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REVIEW OF ENERGY REQUIREMENTS AND RUMEN FERMENTATION IN MOOSE AND OTHER RUMINANTS

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Résumé

Les auteurs dressent un bilan saisonnier des besoins énergétiques et de l'utilisation de la nourriture chez l'orignal (*Alces alces*) en le comparant à celui obtenu chez d'autres ruminants sauvages et domestiques. L'absence de mesures précises du métabolisme basal chez l'orignal et la grande variabilité de ce paramètre chez les autres ruminants domestiques et sauvages rendent très difficile l'estimation de leurs besoins énergétiques. Les auteurs posent comme hypothèse de départ que le métabolisme basal (BMR) obéit à la relation suivante:

$$\text{BMR (kcal/jour)} = 70\ W^{.75}$$

où W représente le poids corporel en kg; ils estiment en outre que le régime d'entretien nécessite 1.7 fois la quantité d'énergie requise par le métabolisme basal. Les besoins énergétiques des femelles gestantes s'accroissent soudainement en mars, en raison du développement du foetus et ces besoins vont atteindre un niveau de trois à quatre fois plus élevé que ceux qu'exige le métabolisme basal durant le mois de juin, conséquence de la lactation et de la lipogénèse.

Les auteurs décrivent les principales différences saisonnières dans le contenu du rumen et dans la consommation de nourriture. Le degré de remplissage du rumen chez la femelle atteint un maximum au début de l'hiver, un minimum à la fin du printemps et une valeur intermédiaire l'été. Le pourcentage de matières sèches dans le contenu du rumen passe par un maximum l'hiver et par un minimum l'été. Le filtrat provenant du lavage du contenu du rumen avait une teneur plus élevée en protéines brutes et plus faible en matières cellulosiques et lignine durant l'été que durant l'hiver, ce qui reflète la meilleure qualité de la nourriture consommée durant la saison chaude. Les sources bibliographiques consultées proposent des estimés fort variables de la quantité de nourriture ingérée, mais toutes semblent établir que la consommation de nourriture est plus forte durant l'été que durant l'hiver. Les auteurs considèrent que les femelles adultes consomment jusqu'à trois et même quatre fois plus de matière sèche l'été que l'hiver. Ils estiment également que l'augmentation du degré de remplissage du rumen et la diminution de la consommation de nourriture durant l'hiver sont, d'une part, le résultat d'un ralentissement dans le transit d'une nourriture de qualité inférieure et, d'autre part, d'une réduction volontaire de la consommation par l'animal.

Environ 57 pourcent de toute l'énergie digestible chez les ruminants provient des acides gras volatils (VFA) dérivés de la fermentation microbienne des hydrates de carbone et des protéines de la diète. Les auteurs ont mesuré les changements saisonniers dans la production d'acides gras volatils chez des animaux à l'état sauvage et ont établi que celle-ci est une fonction directe de la qualité de la nourriture. En hiver, la moyenne du taux de production d'acides gras volatils se situait aux environs de 18 μeq VFA/ml de liqueur du rumen par heure tandis que durant l'été, la moyenne était de 60 μeq VFA/ml par heure.

L'orignal subit des changements considérables de poids corporel durant l'année et ces changements correspondent à des changements dans la production d'énergie dérivée des acides gras volatils. L'énergie utilisable pour le métabolisme (ME), calculée d'après l'estimé de production d'acides gras volatils, passe de 7,300 kcal/jour pour une femelle, l'hiver, à 20,900 kcal/jour pour cette même

femelle durant les mois d'été alors qu'elle est en lactation. Les auteurs évaluent à 6,000 kcal par jour la quantité d'énergie utilisable requise pour le métabolisme basal. Or, durant l'hiver, environ 3,900 kcal par jour doivent être obtenus du catabolisme des graisses et des protéines de réserve pour compenser l'insuffisance de l'énergie fournie par le broutement tandis que l'été, environ 7,600 kcal par jour sont mis en réserve sous forme de protéines et de graisses. Les effets de la malnutrition indiquent que toute réduction, soit de la quantité, soit de la qualité de la nourriture réduit la flore bactérienne ainsi que les taux de fermentation.

Les auteurs expriment enfin divers points de vue sur l'à propos d'utiliser l'un ou l'autre des paramètres liés à la fonction du rumen dans le but d'évaluer la condition physiologique de divers ruminants ainsi que la qualité de leur habitat.

Abstract

A review of seasonal energy requirements and utilization of food by moose, (*Alces alces*) with reference to other wild and domestic species, is presented. Energy requirements are difficult to estimate because no metabolic studies have been conducted with moose and comparative data from other wild and domestic species differ widely. It is assumed that basal metabolic rate (BMR) conforms to the empirical relationship of weight to metabolic rate, where

$$\text{BMR (kcal / day)} = 70\ W^{.75}$$

and where W = body weight, in kg and that maintenance demands approximate 1.7 × BMR. Energy requirements of female moose begin to increase significantly in March due to pregnancy and reach a peak of three to four times BMR in June, due to lactation and lipogenesis.

Major seasonal differences in rumen contents and estimates of food consumption by moose are described. Rumen fill in cow moose was greatest during early winter, lowest during late spring, and intermediate during summer. Percent dry matter was lowest during summer and highest during winter. Washed rumen contents were higher in crude protein and lower in acid detergent fiber and lignin during summer than during winter, reflecting the superior quality of summer forage. Estimates of food intake by moose vary greatly in the literature, although there is considerable evidence indicating that a greater quantity of food is consumed during summer than during winter. Dry matter consumed by adult females was estimated to be three to four times greater during summer than during winter. Increased rumen fill and decreased food intake during winter apparently result from slow passage of low quality food which restricts additional food intake, and from voluntary reduction of forage consumption.

Volatile fatty acids (VFA) produced by rumen microbes from the fermentation of dietary carbohydrates and proteins constitute approximately 57 percent of the digestible energy of ruminants. VFA production, which is directly related to food quality, was determined seasonally on free-ranging moose in interior Alaska using the "zero time rate" method. Production rates varied from a mean low of 18 μeq VFA/ml rumen liquor/hr during winter to 60 μeq VFA/ml rumen liquor/hr during summer.

Moose undergo a large seasonal change in body weight which corresponds closely to seasonal rates of VFA energy production. Metabolizable energy (ME), calculated from estimated VFA production, increased from 7,300 kcal/day in females during winter to 20,900 kcal/day in lactating moose during summer. It was estimated that approximately 6,000 kcal/day of ME was required for BMR. During winter an estimated average of 3,900 kcal/day was obtained from catabolism of fat and protein reserves to meet the energy requirements not provided by forage, while during summer 7,600 kcal/day of fat and protein were deposited.

A review of effects of malnutrition on rumen function show that decrease in food quantity or quality depresses microbial populations and rates of fermentation.

The value and practical application of using various parameters of rumen function to evaluate nutritional status of ruminants and quality of the habitat are discussed.

Introduction

As the management of wildlife species becomes more intensified, the study of wildlife nutrition becomes more critical. Food habits data were once the only food resource information considered important. However, certain deficiencies in this approach have promoted studies of greater scope to better understand relationships between wild ruminants and their food resources.

In vitro digestibility studies have been undertaken on foods of wild ruminants to rate the quality or usefulness of various forages to the animal (Short, 1971; Ward, 1971; Oldemeyer, 1974). Clinical blood chemistry techniques have recently provided a new avenue of approach to gain insight into the nutritional status of wild ungulates (LeResche and Davis, 1971; LeResche *et al.* 1974). Digestibility and maintenance requirements have been studied on wild ruminants held in pens and provide information on how the animals may utilize various diets in the wild (Ullrey *et al.* 1967, 1969, and 1971). Field studies of rumen function have enabled investigators to evaluate nutrition status and energy balance by estimating the energy wild ruminants derive from their diet (Coady and Gasaway, 1972). Wildlife nutrition must be concerned not only with availability and utilization of forage species, but also with the nutrient requirements of ruminants and their ability to convert plants to animal tissue.

The following discussion reviews seasonal energy demands for basal, maintenance and production requirements of moose, and the digestive processes which convert food into useful energy.

Energy requirements

In this review, gross energy of food consumed by an animal will be partitioned into apparent digestible and metabolizable energy. Apparent digestible energy (DE) is that portion of gross energy not excreted as feces, and it represents a first approximation of the efficiency of food digestion. Metabolizable energy (ME) is that portion of DE not excreted in urine or lost as gaseous products of rumen fermentation. ME is a measure of the energy available to or needed by an animal at a particular time for all metabolic requirements, and may be used for work, heat, and tissue synthesis.

Metabolic rate of homeotherms varies greatly within and between species, since it must meet all requirements for diverse physical and physiological activities. Basal metabolic rate (BMR) is the measure of a mammal's minimum energy demand and has been widely used for intra- and interspecies comparisons and as a base-line for computing effects of other metabolic functions. Energy requirements for maintenance (thermoregulation, activity, and specific dynamic action) and for production (i.e. body growth, gestation, milk production) are requirements above BMR and, together, these processes constitute the total energy requirements of an animal. By integrating the temporal pattern of metabolic rate, a seasonal energy budget can be calculated and the total impact of both the animal on its food supply and the environment on the animal can be evaluated.

BASAL METABOLIC RATE (BMR)

BMR is a measure of caloric requirements for minimum physiological functions. Ideally, test conditions for measuring BMR include postabsorptive state, complete inactivity, and "comfortable" microclimate (Benedict, 1938). In practice, however, these conditions may be difficult if not impossible to attain, particularly with wild species. The extent to which psychological, physiological and physical stresses on an animal can be reduced vary greatly among individuals and species. Consequently, the circumstances appropriate for measuring BMR will vary with the species, and the accuracy of measurement will largely depend upon the extent to which stresses can be minimized. While strict use of the term BMR may frequently not be applicable, it is a useful comparative concept, providing the technical difficulties of its measurement are realized.

It is well known that BMR of mammals increases as an exponential function of body weight. Brody and Proctor (1932) and Kleiber (1961) concluded from comprehensive studies that average BMR of mammals equals $70W^{.734}$ and $70W^{.75}$, respectively where BMR = kcal/day and W = body weight in kg. Differences between the two equations are strictly pedantic, although Kleiber's relationship, adopted by the Third Symposium on Energy Metabolism for Interspecies Comparisons (Blaxter and Wainman, 1964), has been more widely used in recent years.

Another useful metabolic term is fasting metabolic rate (FMR), which is greater than BMR by the amount of energy expended is standing and small postural movement during measurement (Silver *et al.*, 1969). Kleiber (1961) preferred measurement of FMR over BMR since he felt it better represented minimum energy requirements among animals unable to remain voluntarily inactive. Blaxter (1962) indicated that differences between BMR and FMR are small among domestic ruminants. However, differences may be greater among wild species due to stress imposed by captivity.

FMR of wild ungulates varies widely among species, within species measured during different seasons, and even within species measured during the same season (Table I). FMR's range from 67.8 kcal/kg$^{.75}$/day to 143.6 kcal/kg$^{.75}$/day. Silver *et al.* (1959) working with white-tailed deer (*Odocoileus virginianus*) during winter and summer, and Maloiy *et al.* (1968) working with red deer (*Cervus elaphus*) recorded metabolic rates similar to those predicted for animals of their size (Table I). However, most values for FMR range from 15 percent to 100 percent higher, and average approximately 40 percent greater than the predicted BMR. The origin of these differences is not known, although numerous factors associated with age, reproductive state, nutrition, activity, insulation, and acclimatization must be considered (Whittow, 1971).

Estimation of BMR of moose is difficult, particularly considering that metabolic data have not been reported for the species. Silver *et al.* (1969, 1971) and McEwan and Whitehead (1970) indicate major seasonal differences in BMR of white-tailed deer and resting metabolic rate of reindeer (*Rangifer tarandus*) respectively. Thus, a constant relationship between heat production and a fixed exponent of body weight may not be adequate to cover all species under all situations. For the purpose of this review and pending appropriate metabolic studies, we assume that moose under basal conditions obey Kleiber's (1961) empirical formula relating metabolims to body weight. Therefore, BMR of a 425 kg (937 lb) animal, for example, equals $70 \times 425^{.75}$ or 6,550 kcal/day. The BMR shown in Figure 1 was calcilated from Kleiber's formula and was considered to be constant throughout the year.

MAINTENANCE ENERGY

Maintenance energy is a composite of requirements for basal or fasting metabolism, thermoregulation, activity associated with obtaining food and water, and the heat increment or "specific dynamic action" of digestion and assimilation of food. It is that portion of the metabolizable energy required for existence at a minimum level of activity, where energy retention by the animal is zero. While clearly an underestimate, BMR does represent a significant portion of maintenance energy requirements.

Energy requirements by moose for thermoregulation in the cold have not been studied. Scholander *et al.* (1950) suggest that most large northern mammals do not increase their metabolic rate until temperatures are at least minus 40°C. In agreement with this hypothesis (Hart *et al.*, 1961) found no increase in metabolic rate of a 9-month old caribou (*Rangifer tarandus*) from 25°C to minus 55°C. Moen (1968) calculated that a 70 kg fasting deer standing under clear night skies with a heat production of 75.1 kcal/kg$^{.75}$/day could maintain body temperature at an ambient temperature of -40°C and wind velocity of nearly 2 mph. Fed deer could tolerate a wind velocity of over 8 mph. at -40°C without increasing their metabolic rate (Moen, 1968).

Factors such as relatively large body size, decreasing the surface to weight ratio, heat production associated with rumen fermentation, and behavioral responses assist in conserving heat and enhance cold tolerance of moose. Activity patterns observed for moose agree with this, as they may bed in open areas during very cold Alaska temperatures, rather than seeking heavy cover where a more favorable energy flux usually exists. Also, substantial movements of radio-collared moose during temperatures of -40° to -50°C have recently been recorded (Coady, 1974). Markgren (1966) noted that captive moose calves in Sweden did not appear inconvenienced by temperatures as low as −28°C and mild wind. Although high winds during very cold temperatures are unusual in most areas, these conditions could create an unfavorable energy balance for exposed moose. However, behavioral response in posture and habitat selection to cold temperature and high wind would bring the animal in a more favorable micro-

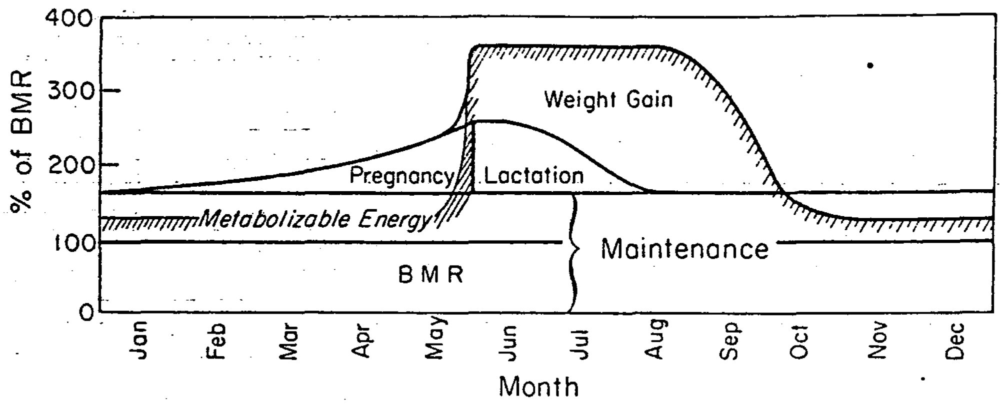

Figure 1. Seasonal energy required and metabolizable energy produced by adult female moose in interior Alaska.

climate. Therefore, it seems unlikely that metabolic thermoregulation ever constitutes a significant energy requirement for moose.

While activity patterns of moose have been studied and reviewed by numerous workers (Murie, 1934; Peterson, 1955; Denniston, 1956; Geist, 1959; 1963; Berg, 1971), duration of daily activity has rarely been determined. Restricted movements and small home range of moose during winter, particularly during periods of deep snow, have been suggested by numerous authors (cf. Coady, 1974). However, limited movement patterns do not necessarily indicate reduced activity and energy expendure. LeResche and Davis (1971) found that tame moose in Alaska fed for an average of 7.7 hours during 12 daylight hours in winter, and for 6.8 hours during 18 daylight hours during summer. No observations were made during periods of darkness. Knorre (1959) found that moose were active, primarily in feeding, 42 percent of the 24-hour day during winter and 58 percent of the 24-hour day during summer. Similar observations have been made for other ruminants. Silver (1971) recorded lowest daily activity and feed consumption for white-tailed deer during winter, and Silver *et al.* (1969) cited unpublished data indicating reduced activity and food consumption of white-tailed deer during winter.

The above studies suggest that duration of activity may be similar or somewhat less for moose during winter than during summer. Reduced activity conserves energy and may be particularly important in minimizing metabolic requirements when snow conditions hinder movement (Coady, 1974).

While maintenance energy for moose is uncertain, maintenance requirements for wild and domestic species have been estimated. Short and Golley (1968) concluded that maintenance energy demands for cattle *(Bos taurus)* in normal range activities, and perhaps for wild herbivores under usual range conditions, is 15 percent above FMR. Blaxter (1962) generalized that maintenance requirements of ruminants averaged 36 percent greater than FMR.

The above estimates appear low, especially considering that increased resting metabolic rate (RMR) of fed but quiet animals may be considerably greater than FMR (Table I). Brockway and Maloiy (1968) found an increase of 29 percent in RMR over BMR in red deer, while McEwan and Whitehead (1970) found an increase of 49 percent in RMR over BMR in reindeer during winter. Similarly, Hart *et al.* (1961) measured an increase of 49 percent in RMR of caribou during winter over BMR determined by McEwan (1970) for caribou during the same season. Energy demands by free ranging ungulates for movement would further elevate requirements above that for RMR.

Brody (1945) suggested that maintenance energy requirements for large herbivores average approximately 2 × BMR. Ullrey *et al.* (1969) calculated maintenance requirements of white-tailed deer during winter to be 1.9 times BMR, where ME = 131 kcal/day and BMR = 69 kcal/kg$^{.75}$/day. However, the excitable nature of white-tailed deer may increase maintenance rerequirements above that required for less excitable moose.

Based on partitioning available energy between BMR, maintenance, and tissue production, we estimate that maintenance requirements for moose range between 1.5 and 1.8 × BMR, and may average near 1.7 × BMR, as shown in Figure 1. Since metabolic requirements for both thermoregulation and activity are considered to remain relatively constant throughout the

TABLE I

Fasting (FMR) and resting (RMR) metabolic rate of wild ruminants

Species	*Season*	*Number of animals*	*$\bar{X}$ body wt (kg)*	*Age (yrs.)*	*Air Temp. (°C)*	*Heat Production FMR (kcal/ $W^{.75}$/day)*	*RMR (kcal/ $W^{.75}$/day)*	*Reference*
White-tailed Deer	Winter	2	56.8	1 ½-2	−0.4 to 3.9	67.8		Silver *et al.* 1959
White-tailed Deer	Summer	2	45.6	1 ½-2	21.2-21.5	71.2		Silver *et al.* 1959
White-tailed Deer	Winter	17	65.3	Adult	16-21.5	97.1		Silver *et al.* 1969
White-tailed Deer	Summer	9	58.6	Adult	16-21.5	143.6		Silver *et al.* 1969
White-tailed Deer	Winter	4	30.6	Fawns	16-21.5	90.2		Silver *et al.* 1969
White-tailed Deer	Summer	2	36.1	Fawns	16-21.5	130.8		Silver *et al.* 1969
White-tailed Deer	Winter	4	67.6	2.5-11.5	17.50-21.5	81.0		Silver *et al.* 1971
White-tailed Deer	Summer	2	49.0	2-11.5	17.4-19.3	139.8		Silver *et al.* 1971
Caribou	Winter	2		9 mos.	15	96.8		McEwan, 1970
Reindeer	Winter	3	74.7	Calves	15	102	157.4	McEwan & Whitehead, 1970
Reindeer	Summer	3	73.3	Calves	15		196.9	McEwan & Whitehead, 1970
Caribou	Winter	1	31.7	9 mos.	25 to -52		144.0	Hart *et al.* 1961
Reindeer		1	100	5-6	−10		132.8	Hammel, 1962
Pronghorn		4		4 mo-6 mo	21	92.8		Wesley, 1969
Red Deer		2	58	Adult	18	90.0	116.0	Brockway & Maloiy, 1968
Red Deer		1	45-50	—	—	70.0		Maloiy *et al.* 1968
Wildebeest		1	—	—	—	91.0		Rogerson, 1966
Wildebeest		1	—	—	28	104.3		Rogerson, 1968
Eland		2	—	—	28	111.2		Rogerson, 1968

year, seasonal maintenance requirements probably follow a similar pattern. Therefore, the maintenance energy requirements during both winter and summer of a 425 kg moose with a BMR of 6,550 kcl/day is estimated to be 1.7 × 6,550 or approximately 11,000 kcal/day.

REPRODUCTION

Energy requirements for pregnancy, lactation, and weight gain are major processes in adults which elevate metabolic rate above the maintenance level. A limited number of studies have been conducted to determine energy requirements among domestic ruminants for various productive processes, while few, if any, such studies have been undertaken with wild species.

Measurements of energy requirements for gestation among domestic ruminants differ widely, but generally indicate a substantial energy accumulation in fetal material and increase in maternal metabolism occurs only during the last one-third of pregnancy (Flatt and Coppeck, 1965; Flat *et al.*, 1969; Halls, 1970; Moe and Tyrrell, 1972). For example, Moe and Tyrrell (1972) found that ME requirements for cattle increased from 15 percent to 75 percent above that for the non-pregnant animal during the last one-third of pregnancy, representing an increase from 21 percent to 107 percent over BMR. Assuming a gestation period for moose of approximately 243 days (Peterson, 1955) and a parturition date of June 1, a significant increase in energy requirements for fetal development probably begins in early March.

Reid (1968) suggested that ME required for gestation can be estimated as 350 kcal/kg/day. Based on fetal growth rates of Alaskan moose (Rausch, 1959), ME for gestation increases form 875 kcal/day in March to 5,250 kcal/day at term near June I (Table II). Since weights of pregnant moose in interior Alaska range near 360 kg during spring, ME requirement per kg body weight$^{.75}$ of the female increases from 15 percent to 91 percent over BMR of the non-pregnant animal (Table II). We assume that energy requirements for gestation in moose are similar to those for cattle, and range from approximately 15-20 percent of BMR after two-thirds of the pregnancy in early March to nearly 100 percent of BMR near term, as shown in Figure 1.

Production of milk by wild ruminants has received little attention, although milk intake by moose calves (Knorre, 1959, 1961) and by reindeer and caribou calves (McEwan and Whitehead, 1971) has been studied. By weighing before and after nursing, Knorre (1959) found maximum milk

TABLE II

Fetal growth rates and energy requirements by moose for gestation in interior Alaska. Fetal growth rates from Rausch (1959)

Date	*Fetus wt (kg)*	*ME Requirement (kcal/day)*	*ME Requirement per kg$^{.75}$ of (kcal/day)*	*% Increase over BMR*
March 1	2.7	875	10.6	15
April 1	4.8	1680	20.3	29
May 1	8.8	3080	37.3	53
June 1	15.0	5250	63.5	91

consumption by moose calves in Russia to range from 1.5 to 2.0 liter per day during June, and to decrease during July to approximately 0.5 liter per day in August. Total milk consumption per calf until weaning in August or September was between 100 to 200 liter. Knorre (1961) noted that after 1.5 to 2 months of age the diet of calves consists primarily of solid foods. We have found considerable amount of herbaceous material in rumen contents of calves in Alaska towards the end of June.

To calculate metabolic requirements for lactation in moose, the gross energy of milk is required. Overman and Gaines (1933) indicated that caloric value of milk can be estimated by a formula where kcal/kg milk = 304.8 + 114.1 × F, and F = percent milk fat. Although fat content of moose milk varies among individuals and with stage of lactation, 10 percent may be considered an average value (Knorre, 1959, 1961; Cook *et al.*, 1970). Therefore, gross energy of moose milk can be calculated as 304.8 + 114.1 × 10 or 1,446 kcal/kg. It follows that maximum milk consumption of two liter/day would represent a caloric intake of about 2,900 kcal.

Knorre's studies (1959, 1961) indicate that milk consumption by moose is somewhat lower than would be predicted from studies on reindeer and caribou, and high-yielding domestic species. Using tritiated water McEwan and Whitehead (1971) calculated that average milk intake of reindeer and caribou calves during the first month of lactation ranged between 1.2 and 1.8 liter/day, or 2,760 to 4,140 kcl/day, assuming a caloric equivalent for reindeer and caribou milk of 2,300 kcal/liter. Luick and White (1971) reported that milk consumption by reindeer calves during the first two weeks of life averaged approximately 0.95 liter/day. This represented an energy intake of approximately 1,900 kcal/day.

If caloric requirements of moose calves for milk were similar to those for reindeer and caribou calves, milk consumption could be estimated. Based upon metabolic body size, if reindeer and caribou calves weighing 5 kg (5 kg$^{.75}$ = 3.34 kg) consume an average of 1,900 kcal/day in milk (Luick and White, 1971), then moose calves weighing 15 kg (15$^{.75}$ = 7.62 kg) consume 4,300 kcal/day as milk. Since caloric value of moose milk is approximately 1,446 kcal/kg, moose calves would consume approximately three liter per day.

Milk production by domestic animals is also considerably higher than that measured for moose. Payne and Wheeler (1968) suggested that milk yield in dairy cattle is represented by the equation kcal/day = 124 W$^{.75}$, where W = body weight of the female in kg. Since average weight of lactating moose in June was approximately 380 kg (380$^{.75}$ = 86.1 kg) (Table III), the calculated milk production based on dairy cattle would be 10,676 kcal/day or 7.4 (liter/day). Both estimates of mild-yield of 3 liter/day and 7.4 liter/day are considerably higher than was measured by Knorre (1961), even by intensive experimental milking.

TABLE III

Body weight and total length of lactating and non-lactating moose over two years of age during June in interior Alaska[1]

	No.	*Mean*	*Range*
Non-Lactating			
Weight (kg)	4	429	395-463
Length (cm)	4	264	242-275
Lactating			
Weight (kg)	4	380	367-390
Length (cm)	4	276	269-284

[1] Coady, unpublished.

Based largely upon the above work on reindeer and caribou, we feel that milk production by wild moose during the first few weeks after birth of a single calf is at least 3 liter/day, and may be greater.

Metabolizable energy is converted into gross milk energy with an efficiency of approximately 70 percent, although it is influenced by a number of factors such as quality of diet and stage of lactation (Reid, 1968; Blaxter, 1962). Therefore, approximately 5,600 kcal of ME are required daily to produce 3 liter of milk with a gross energy of 4,300 kcal. This amounts to 65 kcal/380 kg$^{.75}$ day, or a value almost equal to one BMR of the female during spring, as shown in Figure 1.

Metabolic costs of lactation are illustrated by lower body weights of lactating moose compared with those of dry females (Table III). Average body weight of four non-lactating adult females during late June in interior Alaska was 12 percent greater than that of lactating moose, in spite of a longer total length indicating larger average body size for the lactating animals. Lactating moose had gained approximately 20 kg while non-lactating moose had gained approximately 70 kg at the end of June over average spring weights of 360 kg. Sequential weights of individual females with and without calves at the Kenai Moose Research Center, Alaska, indicated that calf rearing "costs" were 8 to 18 percent of a cow's July-August weight (LeResche and Davis, 1971).

WEIGHT GAIN

Moose experience marked seasonal fluctuation in body weight. Average body weights for breeding female moose older than three years in interior Alaska ranged from near 360 kg in late spring to approximately 475 kg or larger in fall. These values suggest an average weight loss of approximately 115 kg or 24 percent between fall and spring. Weight gain probably occurs during approximately 125 days per year between late May and late September, when live or dead herbaceous plants and deciduous leaves are most available in interior Alaska. Thus, rate of gain is approximately 1 kg per day.

Jordan *et al.* (1970) concluded that seasonal body weight fluctuations of moose amounted to only 6.6 percent for females and 10.3 percent for males. However, Rausch (1959) and LeResche and Davis (1971) reported seasonal body weight fluctuations of 20 percent and 15-30 percent, respectively, for moose in southcentral Alaska. Verme (1970) found that a "winter-killed" bull in Michigan had lost 33 percent of his pre-winter weight.

Seasonal weight loss in moose is probably not limited to fat, but also includes substantial amounts of protein. Paquay *et al.* (1972) have demonstrated that mature cows have a capacity to store and lose up to 20-25 percent of their body protein, depending on level of feeding. Additional studies reviewed by Paquay *et al.* (1972) suggest that mobilization of reserves from liver, viscera, and especially muscle can contribute to maintenance during undernutrition in several species. Since percent protein in a carcass apparently fluctuates with level of protein intake (Paquay *et al.*, 1972) large seasonal variations in dietary protein of moose in interior Alaska suggest that labile protein reserves probably exist in the species. For purposes of this review, we assume that 25 kg or 20-25 percent of the 115 kg seasonal weight fluctuation of moose in interior Alaska is due to loss or gain of protein, while the remaining 90 kg weight fluctuation is due to loss or gain of fat.

Efficiency of fat synthesis has been measured for domestic species. Flatt and Coppeck (1965) concluded from the literature that ME is converted into body fat in the lactating animal with an efficiency of approximately 70 percent, equal to that of milk production. This efficiency averages about 58 percent in the non-lactating animal (Blaxter, 1962; Flatt and Coppeck, 1965). However, lipogenesis is closely related to diet, and the effeciency of converting ME into body fat may decrease on low quality forage (Short and Golley, 1968). Since the efficiency of protein production is uncertain, we tentatively assume that it is similar to that for lipogenesis. Differences in the efficiency of fat and protein production are probably not great and therefore should not cause significant error in estimating metabolic requirements.

Energy requirements for weight gain in moose can be calculated from rate of tissue production. Ninety kg of fat and 25 kg of protein gained during 125 summer days amount to an average weight gain of 0.72 kg of fat and 0.20 kg of protein, or 0.92 kg of tissue per day. Therefore, gross energy of tissue deposited amounts to 6,696 kcal/day of fat (9.3 kcal/g fat) and 860 kcal/day of protein (4.3 kcal/g protein), or a total of 7,556 kcal/day. Assuming 70 percent efficiency for tissue production, an average of 9,800 kcal ME/day are required to produce approximately one kg of fat and protein per day.

Summer fattening in lactating moose is probably not constant. During early summer weight gain is relatively small, while by mid-summer lactation is greatly reduced and weight gain probably occurs at a more rapid rate. Metabolizable energy shown in Figure I which is available for fat and protein production in the lactating moose probably ranges from slightly more than one time BMR during early summer to nearly two times BMR during mid -to late summer. Weight gain in the non-lactating moose is probably more uniform throughout the summer, and maximum fall weights may be somewhat greater than in the lactating animal. Rates of fattening may decline during late summer because of a reduction in quality of forage during the growing season (Oelberg, 1956).

Nutrition

Energy for maintenance, growth and reproduction is supplied through the digestion of plants. Moose, like other ruminants, rely to a great extent on microbial digestion and fermentation of plant carbohydrates and proteins in the rumen to yield useful nutritional products since they lack some of the essential digestive enzymes required to make efficient use of plant tissues. The following discussion will be directed toward the nutrient composition of moose foods, food consumption and the processes of transforming plant material into usable energy to fulfill the needs previously discussed.

NATURE OF RUMEN CONTENTS

Rumen contents include solid particles of food plants, soluble energy sources, microbial waste products, bacteria, protozoa, gases, saliva, water and many other materials. Rumen contents may be thought of as microbial culture medium maintained in relative stability by the steady input, outflow and absorption of constituents.

Dry matter in the rumen

Dry matter (DM) content varies with diet and season, and ranges from 8 to 20 percent of rumen contents in moose and most other ruminants (Short *et al.*, 1969 a, b; Church, 1969; Luick *et al.*, 1972). Dry matter content is influenced by the nature of food ingested, the time since feeding and drinking, salivary flow, passage of materials out of the rumen, and the rates of digestion and absorption (Church, 1969; Waldo *et al.*, 1965; Ingalls *et al.*, 1966). The above factors result in diurnal variations in percent DM of rumen contents. Short *et al.* (1969a), working with white-tailed deer, reported that the highest percent DM occurred early in the morning following feeding, and the lowest percent DM occurred during midday. Intermediate values were found in the late afternoon.

In moose the percent DM changes seasonally. Moose on summer range have low percent of DM in the rumen because of the high moisture content of succulent vegetation and availability of water. In winter the low moisture content of woody browse causes DM to increase to its highest value (Table IV). Moose may also reduce water intake in winter when only snow is available.

Chemical make up of rumen contents

The gross chemical compositions of rumen contents reflects the food eaten by the ruminant (Klein, 1962, 1965, 1968, 1970; Klein and Schønheyder, 1970; Klein and Standgaard, 1972; Short, 1966). Rumen contents which remain on a sieve when washed with water include primarily ingested forage and indigestible residues, and may be used to determine the approximate nutrients in the diet. Washed rumen contents probably represent a minimum estimate of protein in the forage because soluble protein and amino acids are readily digestible components. Analyses of washed rumen contents from moose in interior Alaksa indicate that dietary protein was 12 percent in summer and 6 percent in winter (Table V). LeResche (pers. comm.). also found similar protein levels (6 percent) in washed rumen contents during winter in moose from the Kenai Peninsula and southcentral Alaska (Table V). This protein content reflects a low protein diet. Protein content of winter moose browse on the Kenai Peninsula was slightly greater than that found in rumen contents. Hand picked browse samples ranged between 5 to 9 percent protein and averaged 8 percent (LeResche, pers. comm.).

Food selected by moose in winter is probably near the minimum required protein level. This value is considered to be about 7 percent for ruminants (Corbett, 1969). Murphy and Coates (1966) found that white-tailed deer fed 7 percent protein diets throughout the year were physically stunted and that does fed on low protein diets (7-11 percent) produced fewer fawns than those fed higher protein diets.

Deer in North America select browse similar in protein content to that of moose. Klein (1965) found that winter forage of black-tailed deer (*Odocoileus hemionus sitkensis*) in southeastern Alaska contained about 6 percent protein. Spring forage contained 25 percent protein and late summer forage 12.5 percent protein. Short (1969, 1971) and Torgerson and Pfander (1971) found white-tailed deer foods contained 5-8 percent protein during winter and 15-16 percent during spring.

Forage can be divided into two basic components (soluble cell contents and cell wall components) by the neutral detergent fiber (NDF) analysis of Goering and van Soest (1970). The cell contents are considered 98 percent digestible, while the cell wall component (hemicellulose, cellulose and lignin) varies in digestibility depending on lignin content. Fiber (cell wall component) is an abundant constituent of most ruminant forage and is

TABLE IV

Seasonal changes in body weight and rumen characteristics of moose collected in the Tanana Valley, Interior Alaska[1]

Season month, year	*Sex, age, reproduction status*	*Number in sample*	*Body wt (kg)*	*Rumen contents (kg wet wt)*	*% Rumen contents of body wt*	*% Dry matter in rumen contents*	*Dry matter in rumen (kg)*	*Estimated[2] digested organic matter (kg dry wt)*
Spring May 1971	Female adult pregnant	4	338	29	8.7	12.7	3.7	2.2
Summer June 1972	Female adult non-lactating	4	430	41	9.5	12.5	5.2	5.6
Summer June 1972	Female yearling non-lactating	1	227	18	8.0	11.3	2.1	2.7
Summer June 1972	Female adult lactating with calf	3	379	43	11.4	10.8	4.8	6.3
Early winter October 1972	Female adult non-lactating without calf	5	501	52	10.4	15.9	8.3	2.2
Early winter October 1972	Male adult rut	2	525	51	9.6	16.9	8.6	2.2

[1] Coady and Gasaway, unpublished.

[2] Estimate based on 8.5 moles VFA produced per kg organic matter digested (Weston & Hogan, 1968a). VFA production data is show in Table IX.

slowly digested by rumen microbes (Hungate, 1966). Goering and van Soest (1970) found that low NDF and low lignin: cellulose ratio are characteristic of more digestible forages.

Cell wall components and lignin: cellulose ratios of washed rumen contents from moose in interior Alaska were lower in summer than in winter, indicating the higher digestibility of summer forage (Table VI). We estimated digestibility of forage in June and October to be 50 and 40 percent, respectively, using the lignin ratio method and the summation equation (Goering and van Soest, 1970). High ADF and lignin values noted in Table VI for February and May are partially explainable upon the basis of technique. The rumen contents collected in these months were washed on a larger mesh sieve than those collected in June and October. The large mesh sieve retained proportionally more coarse, woody material than the sieve used for samples obtained in June and October.

Seasonal changes in rumen fill

The weight of female moose rumen contents varies with season and diet in interior Alaska, being greatest during winter and smallest during spring (Ta-

TABLE V

Seasonal variation in percent crude protein of washed rumen contents from moose and black-tailed deer in Alaska

	Percentage crude protein			
	Early winter	*Mid-winter*	*Early spring*	*Summer*
MOOSE				
Interior Alaska[1]	6	6	10	12
Kenai Peninsula[2]		6		
Southcentral Alaska[2]		6		
BLACK-TAILED DEER				
Woronkofski Island Southeast Alaska[3]			24	
Coronation Island Southeast Alaska[3]			16	

[1] Coady and Gasaway, unpubl.
[2] LeResche, pers. comm.
[3] Klein, 1965.

TABLE VI

Fiber content of washed rumen samples taken from moose in interior Alaska[1],[2]

Month	*Cell wall components (NDF)*	*Acid detergent fiber (ADF)*	*Lignin*	*Cellulose*	*Lignin/ADF*
February		67.3	26.1	41.2	0.39
May		66.3	33.2	33.1	0.50
June	51.7	40.2	11.7	28.5	0.29
October	68.9	58.9	18.5	40.4	0.31

[1] Analyses performed by WARF Institute, Inc. Madison, Wisconsin
[2] Coady and Gasaway, unpublished.

ble IV). During winter, the greater rumen fill in moose may act to compensate in part for poorer quality forage. Microbes are provided with more substrate which leads to increased utilization of lower quality food. Rumen fill of cows was lowest prior to calving in late May, possibly because growth of the fetus occurs at the expense of rumen volume as has been demonstrated in domestic sheep and cattle (Campling, 1970). This decrease in rumen fill results in a reduction in total DE attained from the diet. Intermediate rumen fill occurs throughout the summer (Table IV). Increased digestibility and turnover of succulent food in the rumen during summer probably results in lower rumen fill in spite of greater food consumption. By contrast, rumen fill in white-tailed deer is lowest during winter (Short, 1971).

pH of rumen contents

The pH of moose rumen liquor is similar to that of other ruminants. Samples collected from freshly killed moose in interior Alaska during October and February contained rumen liquor with a pH of 6. The pH of rumen liquor in a moose killed in October was monitored for four hours following death. The pH dropped from 6 at death to 5 three hours after death. At this time fermentation had nearly stopped suggesting that pH would probably not decline further. These values were determined using pH indicator paper and are therefore only approximate. pH values are not available from moose in summer, although they may be lower than winter values because of increased fermentation rate and higher volatile fatty acid concentration. Short *et al.* (1966) found a lower pH in rumen liquor of mule deer (*Odocoileus hemionus)* during summer than during winter. Therefore, pH values may be of some use as a very general indicator of relative fermentation rates.

FOOD INTAKE, PASSAGE AND DIGESTIBILITY

Food intake, passage rates and digestibility in moose have received little consideration. However, these parameters are important to the understanding of moose nutrition and require further investigation.

Verme (1970) reported that captive moose consume 18-23 kg fresh browse per day in winter and 23-27 kg food in summer. Palmer (1944) estimated that moose required 16 kg of forage per day (air dried weight). Attempts to estimate food consumption by Alaskan moose are reported by LeResche (1970) and LeResche and Davis (1971). The utilization of winter browse was studied in pens by estimating the biomass of browse removed by known numbers of moose during the winter. Variability in estimates of food intake was high, ranging from 1.3 to 5.4 kg/animal/day (wet weight) and were considered unreliable. A second method was tried where tame moose were observed and number of bites and types of plants were recorded. Bites were then converted into pounds of food consumed. An estimate 1.7 kg/animal/day (wet weight) (1.3 kg dry wt/day) was consumed in winter and 19 kg animal/day (wet weight) during summer (Table VII). The estimate for winter was felt by LeResche and Davis (1971) to underestimate actual consumption. These same moose were capable of consuming 11 to 16 kg of pelletized commercial food per day in the previous winter.

Estimates of required digestible DM and food intake during winter can be made for moose in interior Alaska. Approximate values used in the calculation of DM consumed were the following: organic matter digested = 4,500 kcal/kg digested; metabolizable energy (ME) = 3,690 kcal/kg organic matter digested (ME = 0.82 × DE, Annison and Armstrong, 1970); digestibility of 40 percent in winter and 55 percent in summer, based on estimates made by the summation equation and lignin ratio methods discussed previously. Daily energy requirements for moose during winter are assumed to be near 1.7 × BMR.

Applying the above assumptions an estimate of the required food for moose can be calculated as follows. Cow moose in mid to late winter weigh about 400 kg and have a BMR of about 6,300 kcal/day. Metabolizable energy requirements at that time are approximately 10,700 kcal/day (6,300 kcal/day × 1.7). Body fat and protein reserves were catabolized at an average rate of 3,900 kcal/day (based on winter weight loss of 90 kg fat and 25 kg protein in 240 days). Thus, 6,800 kcal ME were supplied by the forage. It requires 1.9 kg digestible DM to supply this 6,800 kcal ME, and since DM is 40 percent digestible, 4.6 kg DM or about 6.5 kg wet weight of winter browse would be consumed (Table VII).

Dry matter digested and food consumed by moose can also be estimated from volatile fatty acid (VFA) production using the relationship described for domestic sheep by Weston and Hogan (1968a). They found a relatively constant production of VFA per unit of organic matter digested (8.5 mole VFA/kg DM). Using Weston and Hogan's relationship,

TABLE VII

Estimates of food consumption by moose are presented for several studies in kilograms per day. Note that values are in dry, air dried, and wet weights making direct comparison difficult

Summer			*Winter*	*Conditions*	*Reference*
Lactating	*Non-lactating*	*Reproductive Status Unknown*			
		23-27 wet wt.	18-23 wet wt.	Penned, hand cut browse	Verme, 1970
		16 air dried	16 air dried	Estimate for penned	Palmer, 1944
			1.3-5.4 wet wt.	Natural browse, estimated from browse removed in large pen	LeResche, 1970
	19 wet wt.		1.7 wet wt. (1.3 dry wt.)	Natural browse, estimates from bites eaten by tame moose in large pen	LeResche and Davis, 1971
			4.6 dry wt. (6.5 wet wt.)	Natural browse, estimated from energy requirements of 1.7 x basal metabolic rate	Coady and Gasaway, unpubl.
11.5 dry wt.	10.2 dry wt.		5.5 dry wt. (6.0 wet wt.)	Natural browse, estimated from digestible DM required for measured VFA production	Coady and Gasaway, unpubl.

the mean value for production of VFAs in moose feeding on winter browse in interior Alaska was equal to 2.2 kg digestible DM/day (Table IV). Therefore, DM consumed equals 5.5 kg per day with a 40 percent digestibility or about 7.9 kg/day wet weight. Caloric value of food digested is 2.2 kg × 3,690 kcal ME/kg = 8,118 kcal or 1.3 × BMR. This is less than the estimated 1.7 BMR mentioned above. However, when the additional energy (3,900 kcal/day or 0.6 × BMR) from tissue reserves is considered the total energy available equals 1.9 × BMR (12,000 kcal) which is close to the estimated requirement of 1.7 × BMR.

Similar calculations can be made for lactating moose which are in positive energy balance during summer. Estimated digested DM equals 6.3 kg (Table IV), or, assuming 55 percent digestibility for summer forage, 11.5 kg DM consumed. Caloric value of the 6.3 kg DM is equal to 23,200 kcal ME/day or 3.8 × BMR (BMR = 6,035, see Table XI).

Non-lactating cow moose during summer digested an estimated 5.6 kg DM per day equal to 20,700 kcal ME, or 3.4 × BMR (BMR = 6,100, see Table XI). This represents 10.2 kg of DM consumed or 1.3 kg less than lactating cows. Moose appear to increase food intake while lactating as do domestic cows (Campling, 1970). Corbett (1969) reported lactating dairy cows may consume as much as 50 percent more food than non-lactating cows. Dairy cattle have higher energy demands for lactation than moose since they are bred for inordinately high milk production rather than requirements of the calf.

Estimates of food consumption discussed here vary considerably according to the method by which they were calculated (Table VII). Although all food consumption estimates are approximate, they show a marked increase during the plant growing season. The increase in food consumption is reflected in rapid weight gains during the summer and the winter decrease in food intake by weight loss (see Table XI).

It is unlikely that lower food intake during the winter is a result of limited food availability. The probable cause is increased retention time of food in the rumen because of decreased digestibility. Food intake in ruminants is partially regulated by the passage rate of digesta through the gut (Weston and Hogan, 1968b; Corbett, 1969; Corbett *et al.*, 1963, and Balch, 1950).

The more rapidly the breakdown and digestion of foods in the rumen, the faster can be the rate of passage of digesta onward from the rumen to the remainder of the gastro-intestinal tract; hence the greater is the quantity of feed that must be eaten to maintain a certain degree of rumen fill. Food consumption is therefore a function of the rates of digestion in, and of passage from the rumen (Corbett, 1969). Corbett *et al.* (1963) demonstrated this relationship between digestibility and food intake in cattle. During a five week study the digestibility of grass decreased from 80 to 68 percent, and food intake fell about 20 percent. Weston and Hogan (1968b) attribute low food intake of poor quality feed to long turnover time in the rumen of domestic sheep. However, consumption increased when food was ground and pelleted because rumen turnover time was shortened.

Voluntary reductions in food intake during winter have been noted in deer fed good quality food *ad libitum* (Thompson, 1972; Wood *et al.*, 1962). This factor may also play an important role in regulating winter food consumption in moose.

The stage of maturity of pasture plants has a marked effect on rumen function parameters in domestic sheep (Hogan *et al.*, 1969). Similar effects probably occur in moose as the growing season progresses and plants mature. Hogan *et al.* (1969) found that as the grass, *Phalaria tuberosa*, matured food consumption, passage rates through the gut, digestibility and VFA production decreased and chewing activities increased. Short (1971) found that grasses and forbs utilized by white-tailed deer in Texas varied in digestibility with the stage of maturity. He sampled deer browse throughout the year and found that immature stages were more digestible than mature plants.

Since plants in immature stages of growth are most digestible and nutritious it is advantageous for ungulates to inhabit areas with diversity in habitat types, browse, topography, and long seasonal progressions of plant growth. These conditions permit selection of highly nutritious foods for the greatest length of time during the growing season. Klein (1965) found the environmental factors, altitude and topographic variation, to be primarily responsible for differences in the quality of browse and consequently for differences in growth rates of black-tailed deer in Alaska. He suggests that similar factors are of importance to Dall sheep (*Ovis dalli*) and mountain goat (*Oreamnos americanus*). These factors are no doubt important in determining the quality of moose browse and subsequent distribution and seasonal movement of moose.

While information regarding rumen turnover times or forage digestibility in moose are not available, fermentation data can be used to indicate seasonal trends. Quantity of rumen DM was greatest in moose feeding on woody browse during October in interior Alaska, while estimated DM digested was low during this time (Table IV). October forage may have a long turnover time in the rumen because of the low removal rate by digestion. By comparison, moose feeding on green plants in June apparently digested more DM per day than was present in the rumen; hence, the turnover of DM was more rapid than in winter. The only comparable study on wild ruminants of which we are aware was undertaken by Mantz and Petrides (1971) on white-tailed deer. They reported that natural browse had a greater retention time in the rumen than did a ground, pelleted, and readily digestible standard diet which might be considered equivalent to summer forage in terms of turnover. Seasonal turnover patterns described in moose and white-tailed deer are also similar to those observed in domestic ruminants.

RUMEN FERMENTATION AND UTILIZATION OF VFA

Rumen fermentation is one of the major adaptations favoring successful coexistence among ruminants and other large herbivores. The "fermentation vat" has allowed for digestion of the ubiquitous cellulose molecule and other difficult to digest polysaccharides. Over one half of the digestible DM consumed by ruminants is altered by microbial digestion and fermentation in the rumen, and from 53-62 percent of the DE goes through the rumen VFA pool alone (Gray *et al.*, 1967; Bergman *et al.*, 1965; Annison and Armstrong, 1970; Blaxter, 1962).

Rumen metabolism of carbohydrates and proteins

Carbohydrates (CHO) are the most abundant energy source for moose, making up about 60-70 percent of the diet. Carbohydrates found in plants are primarily polysaccharides, cellulose, hemicellulose, pectins, starches, and fructans. A very small portion of CHO is in the form of mono — and disaccharides such as fructose, glucose and sucrose (Church, 1969; Leng, 1970). Microbes digest and ferment much of the CHO consumed, and the ease of digestion varies with the different CHO molecules. Digestion of cellulose and hemicellulose is slower than that of starch and soluble CHO. Large, complex molecules such as cellulose, hemicellulose, and starch are first broken down by extracellular enzymes into small units. This is followed by digestion and fermentation within the microbial cell (Leng, 1970).

The general scheme of CHO metabolism is for conversion of dietary CHO into a common unit, glucose, and then to pyruvate which is metabolized to acetic, propionic, butyric and valeric acids (VFA) plus carbon dioxide and methane (Leng, 1970; Baldwin, 1965; Hungate, 1966; Hungate, 1968; Church, 1969).

Acetic acid is produced in the greatest molar quantity and is followed in order by propionic, butyric and valeric acids in moose and other ruminants (Table VIII). A schematic diagram of CHO degradation in the rumen is shown in Figure 2 (from Church, 1969 and Leng, 1970).

Dietary proteins are broken down into amino acids which are fermented to produce energy for biosynthetic processes. Amino acids may be incorporated directly into microbial cells or deaminated and fermented to produce ammonia, carbon dioxide and VFA. The proportion of VFA originating from protein is not well understood, although feeds rich in highly soluble proteins may yield substantial amounts. Branched chain VFA present in the rumen, i.e. isobutyrate and isovalerate, arise from fermentation of certain amino acids (Hungate, 1966). These branched VFA represent a small percentage of the total VFA, although they provide a relative indication of the magnitude of protein fermentation. Proteins and amino acids may escape fermentation in the rumen and pass into the lower

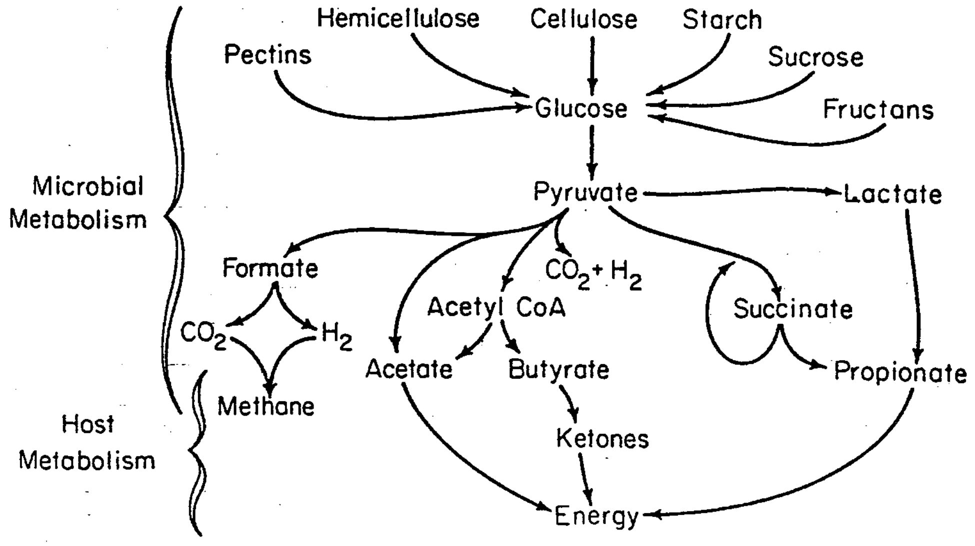

Figure 2. Carbohydrate digestion and metabolism by rumen microbes and their host (from Church, 1969 and Leng, 1970).

TABLE VIII

Comparison of initial concentration and molar percentages of VFA in rumen liquor of several species of ungulates

Species	*Diet or Season*	*Initial concentration* (μ eq/ml liquor)	*Molar percent*				*Reference*
			Acetate	*Propionate*	*Butyrate*	*Propionate*	
Moose	Spring, mixed woody browse + some green forage	65	73	18	9	4.1	Coady & Gasaway, unpubl.
	Summer, green forage	93					
	Early winter, woody browse	69					
	Mid-winter, woody browse	70	74	17	8	4.3	
Mule Deer	Winter to early spring		68	20	10	3.4	Short *et al.*, 1966
	Late spring and summer		63	22	13	2.9	
	Autumn		66	20	11	3.3	
White-tailed deer	Winter, diet largely acorns	108	59	22	15	2.9	Short *et al.*, 1969b
	Winter, diet browse and grasses	107	73	16	9	4.5	
White-tailed deer	Winter — February	97	74	19	7	4.2	Short, 1971
	May	80	72	19	9	3.9	
	July	130	59	32	9	1.9	
	November	110	54	34	12	1.6	
	February	76	62	28	10	2.2	
Domestic sheep	Early growth, low fiber	104	66	20	12	3.3	Hogan *et al.*, 1969
	Intermediate maturity	100	68	20	10	3.4	
	Mature, high fiber	76	71	18	10	3.9	
Domestic sheep	Dry season	118	65	20	16	3.3	Weller *et al.*, 1969
	Wet growing season	117	58	25	17	2.3	
	Dry season	100	68	20	12	4.0	

digestive tract where they are absorbed by the host ruminant (Hungate, 1966; Leng, 1970; Nolan and Leng, 1972; Tillman and Sidhu, 1969; Mangan, 1972). However, the major source of protein for ruminants is of microbial origin (Hungate, 1966; Nolan and Leng, 1972).

Ammonia formed by deamination of amino acids is utilized by the microbes as a nitrogen source for protein synthesis. The host ruminant also absorbs ammonia from the rumen. It is converted into urea and recycled into the rumen via salivary secretion and secretion through the rumen wall. Nitrogen in urea is converted to ammonia in the rumen and used in microbial syntheses (Hungate, 1966; Nolan and Leng, 1972; Weston and Hogan, 1967; Church, 1969). Recycling of nitrogen is an important process which presumably allows all ruminants including moose to effectively utilize low protein diets.

VFA production

More VFA is produced in the rumen from forages containing high levels of soluble CHO and protein than from foods high in fiber and insoluble components. Thus, immature stages of plants generally result in high VFA production rates whereas plants consumed in the winter or dormant period are generally difficult to digest and yield low VFA production rates (Weston and Hogan, 1968a, b, c; Hogan *et al.*, 1969; Hogan and Weston, 1969).

VFA production in moose in interior Alaska was studied during spring, summer and winter using the zero time rate methods of Carrol and Hungate (1954) (Coady and Gasaway, unpubl.). The method was slightly modified for use in field studies. The procedure involves *in vitro* incubation of a rumen content sample under conditions approximating those in the rumen. Isolation of the sample in a polyethylene jar prevented absorption of microbial end products while allowing fermentation to continue for a period of time. Subsamples from the jar were withdrawn at approximately half hour intervals and prepared for total VFA determination by steam distillation and titration with NaOH. Total daily VFA production for moose was calculated by multiplying the *in vitro* production rates per ml of rumen liquor by the total volume of liquor present in the rumen.

VFA production rates per ml of liquor in the rumen of moose varies markedly with season and consequent changes in quality of the diet. Winter diets of woody browse are of low enough quality to limit fermentation rates to approximately one-third of the VFA production rates in summer (Table IX). Apparently, the low fermentation rates in winter result from reduced quality of browse rather than a shortage in quantity, since the moose were collected on quantitatively good winter range. In late May the diet consists of some newly emerging green vegetation mixed with wood browse. VFA production rates at this time were greater than in winter but still only half that of summer values (Table IX).

Seasonal changes in rumen fill and changes in the proportion of liquor have a pronounced effect on the calculated total rate of VFA production observed in moose. Moose in winter have greater rumen fill than in summer. This has the effect of compensating somewhat for the reduced winter VFA production rate per ml of liquor by increasing the volume of substrate exposed to fermentation at any one time. VFA production in the total rumen of moose during summer was 2.6 to 2.9 times that during winter, although the rate of VFA production per ml of liquor was over three times higher during summer than during einter. Thus, the effect of increased rumen fill was that of providing more VFA to the animal than the production rate alone would suggest. The effect of changing rumen fill on total VFA production was more pronounced in cow moose during May when the rumen fill was at its lowest level. Daily VFA production in the May sample equaled that of large rumen volumes in winter because of the increased production rate per ml of rumen liquor due to the recent emergence of green plants. Lactating cow moose during summer had greater total VFA production than did non-lactating cows in spite of the similar VFA production rates. This was due to a greater rumen fill and a higher proprotion of rumen liquor in the rumen contents of lactating moose (Table IX).

Recently, many investigators have measured the VFA production in domestic animals, but few studies of VFA production in wild animals have been undertaken (Table X). To compare animals of different body size, VFA production rates were expressed with respect to metabolic body size ($kg^{.75}$) in Table X. Wide variations in the production rates exist among species depending on the forage fed on and probably the technique used to estimate VAF production. Moose on an annual basis encompass the extreme variation seen in the other species.

Seasonal variations in total VFA production are illustrated in only three studies in Table X. Two studies were carried out on grazing domestic sheep in Australia (Weller *et al.*, 1969, and Weston and Hogan, 1968a) and the other study was on moose in Alaska (Coady and Gasaway, unpubl.). Moose showed greater seasonal extremes in total VFA production than did sheep on their respective high and low quality ranges which are a result of wet and dry seasons. This may be expected since moose have only a short summer period to replenish depleted protein and fat reserves in preparation for a winter of eight months in length. During winter, only low quality food is available and a negative energy balance persists.

VFA concentration in rumen liquor has been used as a seasonal indicator of VFA production for comparing forage quality in wild ruminants (Prins and

TABLE IX

VFA production in moose collected in the Tanana Valley, Alaska[1]

Season, Month	*Sex, Age*	*Number in sample*	*Reproductive status*	*VPA Initial concentration (μ eq/ml)*	*VFA Production rate (μ eq/hr. ml*	*Total VFA production (moles/day)*
Spring May	Female adult	4	Pregnant	65	31	18.81
Summer June	Female adult	4	Non-lactating	98	58	47.75
Summer June	Female adult	3	Lactating	89	61	53.20
Early winter October	Female adult	5	Non-lactating without calf	69	18	18.40

[1] Coady and Gasaway, unpublished.

Geelen, 1971; Short, 1963, 1971; Short *et al.*, 1969a, Short *et al.*, 1969b; Ullrey *et al.*, 1964, 1967, 1968, 1969, 1970; Bruggemann *et al.*, 1968). The correlation of VFA concentration and VFA production described by Leng (1966), Leng and Brett (1966), Leng *et al.* (1968) and Weston and Hogan (1968a, indicates VFA production can be estimated from the concentration once the relationship is established for the species. However, variation in the relationship between VFA production and concentration is considerable. Over a small range of VFA concentration, variability is likely to obscure changes in production. Therefore, in wild game studies we feel VFA concentration can be used only as an approximate indicator of fermentation rates rather than a tool to estimate actual VFA production.

Molar percentages to VFA present in the rumen is related to the gross chemical nature of the diet and fermentation patterns. Generally, forages rich in easily fermented material result in increased propionate relative to acetate. Forages high in fiber result in increased proportion of acetate (Hungate, 1966; Weller *et al.*, 1969; Hogan *et al.*, 1969). Specific incidents in closely controlled studies of domestic animals have revealed exceptions to the generalization cited above (Weston and Hogan, 1968a). Therefore, great significance should not be placed on this parameter as an indicator of food composition and quality, particularly if the investigator has relatively few samples. Table VIII summarizes VFA molar proportions in several species of ungulates. Acetate: propionate ratios show an increase during the winter or dry season which indicates a diet low in soluble CHO and proteins.

Energy value of VFA

The importance of VFA as an energy source in ruminants is well established. The energy contained in the VFA is equivalent to about 57 percent of the DE and about 70 percent of the ME for ruminants assuming that ME is about 82 percent of DE (Annison and Armstrong, 1970). Estimated VFA energy extends our understanding of moose nutrition and energy requirements because ME of free ranging animals may then be estimated.

Metabolizable energy of VFA produced in the rumen of moose which is equal to gross energy of VFA was calculated by multiplying the total moles produced per day by the molar percentage of indivudal VFA. This gave an estimated production of each acid. The number of moles of each VFA times its respective heat of combustion (kcal/mole) equals kcal of ME per day available from each VFA through oxidation. Moles produced per day (Table IX) were converted to kcal of ME as shown in Table XI. Calculated BMR was used as the standard energy unit for moose to which VFA energy was compared. Energy available from VFA in moose feeding on woody winter browse in October was calculated at 69 percent of the BMR (Table XI). This is probably a low estimate because the moose were very fat in this early winter period. Lipid deposits in these moose are approximately 100 kg and adipose tissue is metabolically less active than most other tissues. Correcting for this less active body mass would lower the theoretical BMR and increase the percentage of energy supplied by VFA. The BMR for lean body weight for these moose was about 6,300 kcal per day and VFA energy supplied 81 percent of this amount (Table XI). We suspect VFA production remains relatively constant through a "normal" winter while dormant plant parts are browsed, thus VFA energy contribution

TABLE X

A comparison of rumen VFA production based on body weight in several species of ungulates

Species Sex, Age, No. in Sample	Conditions Season	Diet	Body Wt (kg)	(Body wt)$^{0.75}$	mMoles/ References	mMoles/ day/kg$^{0.75}$	Reference
Moose Cow Adult n = 4	Free ranging Spring, May pregnant	Winter browse + some new green forage	338	79.0	56	238	Coady & Gasaway, unpubl.
Moose Cow Adult n = 4	Free ranging Summer, June Non-lactating	Green forage	430	94.4	111	506	Coady & Gasaway, unpubl.
Moose Cow Adult n = 3	Free ranging Summer, June lactating	Green forage	379	86.0	140	619	Coady & Gasaway, unpubl.
Moose Cow adult n = 5	early winter non-lactating without calf			105.7	37	174	Coady & Gasaway, unpubl.
Eland (*Taurotragus*) n = 1	Free ranging		520	108.9	37	176	Hungate *et al.* 1959
Zebu (*Bos indicus*) n = 1	Free ranging	Grass pasture	241	61.1	52	207	Hungate *et al.* 1959
Grant's Gazelle (*Gazella sp.*) n = 1	Free ranging		49	18.5	34	98	Hungate *et al.* 1959
Thompson's Gazelle (*Gazella sp.*) n = 1	Free ranging		24	10.5	34	98	Hungate *et al.* 1959

Suni n = 1	Free ranging		3.7	2.7	105	146	Hungate *et al.* 1959
Reindeer n = 4	Penned winter	Commercial pellets	52.8	19.5	53	143	Luick *et al.* 1972
n = 2	Penned winter	Commercial pellets + lichens + straw	105	32.8	83	267	Luick *et al.* 1972
n = 4	Penned winter	Lichens	59	21.3	66	183	Luick *et al.* 1972
Domestic sheep, ewes, adult n = 15	Penned	Early stage ryegrass (27 % prot)	43	16.8	128	329	Weston & Hogan, 1968a
		Intermediate ryegrass (12% prot)	43	16.8	125	319	Weston & Hogan, 1968a
		Mature ryegrass (6% prot)	43	16.8	79	202	Weston & Hogan 1968a
Domestic sheep, ewes, adult n = 6	Penned	Lucerne chaff	43	16.8	125	319	Leng & Leonard 1965
Domestic, sheep ewes, adult n = 4	Grazing	Wet season	53	19.6	94	255	Weller *et al.* 1969
	Grazing	Dry season	63	22.4	64	179	Weller *et al.* 1969

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[1] The weight not given by authors and was estimated to be 43 kg for purposes of calculations in table.

TABLE XI

Estimates of VFA and metabolizable energy with respect to the basal metabolic rate in moose, sheep and reindeer

Species, Sex, Age	*Body Wt (kg)*	*Season*	*Diet*	*Conditions*	*Energy Derived from VFA (kcal/day)*	*Theoretical BMR (kcal/day)*	*VFA energy (% of BMR)*	ME *(% of BMR)*	*Reference*
Moose adult cows pregnant n = 4	338	May (1971) Spring	Mixed winter woody browse & new green forage	Free Ranging	5,320	5,505	98	140	Coady & Gasaway, unpubl.
Moose adult cows non-lactating n = 4	430	June (1972) Summer	Green forage	Free Ranging	13,160	6,585 (6,100)	198 (218)	283 (311)	Coady & Gasaway, unpubl.
Moose adult cow lactating n = 3	379	June (1972) Summer	Green forage	Free Ranging	14,660	6,035	243	347	Coady & Gasaway, unpubl.
Moose adult cows non-lactating n = 5	501	October (1972) Early	Woody winter browse	Free Ranging	5,080	7,410 (6,300)	69 (81)	99 (115)	Coady & Gasaway, unpubl.

Domestic sheep ewes n = 6	40		Lucerne Chaff 900 g/day	Penned	1,490	1,110	133	191	Leng & Leonard, 1965
Domestic sheep ewes n = 10	35.5	Growing Season	Grasses	Grazing	1,900	1,020	186	266	Corbett, Leng & Young, 1970
Domestic sheep ewes n = 6	40		Grass Early Stages (high quality)	Penned	1,845	1,110	166	237	Hogan, Weston & Lindsay, 1969
	40		Intermediate		1,525	1,110	137	196	Hogan, Weston & Lindsay, 1969
	40		Mature (poor quality)		855	1,110	77	110	Hogan, Weston & Lindsay, 1969
Domestic sheep ewes n = 9	37.5		Grasses Varying Stages of Maturity	Grazing	1,140	1,06	107	153	Leng, Corbett & Brett, 1968
					990	1,065	93	133	Leng, Corbett & Brett, 1968
Domestic reindeer n = 4	59		Lichens Simulated Winter Diet	Penned	1,075	1,490	72	103	Luick *et al.* 1972
n = 4	53		Commercial Pellets	Penned	765	1,37	56	80	Luick *et al.* 1972
n = 2	105		Commercial Pellets + Straw + Lichens	Penned	2,415	2,295	105	150	Luick *et al.* 1972

[1] Numbers in ( ) are calculated using the estimated lean body weight.

may increase slightly relative to the decreasing lean body weight and BMR.

It may appear that the estimated VFA energy production is insufficient and that maintenance of moose through winter is energetically impossible. However, moose in October derived and estimated 7,300 kcal/day ME from the diet, and an estimated additional 3,900 kcal/day was derived from catabolism of body tissue stores. Therefore, total ME available per day was approximately 11,200 kcal (7,300 + 3,900) or 1.8 × BMR when using the calculated BMR of 6,300 kcal/day. This value, 11,200 kcal, compares closely with the 12,000 kcal ME/day estimate, based on the conversion of VFA into kcal of digestible organic matter using Weston and Hogan's (1968a) data, discussed previously.

The spring greenup appears rapidly during late May in interior Alaska. Within a week, the region where studies by Coady and Gasaway were conducted, turns from a drab brown to a sprakling green and the moose change from a diet of wood forage to lush green foods which are digested more easily. Calories are abundant on the new diet and depleted stores of fat, carbohydrate and protein are rapidly replenished.

Moose collected in May (during the spring transition) in the Tanana Flats were near their annual low body weight. VFA energy at this time amounted to about 98 percent of the BMR, and total VFA production was similar to that during early winter (Table XI). Energy demands at this time were high because of pregnancy which left the cows in a negative energy balance and necessitated a high dependence on catabolism of stored tissues.

By late June, lactating cow moose had gained about 20 kg and VFA energy had increased to 14,700 kcal/day (Table XI). This VFA energy exceeded the BMR (calculated to be 6,035 kcal/day) by about 240 percent (Table XI). Estimated ME is 20,900 kcal/day or 3.5 X BMR, putting the moose into a highly positive caloric balance. The period of weight gain each year was approximately 125 days, and during this time an average of 7,600 kcal per day were put into stored tissue energy.

In late June, non-lactating cow moose were approximately 50 kg heavier than lactating cows, indicating that the cost of pregnancy and lactation is high in terms of potential weight gain. The energy in VFA's produced amounted to about 13,200 kcal/day; thus ME would be approximately 18,800 kcal/day. The lean body mass of non lactating cows is probably slightly greater than that of lactating cows because most of the weight gain is fat. To establish a value for calculation of BMR for nonlactating moose, 15 kg was arbitrarily added to the mean weight of lactating moose. The BMR was then calculated to be 6,100 kcal and VFA energy was 2.2 × BMR and ME was 3.0 × BMR. These values would be less if BMR were calculated using actual body weight, but adjusted weights were considered more representative of energy requirements. Table XI gives values based on actual weights.

Domestic ruminants on open range generally undergo less dramatic changes in seasonal energy balance than some wild ruminants like moose (Table XI. Sheep (*Ovis aries*) did not reach the extremes of negative or positive energy balance seen in moose even when fed very high and low quality forage. Energy balance of free ranging reindeer is probably more like that of moose, but captive reindeer used by luick *et al.* (1972) were in negative balance on all diets tested. These studies were conducted in the winter when intake is lowered which may account for these low energy values. For moose in interior Alaska the seasonal energy picture appears to be feast or famine with little in between.

EFFECTS OF UNDERNUTRITION ON RUMEN FUNCTION

Undernutrition will be considered as reduced caloric intake leading to less than optimal weight gain or weight loss. This definition is broad enough to apply to "normal" winter weight loss, starvation, or even inadequate summer range resulting in reduced fat deposition prior to winter.

During winter, the food intake of moose undergoes a normal decrease, but under certain circumstances intake may be reduced still further. Abnormally deep snow or particularly cold temperatures (−50° C or colder) may decrease food availability by restricting moose mobility.

Decreased food intake lengthens turnover time of rumen contents and decreases rumen fill (Hungate, 1966). Numbers of rumen microorganisms decline as food intake is reduced (Church, 1971) and may drop to very low numbers if inanition is prolonged (Hungate, 1966). Sheep deprived of food for three of four days show marked changes in the composition of bacterial and protozoan populations in the rumen and have reduced digestive capability (Church, 1971). Recent studies by Swope (1972) indicate that starvation in mule deer does not reduce the viability of rumen microbes. Rumen liquor from starved mule deer digested forages about as well as deer on normal rations, and counts of bacteria showed no significant declines during starvation. These results contradict earlier studies on domestic sheep and indicate all species of ruminants may not respond to starvation in similar manners. Hungate (1966) suggests that bacterial populations can remain high in the rumen of starved animals because of reduced saliva flow which cause an increase in rumen turnover time. Bacteria do not leave the rumen as fast and the population remains high. Because the available nutrients in the forage contained in the rumen will eventually become too low to sustain the microbial populations this condition is temporary. The mule deer in Swope's study were starved from 7 to 47 days, which seems too long to sustain normal numbers of viable bacteria yet numbers of bacteria were reported to remain high.

Moose that die from undernutrition in interior Alaska generally have substantial amounts of forage in the rumen. This is a result of consumption of less palatable and digestible browse as well as lengthened turnover time in the rumen. The fact that the digesta found in starving ruminants is large makes the diagnosis of starvation difficult (Hungate, 1966). Hungate suggests the use of VFA concentrations and production rates as indicators of undernutrition. Rumen VFA concentrations are of value only when samples are taken immediately after death. This usually requires that the investigator kill the animal. Although VFA concentrations and production rates are expensive and time consuming to measure, they are relatively conclusive indicators of the animal's nutritional balance at that time.

Summary and conclusions

Seasonal energy requirements of adult moose and ME available for meeting those requirements can be estimated from data presented in Figure 1. Energy required for diverse physiological functions can be described as percent of BMR, where BMR equals $70W^{.75}$ kcal/day. Maintenance energy requirements were considered to remain relatively constant, near 70 percent of BMR, throughout the year. Metabolizable energy requirements for gestation begin to significantly increase in March and reach approximately 100 percent of BMR at term in early June. Metabolizable energy requirements for lactation shortly after birth were approximately 100 percent of BMR. Milk production remains high for a relatively short time, and by August represents a relatively small energy demand. Weight gain by moose in Alaska occurs between late May and late September. Energy available for lactation and weight gain probably averages about 200 percent of BMR throughout the first half of the summer, and then declines as forage quality decreases. However, lactation during early summer significantly reduces the energy available for weight gain.

The quality of foods available to and selected by moose is superior during summer to that consumed in winter based on chemical analysis and rumen fermentation rates. Food consumption data from several studies indicate greater food intake during the plant growing season than during winter. Estimates of food intake that supply the required energy during winter and summer are 4.5 — 5.5 kg and 10 — 12 kg dry weight, respectively. The reduction in winter food consumption results from slower rates of digestion and passage through the gut and probably from a voluntary decrease in food intake as has been observed in other wild ruminants.

Microbial fermentation of plant CHO and protein in the rumen yields VFA. The ME energy in VFA represents about 70 percent of the total ME derived from the diet. Plants in the growing season, particularly immature stages, yielded the highest fermentation rates in the rumen whereas dormant plants and woody browse, being lower in digestible nutrients, resulted in lowest fermentation rates during winter. The total VFA production in moose during summer is nearly three times that of production in winter. Moose undergo greater seasonal variation in the quality of the forage and fermentation rates than do domestic ruminants which have been studied in this manner. The energy derived from rumen fermentation in moose was about 80 percent of the BMR in winter and increased to nearly 250 percent of BMR in summer. Estimated metabolizable energy obtained from forage by moose during winter was only 115 percent of the BMR, where as in summer moose produced up to 350 percent of basal requirements. In late summer and fall the quality of the forage declines until the winter values of fermentation are attained. Lipid and protein stores supply the energy required in winter which is not provided from the dietary sources, thus making ample lipid storage in summer a necessary requirement of annual production.

The quantity or quality of winter browse is occasionally restricted by weather conditions. The effect of reduced intake on rumen function is to lengthen turnover time of rumen contents and decrease rumen fill. Numbers of microorganisms may decline to low numbers if intake remains low for an extended period of time causing a marked reduction in the fermentation rate.

Rumen function studies on wild cervids and bovids will provide comparative information on their seasonal energy balance and status. Ruminants, whether in the tropics, temperate or arctic zone characteristically are exposed to seasonal variation in forage quality. Energy is generally stored as fat and protein during the portion of the year when forage quality is high. Stored fat and protein is catabolized during the remainder of the year when ME is below the maintenance level, and moose are in negative energy balance. The estimated caloric value of VFA produced in the rumen while feeding on the various seasonal diets and subsequent estimates of ME allows for direct comparison of the animals' ability to utilize the forage and derive energy. This provides a clearer understanding of the temporal relationship of the animal to its food resource. Biologists can then recognize the importance of a particular season in relation to others, determine the importance of various foods and determine the duration of seasons based on food utilization and available energy.

Range evaluation techniques can be very time consuming, expensive and often result in information which is difficult to interpret in a usable form. Therefore, the animal utilizing the range may be an alternate evaluator and provide a more direct and sensitive indicator of range quality provided techniques can be developed to measure physiological changes in the animal. While digestive performance of moose on summer and winter range show striking differences, only subtle differences may exist among moose ranges when compared during the same season. A system using digestive information to compare various ranges could include estimates of VFA production rates, energy derived from fermentation and ME, food consumption, digestibility of forage and chemical and botanical composition of rumen contents. Data obtained from this method, especially when used in conjunction with other techniques, may provide a useful means of comparing ranges and the nutritional status of the animals.

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