

INGESTION AND NUTRIENT UTILIZATION

9-1 VARIATIONS IN NUTRIENT INTAKE

There is a continuous flow of nutrients through the metabolic pathways in an animal-range relationship. There is variation in both the ingestion rate and the turnover rate of different forages as the food is processed by the animal. A time lag also occurs in the conversion of forage to metabolically useful energy for activity and tissue synthesis. An analysis of the characteristics associated with ingestion and the subsequent use of food material provides an understanding of the chemical communication between the animal and its range at a fundamental life-support level.

SEASONAL VARIATIONS. Wild ruminants exhibit seasonal differences in the rate of ingestion of different forages. The general pattern observed by many investigators shows a marked drop in consumption that begins in the fall and continues through the winter, with a reversal in the trend in the spring and summer. Males show a greater reduction than females. Silver (unpublished data) reports a 60% decline in intake from September through March for penned adult white-tailed deer on a pelleted diet of grains and alfalfa. Fowler, Newsom, and Short (1967) observed a decline in food consumption of white-tailed deer in Louisiana during the winter, accompanied by a 10% weight loss in bucks and a 3% weight loss in does. A decline in both feeding activity and cedar consumption was recorded for penned animals at the Cusino Wildlife Research Station in Upper Michigan during January and February (Ozoga and Verme 1970).

Nordan, Cowan, and Wood (1968) have studied the intake of black-tailed deer through several annual cycles, and they observed a very obvious decline in feed intake that begins when male deer exhibit rutting behavior. Males on a high plane of nutrition have lost up to 35% of their body weight during the rutting season, refusing food completely for nearly sixty days. Female deer showed a similar pattern of feed intake and weight loss during the breeding season, but not to the extent exhibited by the males.

One interesting and significant observation reported by Nordan, Cowan, and Wood is that a male deer on a low plane of nutrition did not increase his intake when put on *ad libitum* feeding during the rutting season, but exhibited a feed intake that was characteristic of the rut. This indicates that the physiological circumstances of the rut prevailed rather than the available food conditions.

Sexually immature animals do not always show a marked decrease in either food consumption or weight during the breeding season. Two white-tailed deer fawns used for experimental purposes at the University of Minnesota maintained their consumption of a pelleted horse ration, gaining 15 pounds, which was equal to about 30% of their weight in December. The small size of the two fawns when acquired in December (42 and 44 lb) was an indication of malnutrition, but compensatory growth occurred even though they were penned outside during a cold Minnesota winter (Moen unpublished data).

Fawns killed in New Hampshire during the eight-week hunting season in November and December showed a dressed weight loss of 0.6 lb week⁻¹ for males and 0.25 lb week⁻¹ for females. Yearlings of both sexes showed a weight loss of over 2 lb week⁻¹, and adult males lost as much as 5.75 lb week⁻¹ (White 1968). These differences in weight indicate that physical and sexual maturity may be important; Fowler, Newsom, and Short (1967) concluded that weight loss of white-tailed deer is related to the sexual cycle.

The indications that food intake and weight loss vary seasonally and with the age and sexual maturity of an animal suggest that they are subject to some physiological controls that almost certainly involve the endocrine system. The relationship between food intake and weight loss is more than a correlation of intake or weight with "winter stress." There is a real need for experimental work in order to understand the physiological mechanisms employed in the regulation of intake and weight loss in wild ruminants.

INDIVIDUAL VARIATIONS. The selection of particular forage species and even individual plants within a species has been observed by many investigators. Shade-grown sprouts were much preferred to the coarse sprouts produced after clear-cutting procedures (Cook 1939), and marked selectivity in summer feeding was also observed, with the new hardwood sprouts being much preferred to small seedling trees (Cook 1946).

Marked differences in selectivity of forage species has been observed between different geographical areas. Red pine (*Pinus resinosa*) in northern Minnesota was scarcely touched (Burcalow and Marshall 1958), but small red pines planted in western Minnesota were browsed heavily although other food was abundant in

the surrounding fields and woodlots (Moen 1966). Soil fertility appears to be an important factor; Swift (1948) presents data showing that deer grazed preferentially in wheat and clover fields that had been fertilized, often traveling through an unfertilized field to get the preferred plants.

Deer seem to make their initial selection of forage through olfaction. Observations of deer in the field and in pens at the Hopland Field Station, University of California, indicate that they smell the plant first, then if they like the smell they will taste it, and if they like the taste they will continue feeding on it (Longhurst et al. 1968). Healy (1967), using a deer trained to a lead rope, also noted the importance of smell while the deer was browsing in a hardwood forest; it frequently located food items that were hidden from view. He also observed a preference not only for particular forage species, but for individual plants within a species. Individual leaves and twigs on a single plant seemed to be selected rather than chosen at random. The deer also exhibited a greater selectivity in areas where food was more abundant.

It has often been assumed that deer exhibit some kind of beneficial selection when feeding. Some plants produce aromatic and volatile compounds that have an inhibitory effect on rumen function. Longhurst et al. (1968) question whether deer can detect the presence of either nutrients or odors; the relationship between the nutrient content of plants and their palatability was not always a positive one.

The amount of inhibitory activity of plant chemicals on rumen digestion is dependent in part on the concentration of the inhibitory substance. A mixed diet that includes forages that vary from one extreme to the other in nutritive value can be tolerated, but a diet of forages with low nutritive value or with a high percentage of plants inhibitory to rumen function may result in weight loss or mortality. This is another example of a dynamic animal-range relationship that is dependent on the characteristics of both the animal and the range.

9-2 REGULATION OF NUTRIENT INTAKE

RELATIONSHIP TO WEIGHT. The nutritive requirements of an animal are related to weight in a nonlinear fashion that is expressed for energy in the "mouse-to-elephant" curve (see Figure 7-3), or by the mathematical expression $(c)W_{\text{kg}}^{0.75}$. An approximation for basal metabolism can be expressed for mammals using $c = 70$, and a gross approximation of the energy requirement for normal activity can be made with an activity increment (I_{ma}) = 1.33. Thus an active animal may have an energy expenditure equal to $1.33 \times 70 \times W_{\text{kg}}^{0.75}$. Further analyses of this approximation are made in Chapter 16.

A large animal is relatively more efficient at using energy than a small one, requiring less energy for basal metabolism per unit weight. The absolute energy requirement of a large animal is greater, however, so fewer large animals can be supported on any given range. The relationship between animal size and energy

use is important to the range manager who is responsible for managing a finite quantity of resources to support an animal population.

RELATIONSHIP TO ENERGY EXPENDITURE. The energy and protein requirements of an animal are related to both its behavioral and its physiological characteristics since everything an animal does "costs" something in terms of energy and protein. Life itself costs something—expressed as a basal metabolic rate—and activity beyond that which is stipulated as standard conditions in a BMR test results in an additional energy and protein requirement. Walking costs more than lying down, walking uphill costs more than walking on the level, and running costs more than walking. Crampton [Crampton and Harris (1969) and personal communication] believes that the several nutrients required by animals are related to the energy expenditure of the animal, so energy metabolism is the base for determining the nutrient requirements.

Some biological functions require more energy than others. Breeding activity appears to be quite costly for male white-tailed deer inasmuch as they lose 5–6 pounds of body weight per week during the breeding season (White 1968). The reduced food intake that accompanies sexual activity is not sufficient to sustain the activity level of the animal, especially in males.

Pregnancy demands additional energy and protein, especially during the last third of the gestation period. Two living units—the mother and the fetus or feti—are supported by the food ingested by the mother alone. As rapid growth of the fetus occurs in the late stages of pregnancy, the nutrients required are supplied by increased ingestion and by mobilization of body reserves in the female.

Lactation is a costly process. Dairymen know that high feeding levels of concentrated nutrients are necessary to sustain high milk production in the dairy cow, and it is no doubt a costly process for the wild ruminant as well. There are, however, many natural controls operating in a free-ranging population, so lactation is very likely a more efficient process for wild ruminants who are regulated by natural biological constraints rather than economics. Lactation ceases, for example, when the young are weaned naturally. On the other hand, dairy farmers try to sustain a high milk production for as long as possible, and this requires a high feeding level.

CONTROL OF INTAKE. The availability of nutrients in any forage is a function of the quantity of the forage eaten and the efficiency with which the forage is digested and used metabolically. Extensive work has been done on the digestibility of forages, particularly for domestic animals, but little has been done on the factors affecting intake and the turnover rate in the gastrointestinal tract.

Three classes of effects of forage composition upon nutritive value may be distinguished according to how chemical constitution affects intake, digestibility, and the relationship between them (Van Soest 1965): (1) chemical constitution affects intake but has no direct or reliable effect on digestibility; (2) a positive

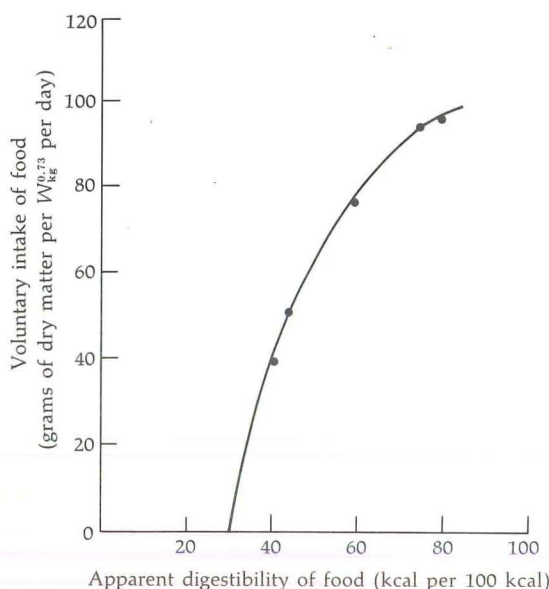


FIGURE 9-1. The relationship between voluntary intake and apparent digestibility by sheep. (Data from Blaxter 1967.)

relationship between intake and digestibility is promoted; and (3) a negative relationship between intake and digestibility is promoted.

The first class includes forages that give off aromatic compounds that may or may not relate to the nutritive value of the forage, such as those reported by Longhurst et al. (1968). The second class includes forage species that can be shown to have a high digestibility and are preferred by the animal. This relationship is illustrated in Figure 9-1. The third class is represented by feeds with a small fiber fraction that has little or no effect on intake. Very young, highly digestible herbage is an example of this class (Compling 1964), as are concentrates and grains. When the feed consumed has a high nutritive value, the intake of digestible energy may then be limited by the requirements of the animal (Van Soest 1965) rather than by some characteristic of the feed.

The three classes presented above are real biological relationships that have been shown to exist by researchers in animal science. It is necessary to consider the chemical and physical characteristics of a particular forage and the efficiency with which that forage can be used by an animal before intake can be considered to be characteristic of any one of these three possible relationships.

The first class—including those forages that give off aromatic compounds without a predictable relationship between intake and digestibility—cannot be useful in predicting the nutritive value of the diet because there is no known mathematical relationship between the odor associated with the forage and its nutritive value. The third class—including very young, highly digestible herbage as well as grains and concentrates—is probably quite unimportant for free-ranging animals because their diets contain a natural mixture of forages and seeds.

The positive relationship between intake and digestibility may be the most important one to consider for free-ranging ruminants, especially when they are

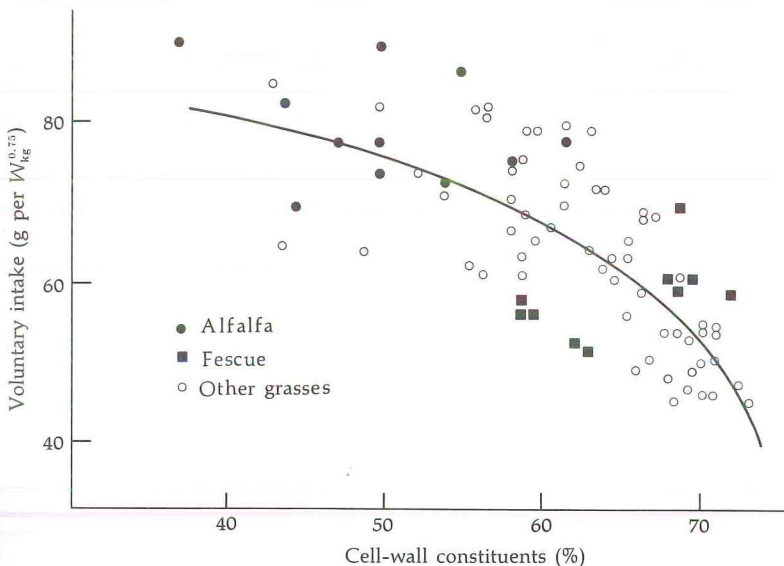
on a browse diet. The basic idea behind this relationship is that the amount of food in the digestive tract limits the amount that can be ingested. It is expressed in the "rumen load" or "fill" theory; the animal does not ingest more food after the rumen is filled to capacity. The more digestible the food mass is, the sooner the rumen will be emptied and the animal will be able to eat again.

What components of the forage material are residual in the rumen for any length of time? The work of Van Soest at Beltsville, Maryland and later at Cornell University indicates that the cell wall is the most indigestible part of the plant cell. The intracellular material, that is, the material inside the cell wall, is highly digestible—on the order of 98% to 100%. The rumen contents include primarily the cell walls of the forage material that is being attacked by the rumen microorganisms. As the volume of cell-wall material increases in comparison with the volume of intracellular material, the voluntary intake declines because the turnover rate of the cell-wall material is slow.

The rumen capacity must be considered together with turnover time. The simple illustration in Table 8-3 of the effect of turnover time on available nutrients is about as much as is known about turnover rates in wild ruminants. The alternative to this lack of knowledge of turnover rates is an analysis of the importance of variation in this parameter.

Voluntary intake by sheep in relation to the cell-wall content and digestible dry matter for 83 forages is shown in Figure 9-2 (Van Soest 1965). The voluntary intake declines rapidly when the percentage of cell-wall constituents is greater than 60. This relationship was observed for the forages from Maryland, Michigan,

FIGURE 9-2. Relationship between voluntary intake by sheep and cell-wall constituents of 83 forages from West Virginia. Reression equation: $Y = 110.4 - 1716/(100 - X)$. (Data from Van Soest 1965, p. 837.)



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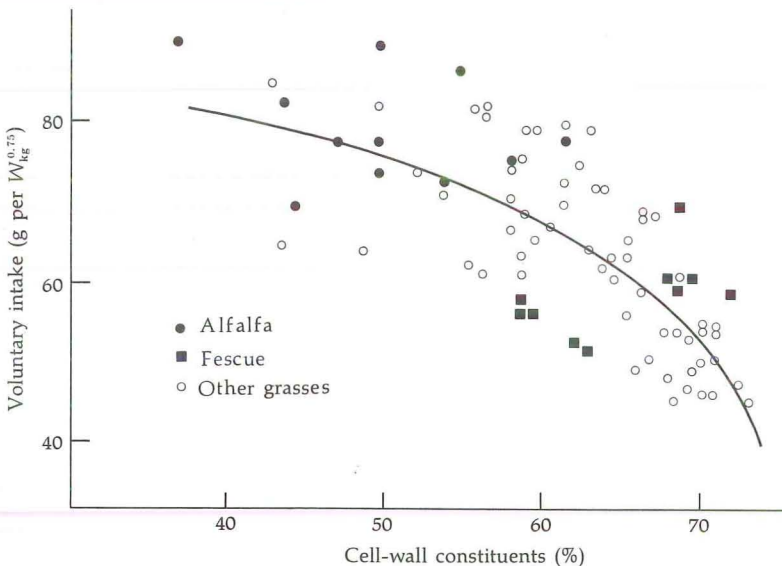


TABLE 9-1 VOLUNTARY INTAKE BY SHEEP OF SOME FORAGES IN RELATION TO THEIR CELL-WALL CONTENT AND THEIR DIGESTIBLE DRY MATTER

Forage	Voluntary Intake		Cell Wall		Digestible Dry Matter	
	(g per W ^{0.75} _{kg})	Rank*	(% of forage DM)	Rank*	(%)	Rank*
Trefoil	89	1	44	1	60	4.5
Good alfalfa	79	2	47	2	60	4.5
Mature alfalfa	67	4	59	3.5	56	6
Early orchard grass	78	3	59	3.5	72	1
Mature orchard grass	29	7	77	7	50	7
Good brome grass	63	5	60	5	65	2
Mature brome grass	51	6	70	6	64	3

SOURCE: Data from Van Soest 1968a.

*Rank added by author.

and Utah; it was the only consistent relationship among many chemical factors that were studied in these forage experiments.

There is a nearly perfect inverse relationship between the rankings of voluntary intake with the percentage of cell wall (Table 9-1). This is biologically reasonable since the cell-wall fraction of the forage, including hemicellulose, cellulose, and lignin, is the fraction that ferments slowly, accumulates in the digestive tract, and limits further feed consumption.

Grinding of domestic animal feeds has been shown to increase intake. This supports the hypothesized relationship between cell-wall constituents and the intracellular components since the mechanical grinding of feed exposes more cell-wall surfaces to be attacked by the microorganisms in the rumen. As might be expected, the grinding effect on plants with a low percentage of cell-wall composition, like alfalfa, is small (Van Soest 1968b).

A considerable amount of time and effort has been spent on the study of browse plants and their relationship to population levels of deer and other wild ruminants. The research has often been started with a vague hope that a correlation may be found between an easily observed parameter, such as plant abundance, and the density of the animal population. It is more useful to consider the basic, biological relationships that exist, however, and the application of basic information is often very straightforward. As Van Soest points out (1968b) "the problem [nutrition] will not be solved by superficial regressions that fail to disclose causative relationships between nutritive value and composition. It is the disclosure and understanding that is required."

Several other theories on the regulatory factors affecting intake have been proposed. These are mentioned here because some of them may have an effect that is superimposed on the basic relationship between the chemical and structural characteristics of the food and intake.

A thermostatic theory [Blaxter (1967) citing Brobeck] states that eating is a response to a drop in heat production. This may be generally true when applied to gross changes in the thermal regime. In a hot environment, in which the relationship between heat production and heat loss may result in an increase in the body temperature, an animal will reduce the food intake and, subsequently, its heat production. In a cold environment, in which heat loss may exceed heat production, an increase in the amount of food consumed and fermented will help maintain or restore the thermal balance.

A theory suggesting that the differences in glucose concentration between arterial and venous blood has been advanced by Mayer [cited by Blaxter (1967)] for man and simple-stomached animals, but this has been shown to be untenable for adult ruminants. Ruminants normally have a low blood-sugar concentration because of the direct absorption of glucose by rumen microorganisms; experimental infusion of glucose does not change the daily intake of food (Blaxter 1967). Glucose concentration may be a factor in the feeding schedule and milk intake of suckling ruminants since they are essentially simple-stomached animals for the first few days after birth.

A lipostatic or fat-balance theory has been advanced by Kennedy [cited by Blaxter (1967)], suggesting that, in the long run, the amount of body fat present regulates the intake of food. This cannot apply to male deer during the breeding season, however, since breeding bucks lose body fat but do not eat an amount of food sufficient to replace it until the following summer. Weight losses are common in adult deer of both sexes during the winter even if sufficient food is available.

In summary, the effect of aromatic compounds in the forage on the olfactory responses of deer and the effect of food quality—in terms of the cell-wall constituency of the forage—seem to be the two most important factors regulating the food intake at the moment at which the animal is ready to eat. There are seasonal changes in the animal's willingness to eat that are related to the maturity of the animal and the hormone balance at the time, especially in relation to sexual characteristics such as breeding, gestation, and lactation. The hormone balance of wild ruminants has received little attention, although it is apparent from the behavior of the animals that it is extremely important as a physiological base for overt behavior.

9-3 ENERGY UTILIZATION

The flow of energy through any living organism follows the Law of Conservation of Energy, which is that "energy can neither be created nor destroyed, but only changed in form." There is a time lag between ingestion and the subsequent

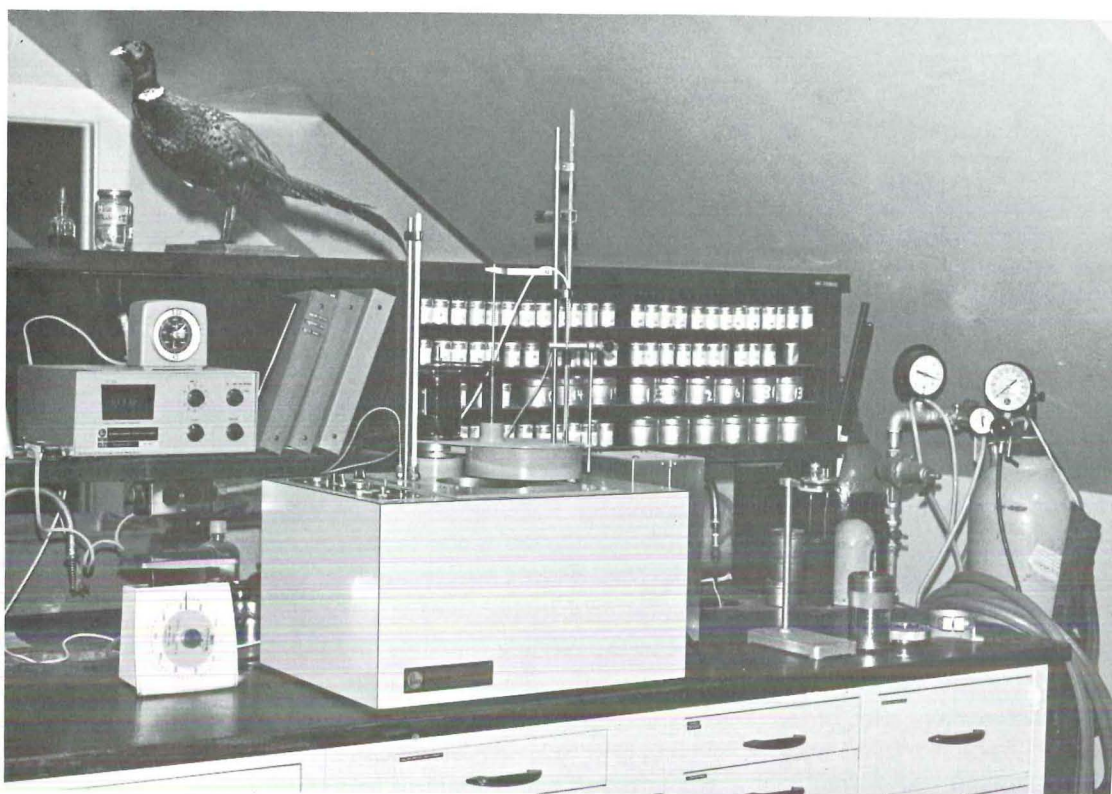


FIGURE 9-3. The bomb calorimeter at the BioThermal Laboratory, Cornell University.

release of energy. This time lag is a necessary characteristic of life for it permits an animal to ingest food whose usefulness will persist for a few hours after eating. Further, those nutrients stored as body tissue will be useful for days or weeks afterwards, increasing the animal's ability to survive periods of food shortages.

PATHWAYS OF ENERGY UTILIZATION. The flow of energy through an animal follows some very logical steps proceeding from gross energy within the food to net energy that is useful to the animal for maintenance and production. The gross energy per unit weight of food is measured in a bomb calorimeter (Figure 9-3) and is usually expressed in kilocalories per gram. Not all of this gross energy is available to the animal because the efficiency of an animal is less than 100%.

Elimination of undigested residue from the gastrointestinal tract is one indication of waste due to a biological efficiency of less than 100%. The gross energy in the food less the heat of combustion of the feces is called the *apparently digestible energy*, expressed as:

$$\left\{ \begin{array}{c} \text{Apparently} \\ \text{digestible energy} \end{array} \right\} = \left\{ \begin{array}{c} \text{Gross energy} \\ \text{in food} \end{array} \right\} - \left\{ \begin{array}{c} \text{Fecal} \\ \text{energy} \end{array} \right\}$$

Two other significant ways in which energy is lost in ruminants are in the gaseous products of digestion and in the heat of fermentation. Methane (CH_4) is the principal gaseous product of digestion and represents a loss of approximately 8% of the gross energy of the food. The amount of energy lost to the animal in methane can be estimated for roughage by the regression equation (9-1) from Blaxter (1967):

$$\text{CH}_4 = 4.28 + 0.059 \text{ DE} \quad (9-1)$$

where

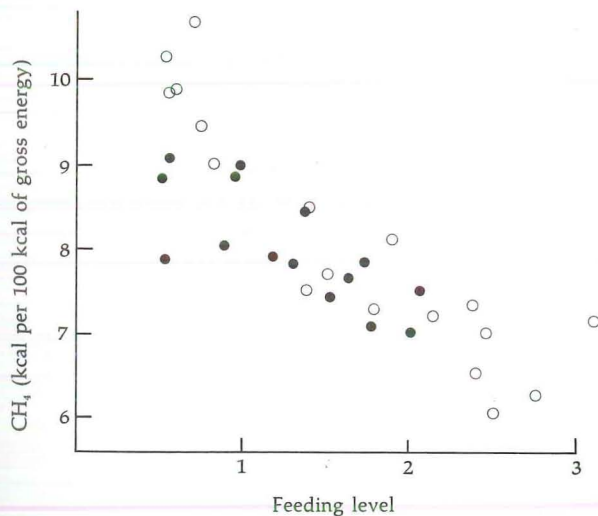
CH_4 = energy lost in methane, expressed in kcal per 100 kcal gross energy
 DE = apparent digestible energy of the food expressed as a whole number
 (50% = 50)

Thus if $\text{DE} = 50\%$, the CH_4 produced is $4.28 + (0.059)(50) = 7.23$ kcal. At 80% apparent digestibility, $4.28 + (0.059)(80) = 9.0$ kcal. Note that these bracket the mean of 8% given above.

The methane produced by the wildebeest (*Connochaetes taurinus*) is 7.0% to 7.6% of the gross energy in the feed, and for the eland (*Taurotragus oryx*), 6.8% to 7.4% (Rogerson 1968). The averages of 7.3 kcal/100 kcal for eland are similar to the amount produced by domestic ruminants.

The level of feeding influences the methane production, ranging from more than 10% on feeding levels lower than maintenance to 6% at three times the maintenance level. These extremes bracket the average of 8%, and the mean value falls between feeding levels of 1 to 2 times maintenance (Figure 9-4).

FIGURE 9-4. Methane production in relation to level of feeding. (From "The Utilization of Foods by Sheep and Cattle" by K. L. Blaxter and F. W. Wainman. *J. Agr. Sci.* 57:419-425, 1961. Cambridge University Press.)



Heat is liberated during digestion owing to the exothermic nature of the chemical reactions in the rumen. It is sometimes called a waste product, but this is not accurate inasmuch as this heat helps the animal to maintain homeothermy when thermal conditions in the environment could cause a decline in body temperature. The energy pathways considered thus far can be expressed as:

$$\left\{ \begin{array}{c} \text{True} \\ \text{digestible} \\ \text{energy} \end{array} \right\} = \left\{ \begin{array}{c} \text{Gross} \\ \text{energy} \\ \text{of food} \end{array} \right\} - \left\{ \begin{array}{c} \text{Heat of combustion} \\ \text{of food residues} \\ \text{in feces} \end{array} \right\} \\ - \left\{ \begin{array}{c} \text{Heat of combustion} \\ \text{of fermentation} \\ \text{gases (methane)} \end{array} \right\} - \left\{ \begin{array}{c} \text{Heat of} \\ \text{fermentation} \\ \text{of feed} \end{array} \right\}$$

An additional way in which energy is lost that has not been measured is the heat of combustion of metabolic products secreted into the intestine. The true digestible energy heretofore illustrated can be called "absorbed energy" since it is the energy that passes through the wall of the intestine and is absorbed by the blood for distribution throughout the body.

Digestible energy that is absorbed by the blood is not completely useful. Some portions of the absorbed nutrients are diverted to urine, and the energy in the remaining food materials available for assimilation is called the *true metabolizable energy*. It can be expressed as follows:

$$\left\{ \begin{array}{c} \text{True} \\ \text{metabolizable} \\ \text{energy} \end{array} \right\} = \left\{ \begin{array}{c} \text{Gross} \\ \text{energy} \\ \text{of food} \end{array} \right\} - \left\{ \begin{array}{c} \text{Heat of combustion} \\ \text{of food residues} \\ \text{in feces} \end{array} \right\} \\ - \left\{ \begin{array}{c} \text{Heat of combustion} \\ \text{of fermentation} \\ \text{gases (methane)} \end{array} \right\} - \left\{ \begin{array}{c} \text{Heat of} \\ \text{fermentation} \\ \text{of feed} \end{array} \right\} - \left\{ \begin{array}{c} \text{Heat of} \\ \text{combustion} \\ \text{of urine} \end{array} \right\}$$

Metabolizable energy is converted to body tissue and is used for basal metabolic processes, activity, production, and other processes basic to life. These conversions require an expenditure of energy, called the heat of nutrient metabolism. Metabolizable energy less the heat of nutrient metabolism is called the *true net energy*, and it is used for the maintenance and productive purposes listed above.

The true net energy available to the animal contributes to two separate energy requirements—maintenance energy and production energy. The entire energy pathway can be expressed as:

$$\left\{ \begin{array}{c} \text{Gross} \\ \text{energy} \end{array} \right\} - \left\{ \begin{array}{c} \text{Fecal} \\ \text{energy} \end{array} \right\} - \left\{ \begin{array}{c} \text{Methane} \\ \text{losses} \end{array} \right\} - \left\{ \begin{array}{c} \text{Heat of} \\ \text{fermentation} \end{array} \right\} - \left\{ \begin{array}{c} \text{Urinary} \\ \text{energy losses} \end{array} \right\} \\ - \left\{ \begin{array}{c} \text{Heat of} \\ \text{nutrient metabolism} \end{array} \right\} = \left\{ \begin{array}{c} \text{Net energy available for} \\ \text{maintenance and production} \end{array} \right\}$$

These diversions are illustrated in Figure 9-5.

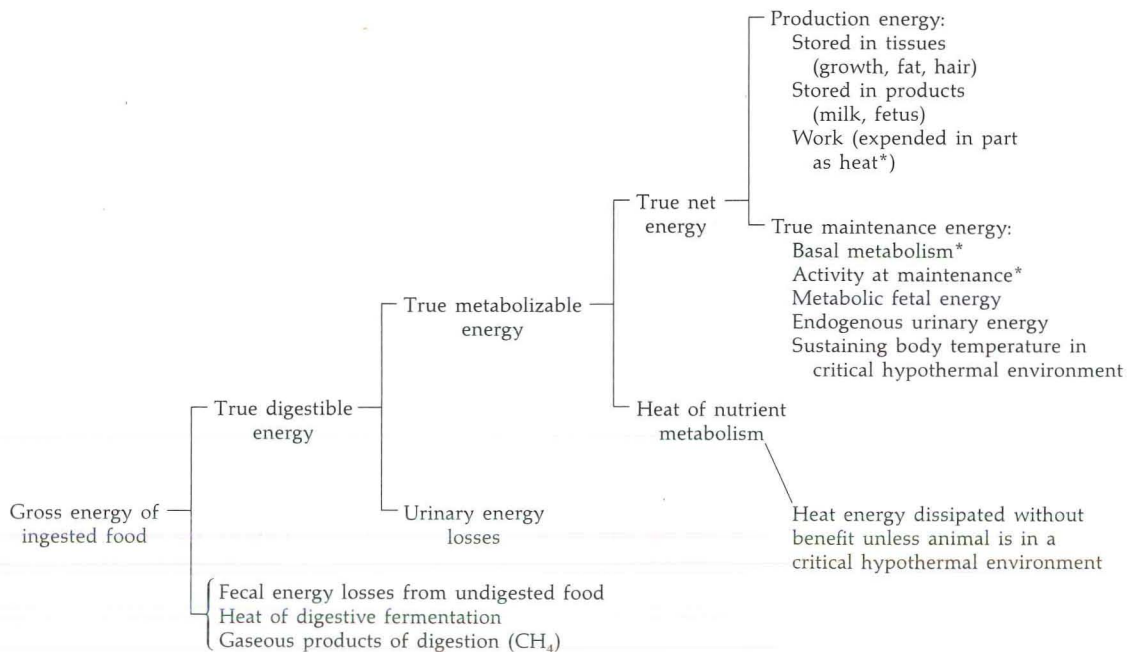


FIGURE 9-5. True biological partitioning of food energy. Asterisk indicates processes that produce heat. (Modified from Crampton and Harris 1969.)

NET ENERGY FOR MAINTENANCE. Maintenance energy includes the basal requirements for cellular metabolism without an increase in body weight and for voluntary activity and other life-support processes in which an animal participates as a part of daily life. This includes feeding behavior, reproductive behavior, flight behavior to escape predators, the maintenance of homeothermy when in a critical thermal environment, the support of a "normal" parasite and pathogen load, and any other requirement that is a part of the animal's life.

Some of the energy in the feces and urine comes from tissue that was produced earlier. Metabolic fecal energy and metabolic urinary energy is of body origin and is derived from the breakdown or catabolism of living tissue. The energy in the cell residues in the feces and urine must be separated from the indigestible food residues that are a major part of the feces and from the excretory products in the urine to allow computation of the net energy derived from the feed. To illustrate, some of the energy in the feces is due to the presence of epithelial cells that have been removed from the lining of the intestinal tract. The energy contained in these cells cannot be attributed to indigestible food material since these cells are the product of metabolic processes, and their loss will be replaced by new cells that are formed at a metabolic cost to the animal. If metabolic fecal and urinary energy is not subtracted from the total fecal and urinary energy, the efficiency of an animal in converting food to metabolic products would be underestimated.

If the thermal conditions in the environment result in a heat loss greater than the heat production by the animal from the heat of fermentation of foods and nutrient metabolism in the cells, the animal is in a critical hypothermal environment (Moen 1968). The animal may increase its heat production in order to maintain body temperature, and this energy demand must be considered a part of the maintenance requirements of the animal under these conditions. When the heat production due to basal metabolism and voluntary activity rises above heat loss, the excess heat energy must be dissipated to prevent a rise in body temperature.

NET ENERGY FOR PRODUCTION. The energy required for production is used for tissue synthesis and storage. The growth of all body tissue, including not only the internal tissue but also the external covering of hair, requires energy, as does the production of ova and growth of the fetus in the pregnant female and the production of semen by the male. Further, lactation requires the production of milk that is ingested by the suckling animal with an energy cycle of its own. Fat is a readily available energy reserve. These production processes are programmed into the computations of the total energy requirement of free-ranging animals in Chapters 16 and 17.

SUMMARY OF ENERGY UTILIZATION. As an animal completes the cycle of conception, birth, growth, and death, all of the energy that went into the animal can be accounted for, with a certain portion of it held in reserve by the body at death, to be dissipated as decomposers use it as a substrate for meeting their own energy requirements. The events that go into the transformation of energy form a very basic foundation on which the survival of an individual and a population, as well as the carrying capacity of the range, can be based. The energy pathways described in this chapter are expressed quantitatively in Chapter 16, which deals with animal requirements, and these equations are used in the calculation of carrying capacity in Chapter 17.

9-4 PROTEIN UTILIZATION

Proteins are complex chemical substances composed mostly of carbon, hydrogen, oxygen, and nitrogen. These elements are arranged into large units called amino acids, which are synthesized by rumen microorganisms from simpler nitrogenous compounds.

Not all of the protein ingested is available to the animal because the efficiency of an animal is less than 100%. Thus there is a difference between the total protein content of the food and the amount of protein actually available to the animal for tissue production. The pathways for nitrogen diversion and use are shown in Figure 9-6. The synthesis of body tissue is a part of the growth process of young animals. Even in adults tissue replacement is necessary because of catabolic processes that result from the maintenance of normal activity and life processes from day to day. Some tissue deposition, such as the production of hair, fetal

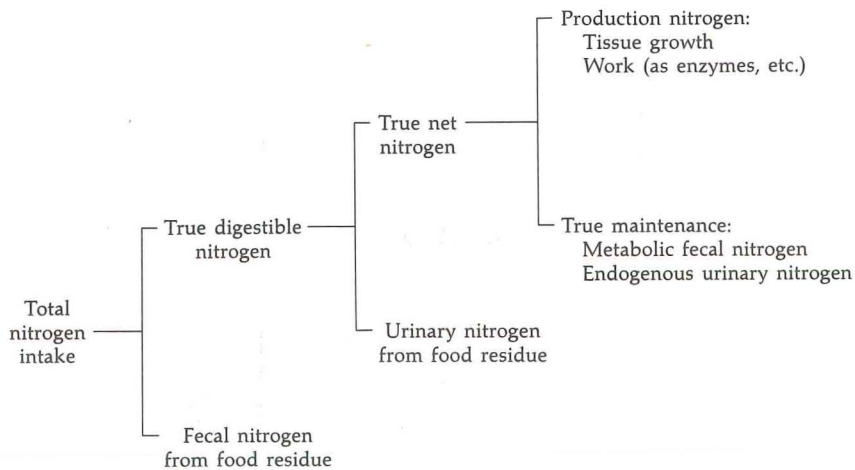


FIGURE 9-6. Biological partitioning of dietary nitrogen (protein/6.25).

tissue, and milk, varies seasonally. Protein requirements for maintenance of body tissue vary much less over time. The protein costs for maintenance and production throughout the annual cycle are expressed quantitatively in Chapter 16.

9-5 EFFICIENCY OF NUTRIENT UTILIZATION

DIGESTION COEFFICIENTS. Food ingested by a ruminant is attacked by microorganisms in the rumen. These microorganisms are engaged in their own struggle for survival, and the end products of their metabolism are of direct value to the ruminant host in this symbiotic relationship. Because of a lack of information on digestibility coefficients for different forages consumed by wild ruminants, it is logical to use instead digestibility coefficients for forage eaten by domestic ruminants. This raises a question about the similarity of different species of ruminants and the validity of comparisons between species.

A review of the literature on both domestic and wild ruminants suggests that any differences observed between different species is not so much due to differences between species per se but is due to the specific history of the different individuals. If two deer were on entirely different diets and rumen fluids from each were used to inoculate *in vitro* fermentation vials containing equivalent forage samples, the results would probably be quite different. If a deer and a sheep were on the same diet and their rumen fluids were used for inoculation, the results would probably be quite similar.

Three mule deer showed differences in cellulose digestion between the animals themselves and between feeding-trial periods (Short 1966). Protein digestion was similar in all feeding trials. It is clear that there is no single value or mathematical relationship available at the present time with which to express these relationships.

NET ENERGY AND PROTEIN COEFFICIENTS. The expression of net energy and net protein in forage is the best way to describe its nutritive value. This is so because

the net values represent the value of the forage actually available to the animal for maintenance and production. Although the expression of net protein and net energy is easy to accept conceptually, there is a loss of accuracy in the predictions because of the number of biological variables and the chance for error in measurement associated with each variable. The calculation of apparently digestible energy by subtracting fecal energy from the gross energy in the food is fairly simple, with a possibility of error only in the measurement of the quantity of food ingested, the caloric value of the ingested food, the quantity defecated, and the caloric value of the feces. If the true digestible energy is to be determined, the caloric energy of the metabolic residues in the feces (separate from the indigestible residues) must be determined, and the measurement of both the quantity and the caloric value of these metabolic products introduces additional errors. Thus it is obvious that as greater detail is sought there will be less precision.

An analysis of basic relationships within any system will ultimately produce more progress in the management of the system than will the continued use of simplified approaches with hoped-for useful results. The use of net energy and net protein coefficients is conceptually sound and is evaluated further within an ecological framework in Chapter 17.

METABOLIC EFFICIENCY. The net energy and net protein coefficients discussed above express the potential value of the forage when it is absorbed and utilized at the cellular level. The efficiency of cellular metabolism is dependent on the presence of cellular enzymes and a cellular environment favorable for particular biochemical reactions.

Vitamins are important constituents of the cellular enzymes. They are small but often essential parts of complex protein molecules and are usually needed in very small amounts. The water-soluble vitamins of the B group are synthesized by the microorganisms in the rumen, and the adult ruminant needs only Vitamins A, D, and E in its diet (Annison and Lewis 1959). The synthesis of some of these vitamins depends on the presence of certain trace elements. Cobalt, for example, is necessary for the synthesis of B₁₂. The young ruminant relies on the ingestion of the full complement of vitamins during the period before the rumen is functional.

Some minerals, such as phosphorus and calcium, are required in larger amounts because they are important components of bone tissue. The young, growing animal has a relatively higher requirement than the mature animal, and this requirement must be met by the diet. Some minerals, such as selenium, are necessary in trace amounts but are detrimental to normal biological processes if present in larger amounts. The mechanism of selenium toxicity is not understood (Crampton and Harris 1969), but symptoms indicate that the nervous system is impaired and normal growth is interrupted.

The requirements and tolerances of wild ruminants for vitamins and minerals are probably quite similar to those of domestic animals. After the computations of carrying capacity described in Chapter 17 are completed on an energy and protein base, the vitamin and mineral requirements can be added as further considerations if the vitamin and mineral composition of the diet is known.

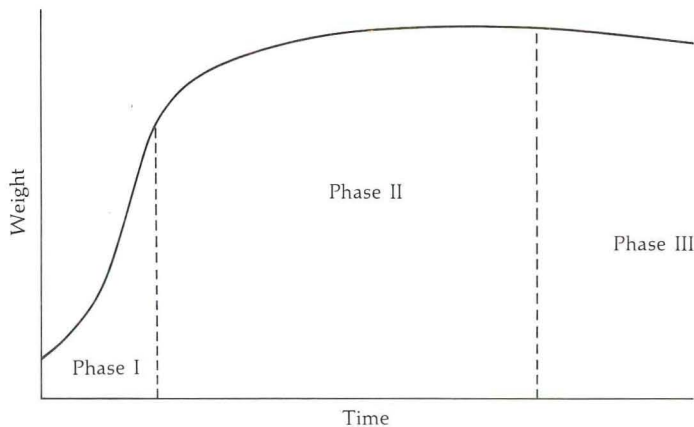


FIGURE 9-7. A theoretical weight change curve showing the three phases of growth during the life span of an individual.

9-6 BODY GROWTH

The growth of animals is a continuous process from conception to the time of death. The rate at which an animal grows is not constant, however. A theoretical weight-change curve (Figure 9-7) can be divided into three phases: (1) an initial phase during which there is accelerating growth; (2) a phase during which the rate of weight change slows considerably; and (3) a phase during which the weight change may be slightly negative. The weight fluctuates within each phase, of course, including rather marked reductions in the weight of many adult wild ruminants during the winter.

At the beginning of Phase I there is a period of adjustment to a vastly different environment immediately after birth. The infant animal goes from a warm constant-temperature uterine environment with an arterial nutrient supply and the mother's excretory system for removal of metabolic waste to an independent life with its own nutrient ingestion. The young animal must metabolize at a rate compatible with its needs as a homeotherm, and this requires energy.

The mother and the young animal begin Phase I as a single nutritional unit, gradually becoming separate units. The young animal grows rapidly on a milk and forage diet, with an increasing dependence on forage. At weaning, the separation is complete nutritionally, but doe and fawn are still united socially to a certain extent.

The transition from Phase I to Phase II of the weight curve is accompanied by the weaning process and, in some of the ruminants, by sexual maturity. Female white-tailed deer, for example, frequently breed as fawns, and male fawns have been reported fertile (Silver 1965). Cowan and Wood (1955) reported the fertile mating of black-tailed deer fawns (*Odocoileus hemionus columbianus*) during their first winter.

The Phase II growth period may continue for several years. The weight of the animal increases, but the rate of increase is slow. There are seasonal increases and decreases that seem to be associated primarily with the breeding cycle and

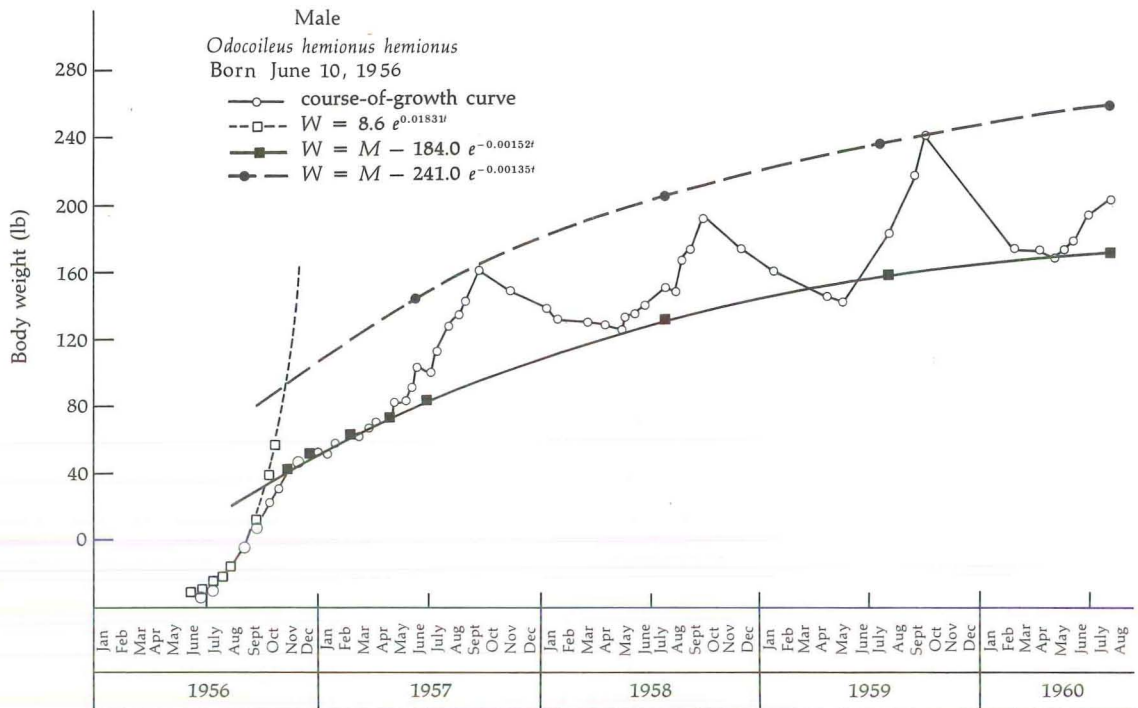


FIGURE 9-8. Growth curves for a representative male of *Odocoileus hemionus hemionus*: W = weight in pounds; t = age in days. [Data from Wood, Cowan, and Nordan. Reproduced by permission of the National Research Council of Canada from the Canadian Journal of Zoology, 40, pp. 593-603 (1962).]

secondarily with the winter range conditions. The reproductive condition of the animal is at its peak during this phase; the animal is in its prime.

The termination of Phase II and the beginning of Phase III, or old age, is a gradual process. Animals lose their biological efficiency owing to a gradual loss of elasticity of body tissue. Further, teeth are becoming worn and the animal is apparently not quite as efficient at utilizing forage as it once was. Concomitant with a loss in weight is a loss in productivity; old white-tailed does produce fewer young than do young does (Cheatum and Severinghaus 1950).

Weight changes of a male mule deer are reported by Wood, Cowan, and Nordan (1962) and are shown in Figure 9-8. Weight during the first summer shows an increasing rate of gain until October when it begins to slow down. If the animal has been on an adequate diet, reproductive behavior appears. The weight increase is greater during the following summer when the animal is a yearling, but a decline follows during the animal's second winter. Note that the weight each winter is higher than the previous winter, and summer weights are progressively higher too. These increases from year to year are a part of the second growth phase, which continues until the maximum weight at maturity is reached. Similar growth equations for other black-tailed deer are reported by Wood, Cowen, and Nordan

TABLE 9-2 AGE-WEIGHT RELATIONSHIPS FOR DIFFERENT SUBSPECIES OF *Odocoileus hemionus*

Species	Sex	Growth Phase I	Growth Phase II
<i>O. h. sitkensis</i>	M	$W_{lb} = 7.8 e^{0.01324t*}$	a† $W_{lb} = M - 325 e^{-0.00283t}$; $M = 240$ b $W_{lb} = M - 132 e^{-0.00174t}$; $M = 165$
<i>O. h. columbianus</i> (Vancouver Island genotype)	M	$W_{lb} = 9.5 e^{0.00996t}$	a $W_{lb} = M - 131.5 e^{-0.00161t}$; $M = 170$ b $W_{lb} = M - 110.5 e^{-0.00123t}$; $M = 140$
<i>O. h. columbianus</i> (California geno- type)	M	$W_{lb} = 8.6 e^{0.01134t}$	a $W_{lb} = M - 166.9 e^{-0.00145t}$; $M = 210$ b $W_{lb} = M - 136.5 e^{-0.00237t}$; $M = 150$

SOURCE: Data from Wood, Cowan, and Nordan 1962.
 *t is time in days.
 †a = summer weights; b = winter weights.

(1962) and are listed in Table 9-2, and for caribou (*Rangifer tarandus groenlandicus*) by McEwan (1968), in Table 9-3.

The number of points in the graphs shown in Figures 9-7 and 9-8 indicate the amount of effort needed to construct a complete weight profile over a period of years. First approximations have been made for white-tailed deer, elk, and moose (Table 9-4). The equations are based on data reported in the literature and are thought to be realistic for first approximations. The effect of error in the age-weight relationship can be analyzed so that decisions can be made about the level of accuracy required in this parameter.

TABLE 9-3 AGE-WEIGHT RELATIONSHIPS FOR *Rangifer tarandus groenlandicus*

Animal	Sex	Growth Phase I	Growth Phase II
U8	M	$W = 7.2 e^{0.020174t}$	$W = M - 130 e^{-0.001429t}$; $M = 150$
U3	M	$W = 6.2 e^{0.020712t}$	$W = M - 120 e^{-0.001347t}$; $M = 150$
V17	M	$W = 6.0 e^{0.019917t}$	$W = M - 116 e^{-0.001311t}$; $M = 150$
V21	M	$W = 4.1 e^{0.022904t}$	$W = M - 120 e^{-0.001172t}$; $M = 150$
Wild	M		$W = M - 130 e^{-0.001429t}$; $M = 125$
Wild	M		$W = M - 120 e^{-0.0004755t}$; $M = 150$
U4	F	$W = 7.2 e^{0.01983t}$	$W = 110 - 80 e^{-0.001597t}$
U7	F	$W = 6.6 e^{0.020542t}$	$W = 90 - 80 e^{-0.003398t}$
V27	F	$W = 6.9 e^{0.018829t}$	
V28	F	$W = 6.4 e^{0.018819t}$	
Wild	F		$W = 90 - 60 e^{-0.001230t}$
Wild	F		$W = 90 - 55 e^{-0.0005852t}$

SOURCE: Data from McEwan [reproduced by permission of the National Research Council of Canada from the *Canadian Journal of Zoology*, 46, pp. 1023-1029 (1968)].

TABLE 9-4 AGE-WEIGHT RELATIONSHIPS FOR DEER, MOOSE, AND ELK

Species	Sex	Growth Phase I	Ref.*	Growth Phase II	Maximum Weight	Ref.*
White-tailed deer	M & F	$W_{kg} = 3.0 + 0.229 t_d$	1			
	M			$W_{kg} = e^{(1.230 + 0.440 \ln t_d)}$	111 kg	1
	F			$W_{kg} = e^{(1.617 + 0.357 \ln t_d)}$	71 kg	1
Moose	M & F	$W_{kg} = 13 + 1.0 t_d$	2	$W_{kg} = e^{(2.198 + 0.549 \ln t_d)}$		3
Elk	M			$W_{kg} = e^{(2.409 + 0.435 \ln t_d)}$		4
	F			$W_{kg} = e^{(2.529 + 0.385 \ln t_d)}$		4

* References include either the equation or the data from which the above equations were calculated.

1. Moen, unpublished data.

2. Verme 1970.

3. Blood, McGillis, and Lovaas 1967.

4. Murie 1951.

9-7 SUMMARY

The ingestion and utilization of food is a complex biological phenomenon. It is a chemical communication between animal and environment, absolutely essential for survival and growth. Wildlife biologists traditionally list the three requirements of an animal as food, cover, and space, but often too little attention is given to food requirements. Food habits and range conditions are often the only things studied in an analysis of the habitat requirements of a wild species. The complex nature of nutritional relationships and the fundamental importance of nutrition for survival and growth must be recognized if wildlife scientists are to develop more reliable knowledge about the habitat requirements of any species.

Other aspects of the total organism-environment relationship are discussed in Parts 4 and 5, with a return to nutritive considerations in relation to carrying capacity in Part 6.

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IDEAS FOR CONSIDERATION

The nutritive pathways discussed in this part of the book are related more specifically to ruminants than to other mammals and birds. Pathways specific to these other animals should be described by students having different interests, utilizing the gross-to-net concept in identifying the pathways and quantifying the nutritive processes.

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