8

DIGESTION

8-1 THE DEFINITION OF DIGESTION

Digestion results in the conversion of food into a form that can be absorbed by the body and assimilated into body tissue. Dukes (1955) defined digestion to include all activities of the alimentary canal and its glands in preparation of foods for absorption and the rejection of residues. The mechanical factors include chewing, swallowing, regurgitation, stomach and intestinal movements, and defecation. Secretory factors are associated with the activity of the digestive glands, and chemical factors include the reactions of the enzymes secreted by the digestive glands with the plant enzymes and other chemicals in the ingested food. Ruminants also have the additional chemical functions of the microorganisms in the gastrointestinal tract.

The transformation of food to metabolically useful nutrients is a biochemical process, and the whole process of digestion must be studied from that point of view if the functional relationships of foods to an animal are to be understood. Identification of different food species that are ingested is only an aid in approaching the study of biochemical aspects of nutrition. Food-habit lists are useful for only the most general analysis of animal-environment relationships. According to Crampton and Harris (1969, p. 5), "Feeds are merely the carriers of the nutrients and the potential energy . . . in a . . . diet."

8-2 A RESEARCH PHILOSOPHY

The utilization of plant species by wild and domestic ruminants on open range has been described in the literature in many different ways, including expressions of the number of twigs browsed, percentage of twigs browsed, volume of food

in the rumen, frequency of occurrence of foods in the rumen, and animal-minutes spent ingesting each species. Statistical analyses of such data have been made, and biological inferences have been published.

Data like these may, however, be quite unrelated to the functional nutritive relationships between an animal and its range. For example, the chemical composition of two plant species may be very much alike, and an animal may be able to digest and assimilate each plant species to a similar degree. The animal makes no biochemical distinction between the two species, but the descriptive biologist separates them according to taxonomic differences. Such a separation of the two species is unnecessary from a nutritional point of view.

Some very pertinent questions can be asked at this point. How much do we know about the chemical interaction between wild ruminants and their environment? What does the environment contain chemically, and of what value is each chemical component to the animals? Do greater chemical differences exist between different plant species than between the same species on different soils? Do deer select different plant species for foraging or do they forage randomly on a variety of species just because they are dispersed throughout the habitat?

We know that there are chemical differences between plant species, and we know there are differences in the chemical characteristics of the soil. Field observations indicate that wild ruminants do have preferences for certain species, but preference lists are not similar for different geographical areas. Knowledge of differences in the food characteristics between habitats or of differences between animal species in their preferences for forage plants does not provide any significant insight into the chemical interaction between wild ruminants and their environment. Little is known about the requirements of wild ruminants and how well the environment supplies these requirements. Much more information is needed before the functional relationships between an organism and its complex and dynamic environment will be understood.

8-3 CHEMICAL COMPOSITION OF FOOD MATERIALS

Foods are complex structures that can be organized into groups having similar physical or chemical characteristics. Chemical analyses of foods have usually followed a proximate-analysis scheme devised by workers at the Weende Experiment Station in Germany over 100 years ago. This proximate analysis results in the grouping of chemically similar components of foods into six categories, including water, ether extract, crude fiber, nitrogen-free extract, crude protein, and ash. A chemical organization of foods is shown in the following outline, with the categories used in proximate analyses shown in parentheses.

I. Water
II. Dry matter
    A. Organic substances
        1. Nitrogenous compounds (crude protein)
            a. True protein
            b. Nonprotein nitrogenous materials

2. Non-nitrogenous substances
   a. Carbohydrates
      (1) Soluble carbohydrates (nitrogen-free extract)
      (2) Insoluble carbohydrates (crude fiber)
   b. Fats (ether extract)

B. Inorganic substances (ash)
   1. Salts
   2. Mineral matter

The Association of Official Agricultural Chemists periodically publishes descriptions of the standard analytical procedures for proximate analyses. Subsequent reference in this book to these procedures is indicated by the abbreviation "AOAC Handbook."

The chemically similar groups measured in the proximate analyses do not necessarily have similar nutritional significance and must be interpreted accordingly for different species of animals. Crampton and Harris (1969) devote an entire chapter to the discussion of the proximate analysis of feeds. The summary that follows is based mostly on their writings.

WATER. Water is a simple food substance chemically, but is difficult to measure quantitatively in different foods. The usual procedure is oven-drying at about 105°C until a constant sample weight is reached. This usually occurs in 24 to 48 hours. Heating at 105°C may also cause a loss of other volatile substances such as essential oils, as well as the decomposition of some sugars. These losses would then be considered a part of water loss. The importance of that error is obviously related to the composition of the plant material. Vacuum ovens are used to eliminate some of these errors, and distillation procedures are also used. Both are more time consuming and expensive than the straightforward drying in a forced-air oven.

NITROGENOUS SUBSTANCES—CRUDE PROTEIN. The total amount of nitrogen in the food is determined by methods of analysis described in the AOAC Handbook, and the crude protein is obtained by multiplying the amount of nitrogen in the food by 6.25. The numerical factor 6.25 is derived from the assumption that protein contains 16% nitrogen, that all of the nitrogen is in the protein, and that all urinary nitrogen excreted is derived from protein oxidation. Thus $100/16 = 6.25$, and urinary nitrogen excreted $\times$ 6.25 = the amount of protein oxidized (Brody 1945). This procedure is not completely valid, since the nitrogen content of the protein of different feeds ranges from 16% to 19%. When the latter percentage is correct for a particular feed, the conversion factor should be $100/19 = 5.26$. Crampton and Harris (1969) include two tables showing (1) the errors resulting from the use of a constant factor 6.25 in estimating the protein content of foods and (2) selected conversion factors for proteins. The greatest errors resulting from the use of 6.25 seem to be characteristic of the oil-seed and cereal proteins that have a higher percentage of nitrogen (greater than 16%) in the protein. Another error is dependent on the amount of nonprotein nitrogen (NPN) in the forage.

In view of the many other unknown factors in the total animal-range relationship, the N × 6.25 calculation seems to be a satisfactory approximation of the quantity of protein in a food. This calculation gives no indication of the amino acid composition of the food, but this is of little importance for ruminants since the metabolic processes of rumen microorganisms result in the synthesis of proteins from nonprotein sources.

CARBOHYDRATES—NITROGEN-FREE EXTRACT. The nitrogen-free extract (NFE) component of carbohydrates is made up of starches and sugars. These are highly digestible sources of energy that are converted through digestion from starches (starch, dextrin, and glycogen) and sugars (monosaccharides, disaccharides, and trisaccharides) to glucose. In a proximate analysis, the amount of NFE is determined by subtraction, with the water, ether extract, crude fiber, crude protein, and ash being subtracted from the original weight of the sample. Errors in the determination of any of these components are reflected in the figure obtained for the NFE.

CARBOHYDRATES—CRUDE FIBER. Crude fiber is the insoluble residue of a food after successive boiling with dilute acid (H_2SO_4) and dilute alkali (NaOH), according to procedures outlined in the AOAC Handbook. This material may not be insoluble when exposed to the digestion process of an animal, however. This is particularly true for ruminants whose microorganisms have the ability to break down cellulose for their own metabolic needs, producing volatile fatty acids (VFAs, including acetic, butyric, and propionic) that are absorbed from the rumen and supply energy to the host animal. Crampton and Harris (1969) present data showing that 50% to 90% of the crude fiber in plants may be digested in ruminants while nonruminants may digest as little as 3% or as much as 78%. The digestibility of crude fiber in mature, dormant, or dead plant material eaten by wild ruminants may be considerably less than 50%.

ETHER EXTRACT. The ether extract obtained from a food consists of glycerides of fatty acids, free fatty acids, cholesterol, lecithin, chlorophyl, alkali substances, volatile oils, and resins. The last four are not biological nutrients; they are extracted only incidentally. The ether extract of foods will depend, of course, on the chemical differences between them. Since an animal cannot use each of the extracted compounds equally well, the value of the ether extract in the diet is dependent on its utilization. Thus the usual practice of attributing 9.35 kcal of gross energy per gram of ether extract or about 9 kcal of metabolizable energy per gram is an oversimplification of the biological situation.

ASH. Ash is the inorganic residue left after food material has been burned at about 600°C. For ruminants, the use of quantitative determinations of ash has limited value because of the high variability in the amount and kind of ash in plant materials. Some of these minerals may depress digestion. For example, the presence of silica in plant tissue may result in an average decline of three units

digestibility per unit of silica in the dry matter of grasses and legumes (Van Soest and Jones 1968).

SUMMARY OF PROXIMATE ANALYSIS. The proximate analysis of feeds is only an approximation of the chemical content of plant materials, which must be related to the digestion processes of living organisms with caution. Differences between the results of analyses completed in different laboratories indicate that they are subject to human error (Dietz and Cernow 1966).

One of the more subtle characteristics of the proximate analysis is that it results in groups that are related to the chemical characteristics of food materials, rather than to the nutrient content of foods. Indeed, the former is useful only because there is some correlation between the chemical characteristics of the isolates and the properties of feeds that have nutritional significance. Crampton and Harris (1969, p. 52) summarize it: "The Weende analysis does not define the nutrient content of feeds. It is an index of nutritive value only because the fractions that it isolates are correlated with some of the properties of feeds that have nutritional significance. Consequently, it is a useful descriptive device in establishing the characteristics of feeds. As with any other specialized tool, to use it correctly and to its fullest potential requires much other nutritional knowledge and judgement. An appreciation of its design, weaknesses, and limitations, though often stressed in destructive criticism, is more correctly an aid in making full legitimate use of a scheme of feed description which has broad and basic value."

8-4 THE NUTRITIVE EVALUATION OF FORAGES

The shortcomings of the proximate-analysis system of nutrient analysis have been recognized for many years. Short (1966*a*, p. 163) states: "The proximate analysis of important species of deer browse has many times been shown to have little value in predicting how a deer digests a particular forage item." Since the value of any food material depends on its chemical constituents and the ability of the animal to use the nutrients in metabolic processes, it is imperative that the real nutritive relationships be described in meaningful terms.

One new approach to the nutritive evaluation of forages is based on the anatomy of the plant cell in relation to the nutritive availability of the different chemical compounds in a plant cell. The distribution of these chemical compounds within a plant cell is shown in Figure 8-1.[1] The new system separates the highly digestible cell contents (98% to 100% digestible) from the differentially digestible cell-wall constituents. The cell contents are soluble in neutral detergent. The fiber-bound protein and hemicelluloses are soluble in acid detergent, but the cellulose, lignin, and liquified nitrogenous compounds are insoluble in acid detergent. The division of forage organic matter by a system of analysis using detergents is summarized in Table 8-1.

[1]Dr. Peter Van Soest, Department of Animal Science, Cornell University, is a leader in this work and has published several articles on the new system.

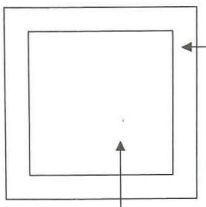


FIGURE 8-1. The composition of a plant cell. (Data from Van Soest 1965.)

How does this approach compare with the older method of proximate analysis? First of all, the nitrogen-free extract in the older scheme includes carbon, hydrogen, and oxygen-rich compounds called carbohydrates. In proximate analysis, the amount of NFE is determined by subtracting all other chemically determined weights from the initial sample weight, resulting in an accumulative error that is dependent on the errors in the determination of other chemical groups. The NFE, however, contains both highly digestible starches and sugars and very indigestible lignin and poorly digestible xylan (Van Soest 1965). Thus the interpretation of the NFE value for a forage analyzed in the older scheme is dependent

TABLE 8-1 DIVISION OF FORAGE ORGANIC MATTER BY SYSTEM OF ANALYSIS USING DETERGENTS

Fraction	*Components*
Cell contents (soluble in neutral detergent)	Lipids
	Sugars, organic acids, and water-soluble matter
	Pectin
	Starch
	Nonprotein nitrogenous compounds
	Soluble proteins
Cell-wall constituents (fiber insoluble in neutral detergent)	
(1) Soluble in acid detergent	Fiber-bound protein
	Hemicelluloses
(2) Acid-detergent fiber	Cellulose
	Lignin
	Lignified nitrogenous compounds

SOURCE: Van Soest 1965.

on the ratio between soluble carbohydrates and indigestible plant-cell materials. This ratio is not known after a complete analysis by the old proximate system, however. The new system of detergent analysis was devised to separate the cell components into chemical groups that had greater biological significance.

What, then, is the role of the proximate analysis data in analyzing the nutritional relationships between animal and range? The determinations of the nitrogen content and the ash in forages are still useful. The NFE and crude-fiber values for a forage may include considerable unknown variation in nutritive quality, and it will be necessary to reanalyze the forages using the detergent system.

8-5 THE ALIMENTARY CANAL

ANATOMY. The alimentary canal in the ruminant includes the mouth, esophagus, four-part stomach, small intestine, large intestine, and rectum. The four-part stomach is unique to ruminants. It includes the rumen, reticulum, omasum, and abomasum. The first three develop as diverticula from the embryonic abomasum, or true stomach.

In the newborn ruminant, milk or water is diverted directly to the orifice entering the omasum through the esophageal groove (Dukes 1955) rather than going into the rumen and then on to the reticulum and omasum. This diversion is a reflex action in the young ruminant that gradually disappears as the animal matures.

The development of the rumen coincides with the increased ingestion of plant materials by the young ruminant. Plant materials that are eaten shortly after birth go to the rumen in which populations of microorganisms are building up as the rumen develops. Concomitant with rumen development is the change from the higher blood-glucose levels of the young ruminant to the lower levels typical of adult ruminants (McCandless and Dye 1950).

The alimentary canal of herbivorous animals has a relatively larger capacity than that of carnivorous animals. This increased capacity permits the extensive fermentation necessary for the breakdown by microorganisms of bulky, fibrous plant materials ingested by the herbivorous host. Carnivore diets, on the other hand, include mainly animal tissue with thin cell membranes, resulting in much more rapid digestion.

The relative sizes and positions of the stomach compartments are not constant throughout the life of a ruminant animal (Figure 8-2). In the newborn, the abomasum or true stomach is larger than the other three parts, and it is not until the age of one or two months that the volume relationship between the omasum plus abomasum and the rumen-reticulum is reversed. After that time, the rumen increases in size. At maturity the rumen comprises about 75% of the total stomach capacity and the reticulum about 10%. The volumetric relationship between rumen + reticulum and omasum + abomasum in white-tailed deer has been determined by Short (1964) and can be expressed as linear regression equations (8-1) and (8-2).

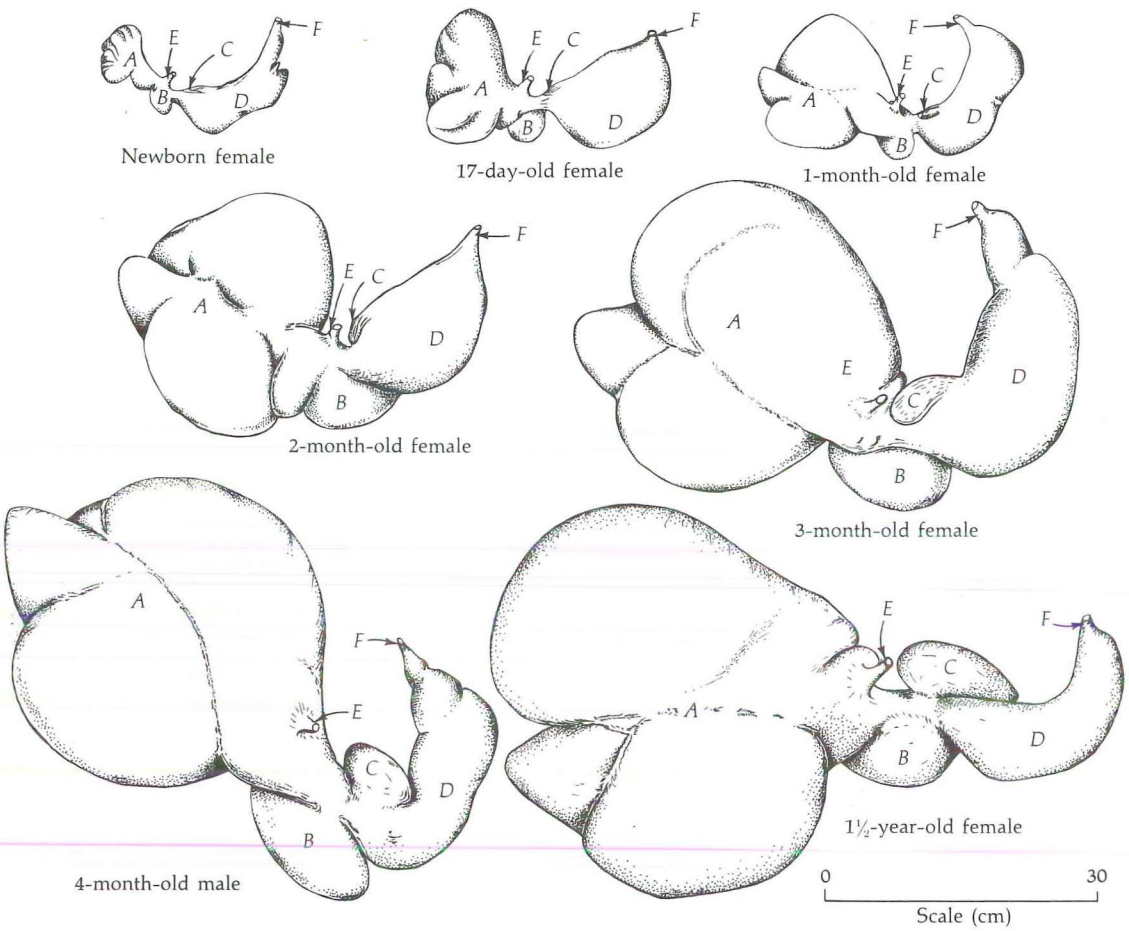


FIGURE 8-2. The sequential development of the stomach of white-tailed deer: *A* = rumen; *B* = reticulum; *C* = omasum; *D* = abomasum; *E* = esophagus; *F* = duodenum. (From Short 1964, *J. Wildlife Management.*)

Rumen + reticulum:

$$Y = 103.35\ W_{kg} + 304.64 \qquad (8\text{-}1)$$

Omasum + abomasum:

$$Y = 11.705\ W_{kg} + 514.64 \qquad (8\text{-}2)$$

where

Y = volume expressed as ml of water

W_{kg} = body weight in kg

The use of these equations and other data in Short (1964) permits an approximation of the relative volumes of rumen + reticulum and omasum + abomasum [equation (8-3) shown in Figure 8-3].

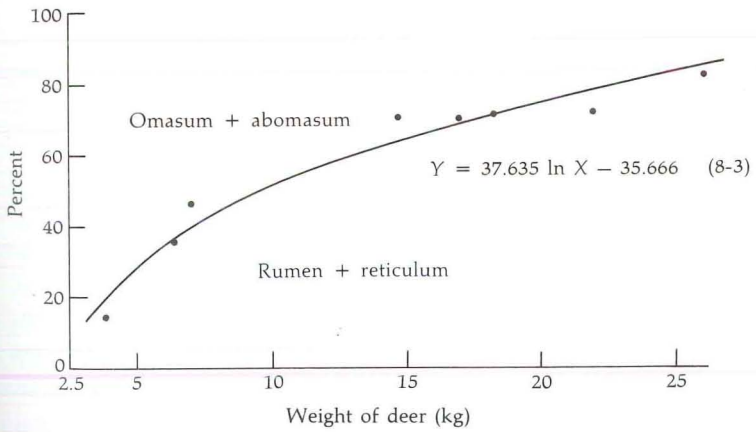
The ruminoreticular volume of mule deer, expressed as liters, is equal to about 10% of the body weight expressed in kilograms (Short, Medin, and Anderson 1965). This is considerably less than the percentage for cattle. The relationship between rumen volume and body weight is important because the rumen is a "holding tank" in which fermentation takes place. The metabolic products are a source of energy and protein for the animal. The capacity of the rumen represents a finite limit to the amount of nutrients that can be made available in a given length of time.

Stomach capacity in relation to body weight for age classes within a species are also worth considering. Short (1964) points out that the relatively small stomach capacity of deer fawns may be an important factor in winter mortality. The browse ingested by deer in the winter in forested areas may not be metabolized rapidly enough to supply the heat production necessary to maintain body temperature during periods of cold weather, thus causing a mobilization of the fat reserve.

One of the interesting deductions that can be made from the comparisons of growth between different stomach compartments is the anatomical and physiological basis for weaning. Tamate (1957) defines weaning as the period during which the capacity of the rumen equals that of the abomasum. He notes three levels of rumen capacities in goats: 20% in the preweaning stage, 44%–48% in the weaning stage, and 82%–85% in the postweaning stage. Adult proportions of the rumen and reticulum in lambs were reached at about 56 days of age (Church, Jessup, and Bogart 1962). *In vitro* fermentations in this study indicated that the rumen digestion was characteristic of that of adults by the time the lamb was three weeks of age, which is the time at which marked growth of the rumen occurs.

Using the time at which the animal achieves equal proportions between the rumen-reticulum and the omasum-abomasum as an indicator of physiological

FIGURE 8-3. The relative proportions of the different stomach compartments of white-tailed deer. The rumen plus reticulum occupies about 85% of the total volume for the remainder of the animal's life.



weaning, Short (1964) concludes that domestic goats and sheep are weaned at about 25 days of age, and white-tailed deer at about 35 days of age.

The weight at which the equal proportions are reached in white-tailed deer is 10 kg (see Figure 8-3). A growth equation in Murphy and Coates (1966) for suckling fawns is:

$$W_{lb} = 4.77 + 0.51t_d \tag{8-4}$$

where

W_{lb} = weight in pounds

t_d = age in days

This equation is $2.17 + 0.23t_d$ if body weight is given in kg. A white-tailed deer can be predicted to reach a weight of 10 kg at age (t_d), using equation (8-5):

$$t_d = \frac{W_{kg} - 2.17}{0.23} \tag{8-5}$$

The solution to equation (8-5) is 34 days, which is very close to the age of 35 days estimated by Short (1964).

White-tailed fawns can be weaned at an earlier age. One female fawn at the BioThermal Laboratory refused to take milk from the bottle at a weight of 15 lb. She was fed calf pellets and had access to grass in her pen, and she weighed as much in the fall as the other fawns on a feeding schedule that included milk.

Wood, Nordan, and Cowan (1961) fed their deer fawns evaporated milk and water in a 1:1 ratio six times per day and weaned them at 15 lb (7 kg) and 5 to 7 weeks of age. Seven-week-old orphaned pronghorn kids survived without milk (Bromley and O'Gara 1967). Thus it is obvious that young ruminants are capable of being fully functional ruminants at a much earlier age than the natural weaning process would indicate since wild fawns are usually not completely weaned until they are 3 months or older.

HISTOLOGY. The four-part ruminant stomach has a tissue and cellular structure that is related to the functions of each of the parts. The rumen is a muscular organ with a middle layer of smooth muscle that is capable of rhythmic contraction. The smooth-muscle layer is enveloped between a highly vascular layer with many papillae and an outer serous layer that is continuous with membranes that support and suspend the stomach (Short 1964). The papillae lining the rumen (Figure 8-4) greatly increase the internal surface area of the organ, resulting in a more rapid absorption of the volatile fatty acids produced by the rumen microorganisms as by-products of their own metabolism.

The papillae are very rudimentary in the very young ruminants, and their development is dependent on the end products of rumen fermentation (Flatt, Warner, and Loosli 1958). The small and nonfunctional rumen at birth develops concomitantly with an increase in the dependence of the host on digestive action of the rumen microorganism. Short (1964) describes the anatomy of internal

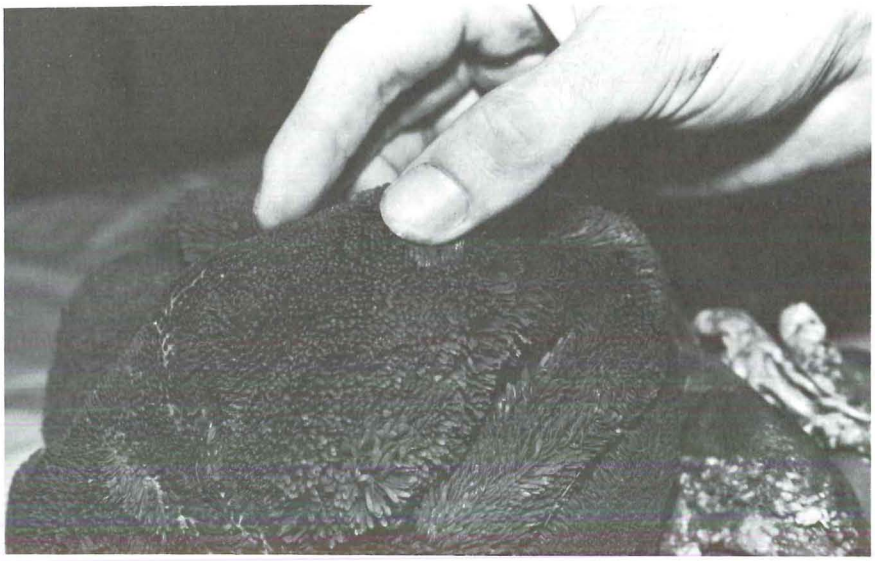


FIGURE 8-4. The papillae lining the rumen of white-tailed deer.

stomach characteristics for deer from birth through $5\frac{1}{2}$-years (Table 8-2). Note that the size of the papillae is nearly maximum by the age of 4 months.

The reticulum is not nearly as muscular as the rumen; the muscular middle layer is thin. It is connected to the rumen through the ruminoreticular fold. Its function is closely associated with the rumen because the ruminoreticular fold acts like a dam, retaining the more solid ingesta in the rumen. Contractions of the reticulum force liquid into the rumen, washing the material in the rumen. The finer particles of ingesta go into suspension. These are washed back into the reticulum by rumen contractions and then move on to the omasum. There are only occasional papillae and the epithelial lining is without glands.

The omasum has many leaves or folds covered by small granular papillae. The leaves increase the internal surface area of the omasum and play an important part in water absorption (Short 1964). The true stomach of the ruminant is the abomasum. It has a muscular layer composed of thin fibers in small bundles, an outer serous layer, and an interepithelial lining that includes secretory glands (Short 1964).

8-6 MECHANICAL AND SECRETORY PROCESSES IN DIGESTION

Mechanical factors function throughout the entire process of digestion to keep the food materials moving through the alimentary canal. The mechanical actions in the ruminant include the prehension and ingestion of food materials, mastication, swallowing, regurgitation, reswallowing, rumen contraction, intestinal contractions, and defecation.

During the mechanical movement of food through the alimentary canal, saliva and digestive juices are secreted and mixed with the food materials. The enzymes

TABLE 8-2 ANATOMICAL MEASUREMENTS (means of each age group) OF THE STOMACH OF WHITE-TAILED DEER

		Rumen			*Reticulum*			*Omasum*					*Stomach Contents*				
														% Distribution		*Nature of Contents*	
Age of Deer	*Number of Deer*	*Tissue Weight (g)*	*Papillae Length (mm)*	*Papillae Width (mm)*	*Polygons (cm)*	*Papillae (mm)*	*Tissue Weight (g)*	*Length (cm)*	*Width of Leaves (cm)*	*Papillae (mm)*	*Tissue Weight (g)*	*Abomasum Tissue Weight (g)*	*Total Weight (g)*	*Omasum and Abomasum*	*Rumen and Reticulum*	*Omasum and Abomasum*	*Rumen and Reticulum*
Newborn	1	7	R*	R*	0.1	R*	2	2.5	0.6	R*	2	25					
½ mo	3	26	0.5–1	0.2	0.4	0.5–1	7	4	0.7	1	5	47	195–300	65–96	35–4	Milk curds	Sand and grass
1 mo	2	47	2	0.5	0.5	1	7	4	1	1	3	32	262–348	33–45	67–55	Vegetation and milk curds	Vegetation
2 mo	2	183	4–5	1	0.6	1	27	4	1–1.5	1	17	70	1,321–1,373	16–22	84–78	80% vegetation, 20% milk curds	Vegetation
3 mo	2	189	5	1	1–1.2	1	21	5	2	1	11	45	1,612–1,720	5–14	95–86	Vegetation and trace of milk	Vegetation
4 mo	2	321	5–8	2	1.2	1	29	5	2.5–3.8	1	19	48	3,407–3,481	3–4	97–96	Vegetation and trace of milk	Vegetation
1½ yr	2	845	10	2	1.2	1	64	7.5	3.8	1	58	101	2,527–4,906	7–8	93–92	Similar contents	
5½ yr	1	935	10	2	1.2	1	75	10	5	1	102	145	3,362	8	92	Similar contents	

SOURCE: Short 1964, *J. Wildlife Management* **28**(3) p. 448.
*Rudimentary.

in these secretions assist the rumen microorganisms in the process of digestion. Since there are no glands in the linings of the rumen and reticulum, digestion is almost totally dependent on the activity of the microorganisms, with only a slight contribution from the saliva.

INGESTION. Ingestion or prehension is the process of seizing and conveying food to the mouth (Dukes 1955). This may seem like a simple process but it is accomplished in different ways among wild ruminants. Deer, for example, remove browse by grinding it off with their molars. When feeding on low herbaceous vegetation, they use the lower incisors and upper gum to seize the plant material. Grains on the ground are picked up with the aid of the tongue.

SALIVATION AND MASTICATION. Three salivary glands in the ruminant have been described by Dukes (1955). The parotid gland, located on the side of the cheek, secretes a thin, watery substance containing protein. The submaxillary gland, located below the lower mandible, secretes a thin watery substance containing the glycoprotein mucin. The sublingual gland, located under the tongue, also secretes both protein and mucin. The saliva functions as a lubricant during chewing, swallowing, and regurgitation. It is also important in maintaining the rumen fluid volume. Its high alkalinity makes it a good buffering agent for the maintenance of an appropriate *p*H in the rumen. The nitrogenous substances that make up the saliva also serve as a substrate for protein synthesis by rumen microorganisms, and this protein is useful to the ruminant host (Annison and Lewis 1959).

RUMINATION. Four phases of rumination are listed by Dukes (1955): (1) regurgitation; (2) remastication; (3) reinsalivation; and (4) reswallowing. Regurgitation occurs with no contraction of the rumen since the skeletal muscles are used instead (Dukes 1955). Dzuik, Fashingbauer, and Idstrom (1963) observed that white-tailed deer would regurgitate ingesta, swallow without mastication, and regurgitate again in less than ten seconds. No possible explanations were given for the rapid reswallowing; it may be associated with some characteristic of the particular bolus.

The first signs of regurgitation appear in domestic goats at the age of 8–12 days (Tulbaev 1959). Goats on solid food assume a normal rumination rhythm during the next 5–8 weeks. At first, each regurgitation and remastication cycle lasts 15–25 seconds followed by a pause of 9–15 seconds. Ten to fifteen days after the introduction of solid food, remastication was prolonged to 20–30 seconds followed by a pause of 6–12 seconds.

The jaw movements during remastication are vertical and lateral, resulting in a circular motion that is centered on one side at a time. The innermost edge of the lower teeth and the outermost edge of the upper teeth are sharp. The teeth wear roughly, increasing the grinding efficiency until old age, when both the efficiency of grinding and the physical condition decline.

STOMACH AND INTESTINAL MOVEMENTS. The rumen and reticulum are both physiologically and metabolically active parts of the ruminant digestive system. They

move, churning the food that is being metabolized by the microorganisms, which results in a separation of the indigestible residue from the more digestible parts of the diet.

Ingested food is retained in the rumen and reticulum until it has a fine consistency. Contractions of the rumen and reticulum result in an interchange of food and liquids. The brisk regular contractions of the reticulum cause fluid to be washed backward into the rumen, flushing the contents with liquid. This is followed by contractions of the rumen, which return the fluid and small food particles to the reticulum and then to the omasum (Annison and Lewis 1959).

The contraction patterns of the rumen and the reticulum of white-tailed deer have been studied by Dzuik, Fashingbauer, and Idstrom (1963). Measurements indicated that contractions of the musculature of the rumen and reticulum are very closely associated with each other. The first or primary rumen contraction follows the "reticular doublet" or two successive contractions of the reticulum. The primary contraction involves all parts of the rumen. A secondary rumen contraction may occur, involving the dorsal sac, posterior dorsal blind sac, and the ventral sac of the rumen. The time required for the contractions that occur between one reticular doublet and the next is considered to be one complete ruminoreticular cycle.

The duration of the ruminoreticular cycle was found to be 20–30 seconds. The frequency of reticular and primary rumen contractions varied with the activity of the deer; they were less frequent when the deer were resting (2.2 contractions per minute). Secondary rumen contractions varied from 0.6 to 0.8 contractions per minute while the deer were standing to 0.2 to 0.5 contractions per minute while reclining. Thus the primary contractions were more frequent during periods of resting, but secondary contractions were more frequent during periods of standing. The significance of that reversal was not explained.

The secondary contractions of the rumen were almost always in a 1:1 ratio with eructation, or belching. This is of interest because the eructation of gases represents an energy loss that is difficult to measure in wild ruminants.

Dzuik, Fashingbauer, and Idstrom (1963) concluded that there is a marked similarity in the ruminoreticular contractions of deer, cattle, and sheep. There were differences in frequencies but these were not stable for a single animal over a period of time. Their work yields insight into the mechanical processes to which food materials and rumen microorganisms are subjected. The similarity between deer and domestic ruminants indicates that domesticated animals are not vastly different from their wild relatives; much can be gained from comparative studies on domestic and wild ruminants.

In the omasum, contractions of the muscular walls compress and triturate or pulverize the food materials. At the same time, 60%–70% of the water content is absorbed. The food materials are then passed on to the abomasum where gastric juice is secreted and the fluid content is restored to approximately the original level in the omasum. The hydrochloric acid content of the gastric juice results in a *p*H of 1.5–3.0. Protozoa disintegrate there and most bacteria are killed. The food materials pass through the abomasum quite rapidly and move on to the small intestine (Annison and Lewis 1959).

DEFECATION. Undigested residues are eliminated by defecation. The fecal mass also includes degraded tissue that has been removed from the internal linings of the alimentary canal, as well as the remains of rumen microorganisms that have escaped digestion in the small intestine.

A considerable amount of emphasis has been placed on the defecation rate as a method of taking a census of wild populations. An assumption about the number of pellet groups released per animal per day (13 is a common estimate) has been used to estimate the number of deer in a given area. Defecation rates vary, however, depending on both the quantity and quality of the diet. Experiments have shown that known populations are generally underestimated by this method (Smith 1964).

8-7 CHEMICAL PROCESSES OF DIGESTION

The study of digestion or any other biological function is complex. There are many variables in digestion, including dietary components and the microorganism spectrum, but the end result of digestion is the same—raw material (food) is converted into a form that can be used by the metabolic machinery of the body for maintenance of basic life processes, support of activity, and tissue production.

One problem in studying an internal system is that the removal of any component may result in the disruption of the normal operation of the system. This is true in studies of rumen function. One technique that permits analyses of the chemical reactions in the rumen with little effect on the animal is the use of a rumen fistula. A fistula is a covered opening into the rumen through an incision on the posterior portion of the body wall (Figure 8-5). The cover is removable so that the contents of the rumen can be removed or altered for experimental

FIGURE 8-5. A rumen fistula in a white-tailed deer.

purposes. It is a useful technique for studying the internal characteristics of the rumen with a minimum of disturbance to the animal.

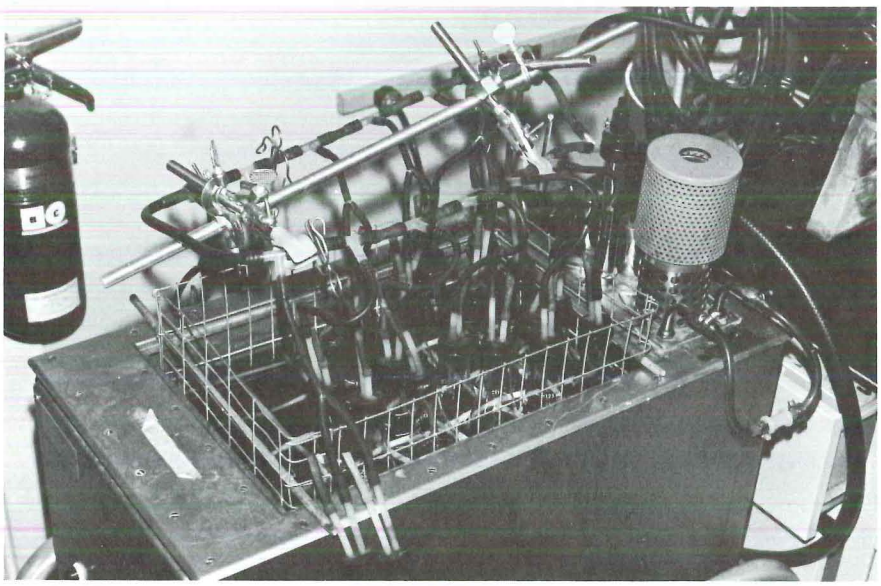
Successful installation of rumen fistulas has contributed to the development of another technique that has considerable promise in the field of ruminant nutrition. This is the *in vitro* method, or artificial rumen experiments. An artificial rumen system consists of a constant-temperature bath that maintains thermal conditions similar to those inside the animal and a container that simulates the rumen itself. This container is filled with the experimental forage and rumen fluid that has been extracted from an animal. The products of digestion are analyzed after an incubation period of about 48 hours. The equipment used for *in vitro* studies is shown in Figure 8-6.

An artificial rumen is not identical to a natural (*in vivo*) one. The dynamics of the living rumen musculature and the motion caused by gross animal activity are missing, as are the histological changes that occur continually in the rumen lining. Used properly, it is an excellent supplementary tool for research in ruminant nutrition.

Another recent technique for studying ruminant digestion is the "sack" technique. A small, indigestible, nylon-mesh sack is suspended in the rumen and the changes in its content of food material are noted. The restriction that the sack imposes on the food material is obviously unlike the natural flow in the rumen, but the results can be useful for interpreting certain aspects of ruminant nutrition.

RUMEN MICROORGANISMS. Rumen microorganisms are absolutely essential for successful digestion. The microorganisms are absent at birth, and experiments

FIGURE 8-6. The *in vitro* fermentation bath at the BioThermal Laboratory, Cornell University.



with axenic (germ-free) animals demonstrate clearly that the microorganisms are symbionts essential to ruminant animals (Pantelouris 1967). The necessity for these symbiotic organisms is due to the absence of the enzyme cellulase in the ruminant stomach. This enzyme is necessary for the breakdown of cellulose, a major component of the cell walls of plants. Both bacteria and protozoans are present in the anaerobic rumen environment. As many as 896 strains of bacteria have been isolated (Pantelouris 1967), and more than 100 species of protozoans (Annison and Lewis 1959).

No animal has the full range of microorganism populations, but the variety of microorganisms in the rumen is large enough so that gradual changes in the diet do not appreciably affect digestion. Further, different species of ruminants throughout the world have almost the same kinds of microorganisms. The number of each species or strains of microorganisms present in the rumen varies, however, even among animals of the same species on the same range. The ciliate *Eudiplodinium* was absent in two elk but was the only large ciliate found in others on the northern Yellowstone elk range (McBee 1964). Other genera were observed to vary among animals during the same season, and one genus, *Enoploplastron*, varied seasonally, disappearing when green grass became a major part of the diet.

The number of microorganisms in the rumen is extremely large. Microscopic counts of organisms in the rumen fluid of thirty-three elk showed from 2.9 to 74.2 billion bacteria per gram of rumen content, with an average of 35 billion per gram (McBee 1964). This is more than the average of 10 billion per milliliter reported by Annison and Lewis (1959) for domestic ruminants.

There are fewer protozoans in the rumen—10^6 or one million in each milliliter of rumen contents (Pantelouris 1967). Their bulk, however, may equal that of the bacteria since the protozoans are much larger (Annison and Lewis 1959).

The bacteria and protozoans in the rumen have their own distinct metabolic characteristics. Most of the important species are obligately anaerobic; they do not require oxygen for metabolism. They have nutrient requirements of their own and must have a certain quantity of protein available to supply their nitrogen requirements before the digestion of starch can occur. Starch is valuable as a substrate for rumen microorganisms, and its utilization is an important factor in maintaining flourishing populations.

Simple sugars are actively metabolized by both protozoans and bacteria in the rumen. Three distinct processes occur: (1) fermentation of sugars, which consists of energy-yielding catabolic reactions; (2) conversion of sugars to glycogenlike polysaccharides and the storage of this material; and (3) endogenous metabolism of the stored polysaccharide. The last two processes are more apparent in rumen protozoans but are undoubtedly part of bacterial metabolism as well. The stored polysaccharide in the protozoan is available for subsequent metabolism by the host animal. Its body protein is also of biological value, and the protozoans themselves are digested in the small intestine (Annison and Lewis 1959).

FERMENTATION. The fermentation of food materials in the rumen is an essential step in the digestion process of ruminants. It takes place in a very particular type

of environment—an anaerobic, highly reducing system at a slightly acid but buffered *p*H—in which a very specialized microorganism population develops (Annison and Lewis 1959). If the supply of food in the rumen is maintained by frequent intake, conditions in the rumen remain fairly constant inasmuch as the microorganisms have a regular supply of carbohydrates and proteins for the maintenance of their own metabolic activities. The soluble products of this activity are readily absorbed through the rumen wall, preventing their accumulation in the rumen.

The rumen functions as an open system that depends on the flow of food materials into it and the flow of microorganism metabolites and food residues out. If food remains undigested in the rumen, the animal's appetite is diminished and rumen movement stops. According to Nagy, Vidacs, and Ward (1967), experiments show that if the rumen is then filled with actively fermenting rumen fluid from other animals, both appetite and rumen movement begin again.

Rumen fermentation continues only if there is an adequate amount of carbohydrates and proteins to support microorganism metabolism. In addition to an adequate quantity, the balance between the quantity of carbohydrate and nitrogen is also important. A minimal level of protein that can be digested by rumen microorganisms is essential for supplying their own nitrogen requirements (Annison and Lewis 1959). Two main conclusions are usually drawn from feeding experiments on the energy and protein relationships in ruminants: (1) the rumen microorganisms attack the fibrous components of the ration more rapidly as the protein intake is increased and (2) they utilize the protein better in the presence of added carbohydrate (Annison and Lewis 1959).

Digestion by the microorganisms results in the breakdown of cellulose in the rumen. The efficiency of this process depends on the metabolism of simple carbohydrates because a large proportion of the energy requirements of the cellulose-splitting organisms is probably supplied by the fermentation of these materials (Annison and Lewis 1959). The complex interaction of the rumen microorganisms with their chemical environment does not result in an unlimited supply of energy to the host. Deer are not super-ruminants; Short (1963) found that *in vitro* digestion of cellulose was often greater for a steer than for white-tailed deer. The relative nutrient value of several browse species was related to the crude-fiber levels of the plant materials—as the crude-fiber content goes up the digestibility goes down. Short, Medin, and Anderson (1965) concluded that the cellulose content seems to limit the digestible energy available to deer in both natural forages and artificial rations.

Two criteria need to be considered in assessing the role of microorganisms in ruminant nutrition: one is that the organisms must be capable of carrying out a reaction known to take place in the rumen, and the other is that the organisms must be present in sufficient numbers to account for the extent of the reaction (Annison and Lewis 1959). Nagy, Vidacs, and Ward (1967) have studied both of these criteria. They determined that short-chain fatty acids were produced by the rumen fermentation of alfalfa hay in the same proportions normally found in the rumen contents of wild deer. This suggests that no major adjustments in

the microbial spectrum are necessary for deer to digest different natural foods.

Changes in the diet of wild deer can cause mortality, however. Cases in which deer have died even though they had had a plentiful supply of hay have been reported in the literature. One possible explanation for this is that as the amount of substrate material decreases during starvation there is a loss of properly functioning microorganisms for the rumen. Food that is difficult for the microorganisms to digest could produce nutritional deficiencies for support of the rumen populations with a concomitant decrease in the rate of fermentation. When the point is reached at which the rumen contains only a small number of active microorganisms, the food residues, in normal passage through the intestinal tract, would tend to mechanically remove these microorganisms at a faster rate than the growth of the resident population (Nagy, Steinhoff, and Ward 1964). Appetite and rumen movement stopped completely when three 7-pound portions of sage brush were introduced into a steer through a rumen fistula. Thus the digestive efficiency of wild ruminants can be reduced when range conditions deteriorate to the point that animals are forced to eat certain plants that might otherwise be avoided.

*p*H. The *p*H of the rumen fluid varies seasonally. For elk, it was found to be generally below 6.0 during the summer, between 6.0 and 7.0 during autumn and most of the winter, and above 7.0 during late winter (McBee 1964). These values are very similar to those reported by Short (1963) for white-tailed deer on different diets. Aspen and white-cedar diets, typical winter forages of deer in the northern range, result in *p*H ranging from 6.42 to 7.09, but an alfalfa-concentrate diet results in a rumen *p*H of 5.23 and 5.48.

8-8 PRODUCTS OF FERMENTATION

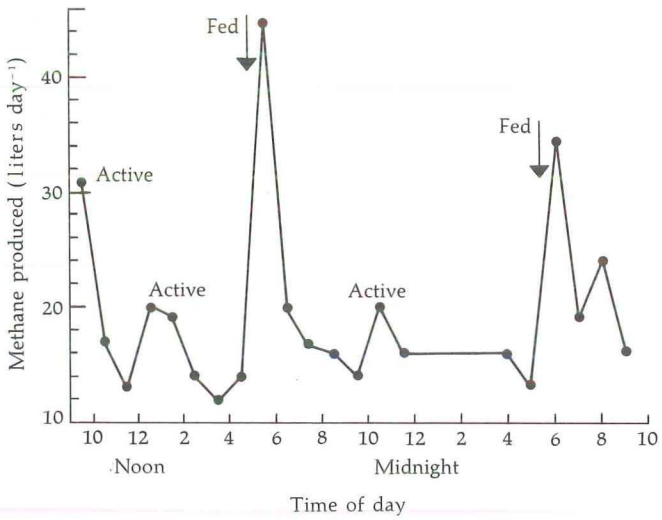
HEAT ENERGY. Rumen microorganisms are metabolically active and consequently must produce certain end products of metabolism. These include heat energy, gases, volatile fatty acids, protein, and vitamins. The first three are waste products from the microorganisms themselves, but only the gases are waste products for the ruminant host. The heat energy is often called a waste, but that is an oversimplification of the role of heat energy in a homeotherm. When the thermal environment of an animal is such that heat production exceeds heat loss, the heat energy produced by the rumen microorganisms must be dissipated from the body surface to maintain a stable body temperature. But, if the thermal environment results in a heat loss greater than the heat produced by nutrient metabolism, then the heat of fermentation in the rumen is important for the maintenance of a stable body temperature.

GASES. The two gases produced by rumen fermentation are carbon dioxide (CO_2) and methane (CH_4). The actual volume of methane produced by cattle can approach 400 liters per 24 hours and by sheep up to 50 liters per day (Blaxter 1967). The amount of methane absorbed by the blood and exhaled through the

lungs of cattle varied from 25% to 94% of the total measured CH_4 before feeding and 9% to 43% after feeding (Hoernicks et al. 1965). The remaining CH_4 was eliminated by eructation. The energy contained in the methane is about 8% of the total food energy. Blaxter (1967) points out that the rate of methane production varies with food consumption and activity. Maximum quantities are produced at the time the food is ingested; lesser amounts are produced when the animal is physically active (Figure 8-7).

VOLATILE FATTY ACIDS. The volatile fatty acids (VFAs) are the most important product of ruminant fermentation, for they are readily absorbed from the rumen and serve as a major source of energy to the animal. Under normal conditions only small amounts of VFAs escape absorption in the rumen and pass on to the small intestine. The amount of energy absorbed from the rumen as a result of VFA production is of real biological significance. Annison and Lewis (1959) cite references indicating that at least 600 to 1200 kcal of energy are absorbed in the form of VFAs from the sheep rumen every 24 hours. In cattle, which have a much greater absolute rumen capacity, 6000 to 12000 kcal become available from the VFAs produced by rumen fermentation. In white-tailed deer, the energy contained in an average gram of rumen acid (with assumptions on molar percentages of the different acids) is estimated to be 4.15 kcal (Short 1963). The average amount

FIGURE 8-7. Typical variation in the methane production of a sheep during a 24-hour period. Note the peaks in production associated with eating and with the physical activity of the animal. (Data from Blaxter 1967.)



of VFA contained in 3000 ml of rumen contents of a deer on an alfalfa-concentrate diet was 25.3 g. This would provide about 105 kcal. If this diet were to provide 1000 kcal in a 24-hour period, the rumen contents would have to be absorbed 9.52 times. The total VFA content of 3000 ml of rumen contents of a deer on an aspen diet was 11.6 g of VFA, and this would provide 48.1 kcal. The VFA content of a deer on a white-cedar diet is 15.8 g, providing 65.6 kcal. The rumen contents due to these two diets would have to be turned over 20.79 times and 15.24 times, respectively, if they were to provide 1000 kcal of energy in a 24-hour period. These turnover rates appear to be unreasonable; further studies of the digestive physiology and the production and absorption of individual VFAs are needed.

The first accurate analyses of the rumen contents of domestic animals were completed in 1945 and 1946 (Annison and Lewis 1959). Acetic, butyric, and propionic acids were invariably found to be present. The total concentration of these VFAs in the rumen and the amount of each individual acid depends on both the composition of the ration and the feeding schedule. Seasonal differences were observed in mule deer (Short 1966*b*), and variations in the proportions of VFAs were observed between white-tailed deer killed at different times of the day (Short 1963).

The concentration of VFAs in the rumen is an indication of the rate of fermentation; higher concentrations of acids are present when easily fermented foods are eaten (Short 1963). High concentrations alone are not precise indicators of the actual rate of production, however. Annison and Lewis (1959) point out that the rumen concentration of VFAs at any given time depends not only on the rate of production of acids in the rumen, but also on the rate of absorption of acids from the rumen, the rate of passage from the rumen to the omasum, the dilution with saliva, the utilization of VFAs by the rumen microorganisms, and the conversion to other rumen metabolites. They also observed that the amount of butyric acid in the blood from the wall of the rumen was less than the amount expected based on the relative amount of butyric acid leaving the rumen. This indicates that the butyric acid was used by the rumen wall itself.

The VFAs in the rumen seem to come from the degradation of carbohydrates. In monogastric animals, most of the caloric energy is absorbed from the small intestine in the form of glucose (Annison and Lewis 1959). Glucose and VFA concentrations in a very young ruminant are very similar to those in a monogastric animal, but as the age of the ruminant increases, the rumen becomes more functional, the concentrations of VFAs increase, and the blood sugar falls to a level about one-half that of nonruminants.

The value of a particular diet should be determined on the basis of the rates at which the nutrients are made metabolically available to the animal through rumen fermentation. Short (1963) stresses the need for additional understanding of energy relationships before management of deer can be properly based on nutritional facts. The framework within which these energy considerations can

be made is discussed in Part 6. The accuracy of any calculations related to the diet depends on the quality of the basic energy data and on the quality of the measurements of feeding data and other factors. It is unfortunate that so little research has been done on basic energy relationships of wild ruminants; the alternative is to make first approximations that will permit analyses of the total animal-environment relationship and an error analysis of the effect of approximations.

PROTEIN. It has been observed that the protein content of the rumen is often higher than the protein content of the food that is being ingested. The terminal two to three inches of growth on browse sampled by Bissel (1959) contained 6.9% crude protein, but the rumen contents of nine deer contained 17.6% crude protein. Fourteen deer were studied in January and February when plants were dormant and the range and rumen values for protein content were 7.1% and 17.2%, respectively, in January and 6.1% and 15.1% in February. Three deer that were fed alfalfa pellets with 15.7% protein content had rumen protein contents of 21.0%, 16.2%, and 14.7%.

The increase in the nitrogen content in the rumen over that of the ingested food materials can be accounted for in several ways. Ammonia that is formed by protein digestion is absorbed by the blood, converted into urea by the liver, and then either excreted by the kidney or returned to the rumen as a component of saliva (Dukes 1955). The urea secreted into the rumen is rapidly hydrolyzed by bacterial urease. On low-nitrogen diets this additional supply of ammonia helps to promote an active microbial population with a concomitant increase in the synthesis of microbial protein (Ullrey et al. 1967, citing Kay 1963).

The microbial protein synthesized is of direct benefit to the host animal. The rumen microorganisms synthesize protein from amino acids and nonprotein nitrogen sources, and the rapid turnover of the microbial population results in the passage of a large number of organisms to the omasum and abomasum where they are digested (Pantelouris 1967). A considerable portion of the protein requirement of ruminants is supplied in this way (Annison and Lewis 1959).

The greatest benefit derived from protein synthesis by rumen microorganisms is their conversion of nonprotein nitrogen to microbial protein that can be digested and absorbed by the host. Urea is such a converted compound. It is currently being used to economic advantage by cattle feeders who add it to the diet as a low-cost supplement to low-protein diets. Deer ingest urea and other nonprotein nitrogenous compounds by consuming water that has been accumulating in pools in which feces and urine have been deposited, by lapping urine from other deer, and by the cleaning of the anal region of the fawns by the doe. Captive white-tail fawns less than two weeks of age have shown varying degrees of interest in lapping the urine from their penmates, sometimes preferring urine to milk.

Other sources of protein are available to the ruminant, including respiratory secretions and the epithelial cells that are sloughed off. These must be replaced, however, so this source of protein cannot be considered of value over a long period of time.

VITAMINS AND MINERALS. Vitamins and minerals are essential components of an animal's diet, with the former being used in nutrient metabolism and the latter deposited as a part of the structural components of different body tissue. It is not practical for the range manager to supply these as additives to feeds as the domestic feeder can. Free-ranging animals should have sufficient quantities of vitamins and minerals when the energy and protein needs of the body are met, except in local areas where the soil may be deficient or overly rich in some materials so a chemical imbalance results. This may develop on several western ranges where the calcium-phosphorus ratio is so high that the metabolism of phosphorus is affected. A deficiency of phosphorus or a wide calcium-phosphorus ratio could cause retarded growth, a high feed requirement, unthrifty appearance, weak young, decreased lactation, failure to conceive, stiffness of joints, and other abnormalities (Dietz 1965).

The vitamin requirements of adult ruminants are satisfied in part by the vitamin syntheses of rumen microflora. Water-soluble vitamins of the B complex are synthesized in the rumen if appropriate foods have been eaten (Annison and Lewis 1959). Vitamins A, D, and E are not synthesized and must be supplied in the diet, but fat-soluble vitamin K is synthesized in the rumen (Annison and Lewis 1959). The young animal that does not have a functional rumen requires the full vitamin complement as a component of the diet. In the wild, this is apparently met by the ingestion of milk and herbaceous plants.

The role of minerals and vitamins in the nutrition of wild ruminants needs to be analyzed in a dynamic way over the entire annual cycle. The methods used for energy and protein analyses in Part 6 are applicable to minerals and vitamins.

8-9 PASSAGE OF DIGESTA THROUGH THE GASTROINTESTINAL TRACT

The rate of passage of digesta through the gastrointestinal tract is an important factor in an evaluation of the nutritive relationships between an animal and its range. Although it is common practice to report the rumen contents of animals killed in the field, this may give a false picture of nutrient absorption and assimilation. The forages more resistant to the enzymatic activities of rumen microorganisms will remain in the rumen the longest. Hence the forages that may be least important nutritionally may be most abundant in the rumen.

An exercise illustrating the importance of turnover rate is shown in Table 8-3. Different foods (marbles) are placed in the rumen (a dish) at different rates, and they pass through the rumen at different rates. The absolute quantities of the different colored marbles at a given time are measured. These represent the "standing crop" or food in the rumen. The number of different marbles that enter the dish and pass on as digested food is then compared with the daily estimates. Over a 12-day period, a distinct difference between the percentage of observed abundance of marbles of each color through daily sampling and the actual abundance of marbles that have passed through is observed. It is a clear indication of the need to consider both the quantity of food in the rumen and the rate of its passage through the rumen.

TABLE 8-3 TURNOVER RATE IN THE "RUMEN" AND ITS RELATIONSHIP TO ACTUAL ABUNDANCE

Data

Black marbles	Enter 3 every third day, 3-day turnover time
Blue marbles	Enter 2 every other day, 1-day turnover time
White marbles	Enter 1 every other day, 2-day turnover time
Yellow marbles	Enter 1 every other day, 1-day turnover time

Abundance Through Time

	Days													
	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*Total*	*% of Total*
Black marbles	3———			3———			3———			3———			12	29
Blue marbles	2	0	2	0	2	0	2	0	2	0	2	0	12	29
White marbles	1——		1——		1——		1——		1——		1——		6	14
Yellow marbles	1	1	1	1	1	1	1	1	1	1	1	1	12	29
													42	

Observed Abundance Through Daily Sampling

	Total Observed	*No. of Days*	*Average*	*% Observed Abundance*	*% Actual Abundance*
Black marbles	36	12	3	50	29
Blue marbles	12	12	1	17	29
White marbles	12	12	1	17	14
Yellow marbles	12	12	1	17	29

Several factors contribute to variation in the results of experiments on the rate at which digesta passes through the gastrointestinal tract of domestic ruminants. Church (1969) has concluded that the physical nature of the feed appears to be a most important factor controlling the rate of passage from the rumen. Other factors include the specific gravity of the ingesta, particle size, digestibility of the food, and the level of feed intake.

Some of the variation in reported results can be attributed to the methods used for marking the food. Dyes, polyethylene markers, and chemical markers in the forage have their own unique rate of passage and do not follow perfectly the movements of the ingesta. This error does not eliminate the usefulness of the data, but it must be considered when interpreting the observed results.

Some general relationships between the retention time for the forage and the characteristics of the forage are evident from the literature. Ingalls et al. (1966) calculated passage from the rumen by dividing the amount of food in the rumen by the daily intake. The retention time of alfalfa dry matter was 0.62 days, trefoil, 0.68 days, timothy, 0.84 days, and canary grass, 0.94 days. The more rapid digestion of legumes compared with grasses is reflected in the faster turnover

rate. The retention time for browse species that make up major portions of the diets of some wild ruminants, especially in the winter, is probably longer.

Smaller particles are digested more quickly and pass through the gastrointestinal tract faster than larger ones. The surface area of a given weight of smaller particles is greater than the surface area of an equivalent weight of larger particles. This results in more efficient digestion. Thus the faster rate of passage does not necessarily mean a loss of nutrients. If the level of feeding is high enough so that the rate of passage results in incomplete digestion, the nutritive value of the forage may be reduced.

The many factors that affect turnover rates are difficult to study, but they appear to be very important in determining the nutritive characteristics in an animal-range relationship. A faster turnover rate may compensate for a lower digestibility up to a point, and conversely, the benefit of a high digestibility may be reduced by a rapid turnover rate. The relationship between turnover rate, digestibility, and nutritive value to the animal is considered in the calculations of carrying capacity described in Chapters 16 and 17.

8-10 DIGESTION AND ABSORPTION IN THE GASTROINTESTINAL TRACT

Most of the research on nutrition in ruminants has been directed toward the four-part stomach. This can be attributed to two things: (1) it is the unique characteristic of ruminants, and (2) it is considerably easier to study than are the remaining parts of the gastrointestinal tract.

There are no data available on the digestion and absorption characteristics of the entire gastrointestinal tract of wild ruminants. The pattern is probably similar to that of domestic ruminants in which most digestion takes place in the rumen, but some active digestion also takes place in the small and large intestines. Nutrients are absorbed all along the gastrointestinal tract. Research on lambs by Vidal et al. (1969) illustrates the importance of the lower gut in the ruminant, not only in the absorption of nutrients of dietary origin but also in both the production and reabsorption of endogenous material.

8-11 SUMMARY

The physiology of ruminant nutrition has been given considerable attention by researchers in the past 100 years, and the basic processes are generally understood. These have been described briefly in this chapter. Comparative work on the nutrition of wild ruminants indicates that the basic patterns are similar to those of domestic ruminants.

The relationships between the nutritive processes within the animal and between the animal and its range have not been studied as a complete system. The analysis of the relationships between nutrient use, animal requirements, and the range supply follows in the next chapter, and again in Chapters 16 and 17.

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