamins except ascorbic acid, inositol, and PABA.

ENERGY

Quantitatively, energy is the most important item in an animal's diet, and all feeding standards and ration formulation (Ch. 12) are based on some measure of energy with additional inputs on protein or amino acids, essential fatty acids, vitamins, and minerals.

The animal derives energy by partial or complete oxidation of organic molecules that are absorbed from the GI tract, including some of the amino acids or fat. In practice the individual nutrients are ignored and some form of energy is utilized when computing animal requirements or formulating rations. Thus it is necessary to discuss energy terminology, although a complete discussion of energy is beyond the scope of this chapter and the reader is referred to other books for more detail (1, 2, 3, 4).

Terminology

Energy is defined as the capacity to do work. In nutritional use it is quantitated by measuring heat production resulting from biochemical oxidations in the body or loss of energy from body excretions. Energy may be expressed in units such as calories, British Thermal Units (BTU), or joules. In the United States the calorie (cal), kilocalorie (kcal) or megacalorie (Mcal) are commonly used in animal nutrition. European coun-

tries have changed to the use of the joule, but it makes no difference whether calories or joules are the basal measure. A cal is the amount of heat required to raise the temperature of 1 g (gram) of water 1 degree C (= 4.1855 joules). A kcal = 1,000 cal and a Mcal (or therm) = 1,000 kcal. Animal use of energy is partitioned in the following way.

Gross Energy (GE). GE is the amount of heat resulting from oxidation of feed in an instrument called an oxygen bomb calorimeter. This is a reference point which tells how much energy is in the feed, but values are of little use otherwise because the energy value of a poorly digested and low-quality feed, such as straw, may be similar to a highly digestible ingredient such as sucrose. It is, however, the term used for energy in human diets. For humans it is more appropriate, because the average diet is highly digestible.

Digestible Energy (DE). DE is a measure of the amount of energy absorbed by the animal after consuming a particular feed or diet. The values are obtained by subtracting fecal energy from GE consumed. It is not strictly a measure of absorbed energy, because some of the energy of fecal excretion is derived from body tissues rather than undigested food. However, DE is a common energy base that is used in the United States and other countries as well.

Metabolizable Energy (ME). ME is determined by subtracting energy losses in urine and combustible gases from DE consumed. It is slightly more accurate than DE but is more expensive to obtain data on most species except for birds. It is the common base used for feeding standards and ration formulation for birds, and it is the common standard used in European countries for other domestic animals.

Net Energy (NE). NE is measured by subtracting energy losses in rumen fermentation and tissue metabolism from ME. It is energy available for maintenance or some type of production such as work or lactation. In theory, it is more accurate than DE or ME. In practice, information is not available on very many feed-stuffs or production situations. If an animal is outside its normal comfort zone (temperature range where nutrients are not oxidized to keep the body warm or cool), NE values will be different than if determined within the comfort zone. Nevertheless, NE values are currently in vogue and are often used in formulating rations or estimating animal performance. NE may also

be divided into NEm (NE for maintenance) and NEg (NE for gain) or expressed as NE^l (lactation) when applied to lactating animals.

Total Digestible Nutrients (TDN). TDN is an old method of calculating energy and is the sum of digestible crude protein, crude fiber, nitrogen-free extract (carbohydrates), plus ether extract $\times 2.25$. The ether extract (lipids) is multiplied by 2.25 in an attempt to give it an increased value equivalent to the higher caloric value of fats. The chief criticism of TDN is that it tends to overvalue roughages as compared to ME or NE methods. Nevertheless, it is still widely used, and some nutritionists feel that it works as well as ME or NE bases. TDN is quite similar to DE, but DE or NE are gradually taking the place of TDN in the United States.

Energy Metabolism and Requirements

Energy metabolism is a very complex topic that is beyond the scope of this book. However, there are a few points that should be made for clarity if the reader is not familiar with the topic.

In the process of digesting and metabolizing energy, the greatest loss is that of undigested material excreted in feces. However, this general statement is subject to many modifications. For example, monogastric species generally consume more digestible diets than herbivorous species; thus the digestibility of energy will usually be higher. Young animals, particularly mammals, also consume more digestible diets than do adults, so digestibility will be higher. High-quality diets fed to poultry or swine may be digested to the extent of 85+ percent. At the other extreme, poor-quality diets such as straw fed to ruminants may be less than 35 percent digestible. In ruminants, digestibility will decrease as the level of feed intake increases, but there is little effect in other species. Factors which disturb the normal intestinal or stomach functions—diarrhea, toxins, parasite infections, and the like—will normally result in reduced digestibility. Digestibility can usually be enhanced in many species by proper feed processing.

Other losses occur in energy metabolism. Energy lost through urine and methane production in the GI tract will amount to about 10 percent of GE in ruminants, but less in most monogastric species. Losses after absorption can vary greatly, depending on level of intake, quality of the diet, and other factors. Heat is produced as a result of microbial fermentation in the stom-

ach or gut (heat of fermentation). While such heat can be used to warm the body if necessary, the animal is not capable of storing the heat by chemical means such as synthesis of fat. In addition, heat is produced by oxidation of nutrients (particularly amino acids); this is referred to as the heat increment. Proteins produce the greatest losses, followed by carbohydrates and then fats. As with the heat of fermentation, such heat can be used to warm the body but cannot be stored. Thus both the heat of fermentation and the heat increment are detrimental in a situation where the animal is heat stressed.

Energy requirements are affected by many different factors, such as age, species, activity of the animal, level of production, environmental temperature, nutrient deficiencies, and various other factors. However, for a healthy animal, energy requirements are directly related to body surface area; this is so because heat is lost or gained in proportion to the area exposed. If body weight is multiplied by a fractional power (0.75 is commonly used), this gives a reasonably good means of relating weight to surface area for different species and sizes of animals (see reference 1, 3). This method of calculating energy requirements for the various domestic species is used in all current feeding standards.

Effective surface area can be altered in various ways. For example with sheep, shearing increases their susceptibility to cold temperatures but reduces heat stresses. Winter hair coats provide more insulation as does a thick layer of fat under the skin. In dry areas, sprinkling animals with water during hot periods will increase evaporation from the body surface and help to reduce heat stress as a result. Other examples could be given, but these will suffice to illustrate the point.

All homotherms (species which maintain a rather constant body temperature) operate within a so-called comfort zone. Within this temperature range the animal does not need to increase oxidation of nutrients to either cool or warm itself. The comfort zone will be affected greatly by humidity because evaporation from the body surface or from the lungs will be decreased when humidity is high and evaporation is the most efficient means of increasing heat loss. Likewise, wind will increase heat loss greatly in a cold climate and add to discomfort in a very hot situation, particularly if humidity is high. Normal activity or an increased level of feeding will increase body heat production and

lower the temperature at which the animal is comfortable. Immersion in cold water greatly intensifies heat loss. If an animal, such as a human, with little body surface protection is immersed in cold water for any length of time, body temperature will decrease rapidly to the point at which the animal cannot survive.

Energy Deficiency

Many wild species go through alternating periods of energy surplus, adequacy, and deficiency as the seasons change or as they go from dry to rainy seasons in tropical areas. This also may happen to free-ranging domestic animals, but usually the extremes of deficiency are less severe because of supplementary feed supplied by the livestock feeder. Such extremes should not occur with animals in confinement. Energy deficiency, if severe, results in a loss of body fat, weight losses, and emaciation. Pregnancy may be interrupted by resorption or abortion, milk or egg production will be decreased drastically, and animal fertility will inevitably be reduced. Energy deficiency is usually accompanied by deficiencies of other nutrients, but the overriding importance of body energy need may prevent the appearance of signs of the other deficiencies.

FEEDING STANDARDS

Feeding standards are statements of quantitative descriptions of the amounts of nutrients needed by animals. Use of such standards dates back to the early 1800s. There has been a gradual development over the years to the point where nutrient requirements for farm animals may be specified with a reasonable degree of accuracy, particularly for growing chicks and pigs. Although there are still many situations where nutrient needs of animals cannot be specified with great accuracy, nutrient needs of some domestic animals have been defined more completely than those of humans. This is due to the simple fact that people do not lend themselves to the types of experimentation needed to collect good quantitative data.

In the United States the most widely used standards are those published by the various committees of the National Research Council (4) under the auspices of the National Academy of Science. These standards (see the appendix tables) are revised and reissued at intervals of a few years. In England, the standards in use

are put out by the Agricultural Research Council (3). Other countries have similar bodies which update information and make recommendations on animal nutrient requirements.

Terminology Used in Feeding Standards

Feeding standards are usually expressed in quantities of nutrients required per day or as a percentage of a diet, the former being used for animals given exact quantities of a diet and the latter more commonly when rations are fed *ad libitum*. With respect to the various nutrients, most are expressed in weight units, percentage, or ppm (parts per million). Some vitamins—A, D, E—are often given in international units. Protein requirements are sometimes given in terms of digestible protein (DP), although crude protein is used more commonly and amino acids can be substituted for DP in monogastric species when adequate information is at hand. Energy is expressed in a variety of different forms. The NRC uses ME for chickens and turkeys; DE, ME, or TDN for swine; DE, ME, and TDN for sheep; ME and TDN for beef cattle, with alternative use of NEm and NEg for growing and fattening cattle. For dairy cattle, values are given in DE, ME, TDN, NEm, and NEg, with additional values as NE^l for lactating cows. The ARC uses ME almost exclusively, with energy expressed in terms of MJ (megajoules) rather than Mcal (megacalories). Other European standards are based on starch equivalents, Scandinavian Feed Units, and so forth. Regardless of the units used, feeding standards are based on some estimate of animal needs and have been derived from data obtained from a great many experimental studies done under a wide variety of conditions with a diverse list of feed ingredients.

Some comments are in order regarding the use of NEm and NEg for beef cattle and growing dairy cattle and NE^l for lactating cows by the NRC publications. If one looks at the tables on feed composition in the respective publications, it is apparent that values are given in this energy terminology for almost all of the feedstuffs listed except for mineral supplements. The reader should be aware that most of these NE values have been calculated from older data that were generally expressed in other ways. Most of it was originally given as TDN or DE, as there is a wealth of older data expressed in these forms. Some values have also been derived from ME. Only a few feedstuffs have been evaluated directly in terms of NEm, NEg, or NE^l.

However applicable these values may be for these respective classes of cattle, recalculating from existing data does not necessarily improve the original data.

Inaccuracies in Feeding Standards

The means and methods of arriving at quantitative values for feeding standards have been discussed elsewhere (1, 3, 4). For the nutritionist, feeding standards provide a useful base from which to formulate rations or to estimate feed requirements of animals. Feeding standards should not, however, be considered as the final answer on nutrient needs, but should be used as a guide. Current NRC recommendations are specified in terms believed by the committees to be minimum requirements for a population of animals of a given species, age, weight, and productive status. Some of the earlier versions were called allowances and, as such, included a safety factor on top of what was believed to be required. It is well known that animal requirements vary considerably, even within a relatively uniform herd. For example, a protein intake that may be satisfactory for most animals in a given situation will probably not be sufficient for a few of the more rapid gainers or high producers; conversely, some of the herd will probably be overfed. With our present production methods, this usually is the most feasible basis of feeding. The poor producers would be culled and the high producers can be given extra allowances.

It is quite obvious from published literature that management and feeding methods may alter an animal's needs or efficiency of feed utilization apart from known breed differences in nutrient metabolism and requirements. In addition, most current recommendations provide no basis for increasing intake in severe weather or reduction in mild climates. The effect of climate may be very great. For example, recent data show that pregnant cows with no shelter have metabolic rates which were 18–36 percent higher than cows provided with shelter.

Nor is any allowance made for the effect of other stresses such as disease, parasitism, surgery, and so forth. Furthermore, beneficial effects of additives, hormones, or feed preparatory methods are not always considered when devising quantitative requirements in feeding standards. Thus many variables may alter nutrient needs and nutrient utilization, and these variables are not normally built into the feeding standards.

Nutrient Needs and the Productive Functions

The remainder of this section will be devoted to some general discussion which will relate the effect of various productive functions on nutrient requirements. This should give the reader a better understanding of nutrient requirements as affected by growth, fattening, reproduction, lactation, and work.

Maintenance. Maintenance may be defined as the condition in which an animal is neither gaining nor losing body energy (or other nutrients). With productive animals there are only a few times when a true maintenance situation is approached. It is closely approximated or attained in adult male breeding animals other than during the breeding season and, perhaps, for a few days or weeks in adult females following the cessation of lactation and before pregnancy increases requirements substantially. However, as a reference point for evaluating nutritional needs, maintenance is a commonly used benchmark.

Other things being equal, nutrient needs are minimal during maintenance. In field conditions during dry periods of the year or during winter months, we may find that range animals need to expend considerable energy just to obtain enough plant material for their needs, as opposed to the amount of energy expended when forage growth is more lush, but this does not alter the fact that nutrient needs are less during maintenance than when an animal is performing some productive function.

Growth and Fattening. Growth, as measured by increase in body weight, is at its most rapid rate early in life. When expressed as a percentage increase in body weight, the growth rate gradually declines until puberty, followed by an even slower rate until maturity. As animals grow, different tissues and organs develop at differential rates and it is quite obvious that the conformation of most newborn animals is different from that of adults; this differential development has, no doubt, some effect on changing nutrient requirements. Growth rate probably decreases because the biological stimulus to grow is lessened, because young animals cannot continue to eat as much per unit of metabolic size, and, as measured by increase in body weight, because relatively more of the tissue of older animals is fat, which has a much higher caloric value than muscle tissue.

Nutrient requirements per unit of body weight or metabolic size (body weight^{0.75}) are greatest for very young animals. These needs gradually taper off as the growth rate declines and as the animal approaches maturity. In young mammals, nutrient needs are so great that, because the capacity of the GI tract is relatively limited in space and function, they must have milk (or a milk replacer) or milk and additional highly digestible food to approach maximum growth rates. As the young mammal grows, quality of the diet generally decreases as more and more of its food is from nonmilk sources, with the result that digestibility is lower and the dry matter of food is used less efficiently.

Dry matter consumption for all young animals is usually far greater per unit of body weight during their early life than in later periods. This high level of food consumption provides a large margin above maintenance needs, thus allowing a high proportion to be used for growth and development. Due to differences in capability of the GI tract for food utilization and because the rate, duration, and character of body growth vary with age and animal species, nutrient requirements may be quite different for different animal species. Nevertheless, it is characteristic for all species that nutrient requirements (nutrient concentration/unit of diet) are highest for the very young and then gradually decline as the animal matures. Naturally, total food and nutrient consumption are less for young animals because of their smaller size.

Nutrient deficiencies show up quite rapidly in young animals, particularly when the young are dependent in the early stages of life on tissue reserves obtained while *in utero*. With few exceptions, tissue reserves in newborn animals are low. Milk or other food may be an inadequate nutrient source, so that deficiencies may occur frequently until the food supply changes or the young animal develops a capability to eat the existing food supply. The young pig is an example. Iron reserves are low and rapid growth soon depletes body reserves; because milk is a poor source of iron, young pigs often become anemic unless supplemented with iron.

It should be pointed out that young mammals are dependent upon an intake of colostrum early in life. In very early life the intestinal tract is permeable to large protein molecules. Colostrum has a large supply of globulins and other proteins that provide nutrition as well as a tem-

porary supply of antibodies which greatly increase resistance to many diseases. In addition, colostrum is a rich source of most of the vitamins and trace minerals, and the young animal's tissues can be supplied with needed nutrients which may not have been provided adequately *in utero*.

From a production point of view, nutrient requirements per unit of gain are least and gross efficiency (total production divided by total food consumption) is greatest when animals grow at maximal rates. However, net efficiency (total production divided by nutrient needs above maintenance) may not be altered greatly. In a number of instances it may not be desirable or economical to attempt to achieve maximal gain. For example, if we want to market a milk-fed veal calf at an early age, maximal gain and fattening are desired. On the other hand, if the calf is being grown out for a herd replacement, then less than maximal gain will be just as satisfactory and considerably cheaper.

The biological stimulus to grow cannot be suppressed to a marked degree in young animals without resultant permanent stunting. It is possible to maintain young animals for a period during which they do not increase body energy reserves, yet they will—if other nutrients are adequate—continue to increase in stature. Following a period of subnormal growth due to energy restriction, most young animals will gain weight at faster than normal rates when given adequate rations. This response is termed compensatory growth. This phenomenon has practical application when young calves are wintered at low to moderate levels (submaximal). When new grass is available in the spring or if calves are put in the feedlot, weight gain occurs at a very rapid rate initially. Efficiency for the total period and especially for a given amount of gain is greater, however, if the animal is fed at near maximal rates, but feeding at a lower level may allow the use of much cheaper feedstuffs or deferred marketing and, as a result, be a profitable management procedure.

Lactation

Heavy lactation results in more nutritional stress in mature animals than any other production situation, with the exception of very heavy, sustained muscular exercise. During a year, high-producing cows or goats typically produce milk with a dry-matter content equivalent to four- to fivefold that of the animal's body, and some animals reach production levels as high as

sevenfold that of body dry matter. High-producing cows give so much milk that it is impossible for them to consume enough feed to prevent weight loss during peak periods of lactation.

Milk of most domestic species runs 80-88 percent water; thus water is a critical nutrient needed to sustain lactation. All nutrient needs are increased during lactation, however, as milk components are either supplied directly via the blood or synthesized in the mammary gland and, thus, are derived from the animal's tissue or from food consumed. All recognized nutrients are secreted to some extent in milk, although the major components of milk are fat, protein, and lactose, with substantial amounts of ash, primarily Ca and P.

Milk yield varies widely among and within species. In cows, peak yields usually occur between 60 and 90 days after parturition and then gradually taper off; thus the peak demand for nutrients follows the typical milk flow characteristic for the species concerned. Milk composition and quantity in ruminants may be altered by the type of ration. This is true particularly of the fat content and, to a lesser extent, the protein and lactose. In monogastric species, diet may affect fat, mineral, and vitamin composition of milk.

Limiting water or energy intake of the lactating cow (and probably any other species) results in a marked drop in milk production, whereas protein restriction has a less noticeable effect, particularly during a short period of time. Although deficiencies of minerals do not affect milk composition markedly, they will result in rapid depletion of the lactating animal's reserves. The need for elements such as Cu, Fe, and Se will be increased during lactation, even though they are found in very low concentrations in milk. The effects of marked nutrient deficiencies during lactation will often carry over into pregnancy and the next lactation.

Reproduction

Although nutrient needs of animals for reproduction are generally considerably less critical than during rapid growth or heavy lactation, they are certainly more critical than for maintenance. If nutrient deficiencies occur prior to breeding, the result may be sterility, low fertility, silent estrus, or failure to establish or maintain pregnancy.

It has been demonstrated many times that underfeeding (of energy and protein) during

growth will result in delayed sexual maturity and that both underfeeding and overfeeding (of energy) will usually result in reduced fertility as compared to animals fed on a medium intake. Of the two, overfeeding is usually more detrimental to fertility.

Energy needs for most species during pregnancy are more critical during the last one-third of the pregnancy. Information on deposition of nutrients in fetal tissues suggests only relatively small percentages of total animal requirements are needed for this function, even late in the term, however other information indicates a somewhat greater need. Pregnant animals have a greater appetite and will spend more time grazing and searching for food than will nonpregnant animals. Furthermore, the basal metabolic rate of pregnant animals is higher. By the end of pregnancy the basal rate of a cow is about 1.5-fold that of a nonpregnant identical twin.

Protein deposition in the products of conception follows the same trend as energy, but protein is relatively more critical for development of the fetus in the late stages than early in pregnancy as is true for Ca, P, other minerals, and vitamins.

Inadequate nutrition of the mother during pregnancy may have variable results, depending on the species of animal, the degree of malnutrition, the nutrient involved, and the stage of pregnancy. Nutrient deficiencies are usually more serious in late pregnancy, although there are exceptions to this statement. With a moderate deficiency, fetal tissues tend to have a priority over the mother's tissues; thus body reserves of the mother may be withdrawn to nourish the fetus. However, a very severe deficiency will usually result in partial depletion of the mother's tissues and such detrimental effects as resorption of the fetus, abortion, malformed young, or birth of dead, weak, or undersized young with, sometimes, long-term effects on the mother. When the mother's tissues are depleted of critical nutrients, then tissue storage in the young animal is almost always low, nutrients excreted in colostrum are also low, milk production may be nil, and survival of the young animal is much less certain than when nutrition of the mother is at an adequate level.

Work

Experimental studies with humans and animals indicate that work (physical effort) results in an

increased energy demand in proportion to the work done and the efficiency with which it is accomplished. Carbohydrates are said to be more efficient sources of energy for work than fats. With respect to protein, balance studies show little, if any, increase in N excretion in horses or humans as a result of muscular exercise, provided energy intake is adequate and protein does not need to be metabolized for energy. Although this evidence has been obtained in a number of studies, data on men indicate reduced quality and quantity of work when protein intake is on the low side, but still above maintenance levels.

If appreciable sweating occurs, work may be expected to increase the need of Na and Cl, particularly. P intake should be increased during work, as it is a vital nutrient in many energy-yielding reactions. Likewise, the B-vitamins involved in energy metabolism, particularly thiamin, niacin, and riboflavin, probably should be increased as work output increases, although data on this subject are not clear.

COMMON NUTRITIONAL ANALYSES

It is necessary for the reader and user of this book to have some idea of the common methods and terms used in analyzing and describing nutrients in feeds and other items. This topic, of course, could be one for a book by itself. For the reader interested in the details of standard methods used in most nutrition laboratories, the writer would recommend the book entitled *Official Methods of Analysis* (8).

There are thousands of different kinds of analyses that might be done on feeds (or foods), animal tissues, excreta, and the like at one time or another. These can be lumped broadly into qualitative tests (which can be used to indicate the presence of a substance, for example, mold) and quantitative tests which will provide information on how much of a given substance is present in the food.

Qualitative tests are used like keys for classifying a plant, bird, or animal. Many things can be eliminated very quickly. For example, is the material liquid or solid? Is it soluble in water or one of many different types of solvents? Does it melt when heated or does it decompose and burn?

In recent years there have been marked improvements in the instrumentation, much of which is automated, for doing analyses on nutrients. Consequently, quantitative informa-

tion is obtained more easily and qualitative tests are used less frequently. Discussion follows on the most common methods in use.

Dry Matter

Although water is a useful substance to the animal, its presence in feed acts as a diluent. Therefore, most feeds are analyzed and the data presented either on a dry matter (DM) basis or an as-is basis with information shown on the moisture content. DM is determined by grinding the material (unless it is not feasible to grind) and drying in an oven of one type or another. Microwave ovens make this a very speedy process. Older ovens using temperatures of 60 to 105°C require 24 hours or more, depending on the nature of the product.

Crude Protein

For common nutritional use, most feedstuffs are analyzed with a procedure called the Kjeldahl process, which measures the N content of the feed, regardless of its source. For this method, feeds are digested in hot, concentrated sulfuric acid, with eventual measurement of ammonia expressed as percent N. This is done because all proteins contain N, although not all N-containing compounds are proteins. The average protein contains about 16 percent N; thus multiplying the percent N $\times 6.25$ gives the crude protein equivalent ($16 \times 6.25 = 100$).

The N from the Kjeldahl analysis could be from urea, manure, an insoluble protein such as uncooked feathers, or from high-quality proteins in milk, but this method will not provide any measure of quality, only of quantity of N present. The advantages of the procedure are that it is relatively rapid and repeatable, it has been used for many years, and most people are somewhat familiar with it.

If more precise information is needed, there are many different types of analysis that could be used. Automated methods are available for analyzing for amino acids, but they require quite a bit of time and are much more expensive. Analyses are available for different types of proteins, for solubility of proteins, for protein bound in an undigestible manner to other components, and so on.

Ether Extract (Crude Fat)

Crude fat is the product resulting from extracting a feed item with hot ethyl ether or some other organic solvent or combination of solvents

such as chloroform + ethyl alcohol. A small sample of feed is put in the proper container and the hot solvent drips through it. The ether extract resulting from this process may contain many things other than true fats. For example, most plant leaves are covered with a certain amount of waxy material which, although soluble in ether, is essentially undigestible and of no nutritional value to animals. As with the crude protein analysis, the information provided is quantitative rather than qualitative in nature. No information is provided on the different types of fatty acids or different types of lipids. In the event that such information is needed, there are methods available for determination of fatty acids, for different types of lipids, and so on (8).

Crude Fiber

The analysis for crude fiber was developed many years ago. It involves boiling the ground feed (usually fat-extracted first) in a weak solution of acid, filtration and boiling in a weak solution of alkali, filtration, and drying. This was an attempt to simulate digestion in the stomach and then the intestine. The procedure is intended to be an analysis for cellulose, hemicellulose, xylans, lignin, and any other components associated with fibrous carbohydrates. It has a number of disadvantages. It is slow and tedious, not very repeatable, and the information is less applicable to some feeds than to others. The reason for the latter statement is that some hemicelluloses will be dissolved by the chemical treatment and, if protein is bound to the lignin or other chemicals in an insoluble form, it will also show up in the crude fiber fraction. Unfortunately, most state regulatory agencies still require crude fiber analyses on commercial feedstuffs (see Ch. 5).

Neutral-Detergent Fiber, Acid-Detergent Fiber

Methods using detergents have been developed to overcome some of the problems with the crude fiber analysis. If feed is extracted with the appropriate neutral-detergent solution, the solution will extract (remove) materials that are essentially the same as the contents of the cell, thus dividing the feed into fractions of cell contents and cell walls. Neutral-detergent fiber and cell wall content are synonymous terms. Most of the soluble material in the cell contents (proteins, lipids, sugars, starch, pectins, other

normally, be a problem for confined animals raised under intensive situations. Energy utilization can be affected markedly by deficiencies of other nutrients and by feed preparatory methods.

Feeding standards were discussed. Feeding standards are intended to define nutrient needs of domestic animals of different species and at different ages or in various production situa-

tions. They are reworked and redefined from time to time in an effort to improve them. There are a number of inadequacies in most standards, but they serve as a most useful base from which to project animal needs for feed.

Common nutritional analyses of feedstuffs were discussed, and some of the problems associated with analytical work were pointed out.

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solubles) are highly utilizable by animals of all types, whereas the cell walls contain most of the fibrous carbohydrates, lignin, heat-damaged protein (if any), and silica. Now, if the cell walls (or neutral-detergent fiber) are extracted with an acid-detergent solution, the hemicellulose is removed, leaving acid-detergent fiber which contains cellulose, lignin, heat-damaged protein (if any), and silica. Hemicellulose and cellulose utilization is low to moderate by ruminants, and they are only partially utilized by nonruminant species. The other materials in acid-detergent fiber are indigestible by all species for all practical purposes.

Ash

As the term implies, ash is obtained by burning feed at a temperature of 350-600°C until nothing is left but metallic oxides or contaminants such as rocks and soil. No qualitative information is provided. If information is needed on individual mineral elements, there are many different methods available. However, nutritional information on some of the trace elements is not too precise because the very low concentrations make analytical results less certain.

Nitrogen-Free-Extract (NFE)

This fraction of feed, which is primarily composed of readily available carbohydrates (sugars, dextrins, starches), is one utilized in an old scheme called the proximate analysis. In this scheme all of the other analyzed items are subtracted from 100, leaving NFE. The formula is as follows:

$$\text{NFE} = 100 - [\text{crude protein} + \text{crude fat} + \text{crude fiber} + \text{ash}]$$

Analysis was done in this manner because there were no quick, simple analytical methods (at that time) for starch, which must be hydrolyzed to sugar, and then an analysis must be done for sugars.

The values on NFE for the grains and other components high in sugar and starch are a reliable estimate of the readily available carbohydrates, but they are not for feeds high in hemicellulose if the crude fiber procedure is used. This is so because a substantial portion of hemicellulose is dissolved in the crude fiber analysis and, using the formula above, would end up in the NFE fraction. If the detergent methods are used, this criticism would be taken care of.

Energy

Energy content of feed is obtained with an instrument called an oxygen bomb calorimeter. A small sample of ground feed is introduced into a thick-walled container (bomb) which is then filled with oxygen under pressure. The bomb is then placed in a container of water, the feed is ignited, and the increase in the temperature of the water is determined. In this way the fuel value (gross energy) of the feed can be determined. In order to develop information on animal utilization of the feed, animal trials of one type or another must be carried out (see the previous section on energy).

SUMMARY

Animals need an adequate source of good-quality water for maximum levels of production. At times water may contain too many mineral salts or other contaminants, but water can also be an important source of mineral elements. Animals need nitrogen or amino acids in their diet. Ruminant animals can use largely non-protein N sources, but the simple-stomached animals need at least nine essential amino acids in their diet. Other amino acids needed for protein synthesis can, usually, be synthesized by the animal's tissues. Carbohydrates provide the majority of most animal diets (except for carnivores), but no specific carbohydrate is required to the diet. Sugars and starches are highly utilized. Fibrous carbohydrates such as hemicellulose and cellulose are utilized by animals only because of digestion in the gastrointestinal tract by microbial organisms; animals do not produce the enzymes needed to digest these compounds. Lipids are normally only a small percentage of animal diets. There are two essential fatty acids, but only in very rare situations are they likely to be inadequate.

Many different mineral elements are required in animal diets. Those that may be a problem at times include Ca, P, and Mg, of the major elements. Of the trace minerals, Cu, Fe, I, Mn, and Zn are usually most likely to be insufficient in animal diets. Vitamins may also be problems in animal diets. Vitamin A is usually thought to be limiting for many species. Vitamin D may be deficient at times. With the B vitamins, the most likely problems are with poultry, which may need to have diets supplemented with a number of these vital nutrients.

Energy is often a limiting dietary component for free-ranging animals, but it would not,