THERMOREGULATORY AND BEHAVIORAL RESPONSE OF MOOSE: IS LARGE BODY SIZE AN ADAPTATION OR CONSTRAINT?

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ABSTRACT: The basis of the "Bell-Jarman Principle" is that body size of ruminants is related to both food requirements and digestive capacity. Large herbivores require greater absolute quantities of forage than smaller ones. But smaller herbivores have higher maintenance costs and require higher quality food. Trade-offs between time-energy constraints and food acquisition determine the limitations of each herbivore. The moose (*Alces alces*) is a particularly interesting herbivore because it is an apparent exception to the "Bell-Jarman Principle". Numerous bioenergetic, digestive, and morphological forces have shaped the adaptive specializations of moose. The large body size is an adaptation to travel through deep snow, to minimize heat loss in seasonal northern environments, and perhaps to minimize predation. The large body size and effective insulation make the moose extremely cold tolerant by conserving heat and reducing energy requirements during harsh weather. Warm environments favor smaller cervids such as white-tailed deer (*Odocoileus virginianus*) which dissipate heat rapidly. Heat loading in moose occurs at relatively low ambient temperatures in both winter and summer. The simulation model in this paper summarizes work on bioenergetic, behavior, and digestion in moose. Behavioral patterns were predicted favorably. High temperatures result in a preemption of feeding and a loss of potential energy that could not be recovered the subsequent day. It appears that the enigmatic moose is pressured by the "Bell-Jarman Principle" to remain smaller on an energetic basis, however, other forces require the largest size possible and more precarious budgets.

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Both food requirements and digestive capacities of ruminants scale allometrically. Energy requirements are proportional to metabolic weight ($W^{0.75}$) (Kleiber 1975) whereas digestive capacity scales isometrically ($W^{1.0}$) (Van Soest 1982). This confers on small selective feeders a penalty of high maintenance costs per unit of body weight but limited digesta storage capabilities (Parra 1978, Demment and Van Soest 1985). This may explain why roughage-feeders are often large but, of course, not why concentrate selectors tend to be small. This pattern has been explained by relative absolute feed requirements to potential feeding rates and is related to the distribution and abundance of high and low quality plants. In many environments, nutritious forbs and shrubs are simply more widely scattered and of lower biomass than low quality grasses.

Nutrient requirements of browsers are met through selection of concentrated nutrients in fruits, foliage, and forbs which may have higher rates of passage (Hofmann 1985). Alternatively, grazers with a large body size, such as bison (*Bison bison*) have lower metabolic requirements per unit of body weight and can tolerate the more fibrous diets of slowly digesting grasses. However, the greater absolute requirements of large body size obviates highly selective feeding (Hanley 1982).

Large size is a common characteristic of ruminants which exploit open environments with more abundant, but lower quality food resources (for example, grasslands). Evolution of this trait was probably shaped by a need to reduce the risk of predation, enhance mating opportunities, and increase mobility of the species in the absence of cover (Hudson 1985). Accordingly, a relationship also exists between body size, habitat characteristics, and food habitats. Ruminants with large body size require large absolute amounts of food and are normally constrained by the time required to search for large quantities of rare foods which would limit their ability to consume sufficient quantities. Consequently, trade-offs between time-energy constraints and food acquisition will determine the limitations of each ruminant (Hanley 1982).

These relationships collectively have been called the "Bell-Jarman Principle" in reference to pioneering work in East Africa (Bell 1969, 1971, Jarman and Jarman 1974). For the past 20 years, the principle has guided research on nutritional ecology and evolution (Geist 1987a, b, Gutherie 1984), simulating studies of energy expenditures (Hudson and White 1985a), digestive anatomy/physiology (Langer 1988, Hofmann 1989), and foraging behavior (Belovsky 1981, Illius and Gordon 1987, Gordon and Illius 1988, Wickstrom *et al.* 1985, Berger and Cunningham 1988).

The giraffe (*Giraffe* spp.) (world's largest ruminant) and the moose (*Alces alces*) (world's largest cervid) appear to be exceptions to the general relationship between diet and body size. The most likely explanation is that both large browsers use a forage resource which, although of average biomass, is highly clumped so high feeding efficiency is possible (e.g. Astrom *et al.* 1990). For the giraffe, these clumps are mainly individual *Acacia* spp., *Grewia* sp., *Balanites* sp., and *Ziziphus* sp. trees and shrubs that provide new shoots that are selected in relation to availability and seasonal quality (Sinclair 1979, Pellew 1984). For the moose, they are riparian *Salix* spp. stands throughout much of their range (Risenhoover 1985), patches of aspen (*Populus tremuloides*) in central Alberta, Canada (Renecker 1987), or combinations of paper birch (*Betula papyrifera*) and aspen in the Kenai Peninsula, Alaska (Oldemeyer *et al.* 1977). But other factors also may determine optimal body size including population dynamics (Western 1979), social dominance (Geist and Bayer 1988), mobility (Pennicuik 1979), predation (Hennemann 1983), snow cover (Telfer and Kelsall 1984), and thermal environment (Parker and Robbins 1984, 1985), all of which have seasonal dimensions.

Although a great deal can be learned from allometry of various physical, physiological, and ecological traits, questions of optimal body size and patterns of behavior can be addressed by finer-grained analysis (Belovsky 1986, Reiss 1986). Of particular significance are activity budgets with which animals adapt to seasonally-changing environments. They optimize trade-offs between searching and foraging time in terms of foraging efficiency, activity patterns, and habitat selection.

THE ENIGMATIC MOOSE

Moose are a particularly interesting species because they apparently violate the "Bell-Jarman Principle" in terms of body size and foraging strategy. It is surprising to find a large ruminant species aligned along the relatively selective gradient of a browser in northern latitudes where forage resources are limited and the seasonal growth pulse is short. Although their large body size can clearly be considered an advantage in terms of cold tolerance, ability to cope with deep snow, and defend themselves against wolves (White *et al.* 1987), large body size may create a precarious energy budget. The success of moose may be linked to their ability to harvest forage efficiently and selectively, however, foraging time is a function of both energy demands and environmental constraints.

ENVIRONMENT

A number of climatic factors influence the boreal environments but snow and temperature are paramount during winter when conditions are harsh and cold. In montane environments, throughout western North America, temperatures frequently fluctuate from below -30°C to above 0°C as a result of short-lived moderating weather conditions. Similar moderating weather is often experienced in other northern environments during winter.

Summers are brief, but daily temperatures are warm. In the boreal forest, cooler microclimates can be afforded under the closed canopy of the boreal forest, wetlands, and aquatic regions to relieve animals from discomfort of extreme heat. Daytime ambient temperatures can exceed 30°C.

Our approach to evaluating bioenergetic adaptations of moose has been to evaluate components of the time-energy budget on a seasonal basis (Hubbert 1987, Regelin *et al.* 1985, Renecker and Hudson 1985, 1986a,b, 1988, 1989a, b, 1990a, b, Renecker 1987, Risenhoover 1986, Schwartz *et al.* 1988a, b, Van Ballenberghe and Miquelle 1990). In this paper, we present a simple model of daily behavior and energy exchanges of moose on typical summer and winter days. We adopted the simulation approach as a summary of our work over the previous six years rather than a test of hypothesis. Our interest was to illustrate the degree to which diel feeding cycles were determined by: a) digestive repletion-depletion cycles; and b) thermal environment.

MODEL

Using the Stella™ continuous simulation package, the model was constructed with three main conservative subsystems: one describing the gut dry matter pool, one monitoring the pool of surplus metabolizable energy, and another accumulating time spent feeding. Controlling rates, auxiliary variables and their interrelationships are presented schematically (Fig. 1). Simulation length was set at 48-hr to obtain 2-day averages, rates were expressed on a hourly basis, and the time step was set at 0.25 hr. Parameters used for winter and summer simulations are compared (Table 1).

Foraging Behavior

Foraging behavior provided the major tracking variables for comparison with empirical observations on free-ranging moose. Total grazing time (TGRAZ, in hr)was accumulated for a daily total (TGRAZ). Dry matter intake (DMI, g/hr) was modelled as the most limiting of three hierarchical constraints: metabolic demand, digestive fill, and foraging logistics. In the absence of precise information, we used our general impression that thermal stress preempted feeding when ambient temperatures rose above 0°C in winter and 22°C in summer (Renecker and Hudson 1986a, 1990b).

Metabolic Demand

We assumed that moose eat to meet their

Table 1. Parameters used for summer and winter simulations.

	Winter	Summer	Source
Body weight (kg)	300	300	
Maximum daily temperature (°C)	-10	22	
Minimum daily temperature (°C)	-25	15	
Forage biomass (kg/ha)	450	2000	Renecker and Hudson 1986b
Initial rumen dry matter (g/kg BW)	13.6	11.2	Renecker and Hudson 1990a
Asymptotic digestibility (%)	48	58	Renecker and Hudson 1990a
Passage rate (fraction/hr)	0.05	0.07	Renecker and Hudson 1990a
Digestion rate (fraction/hr)	0.05	0.08	Renecker and Hudson 1990a
Upper critical temp. (°C)	5	15	Renecker and Hudson 1986a, 1990b
Maximum feeding rate (g/min)	11	23	Renecker and Hudson 1986b
Biomass at 50% feeding rate (kg/ha)	200	500	Renecker and Hudson 1986b

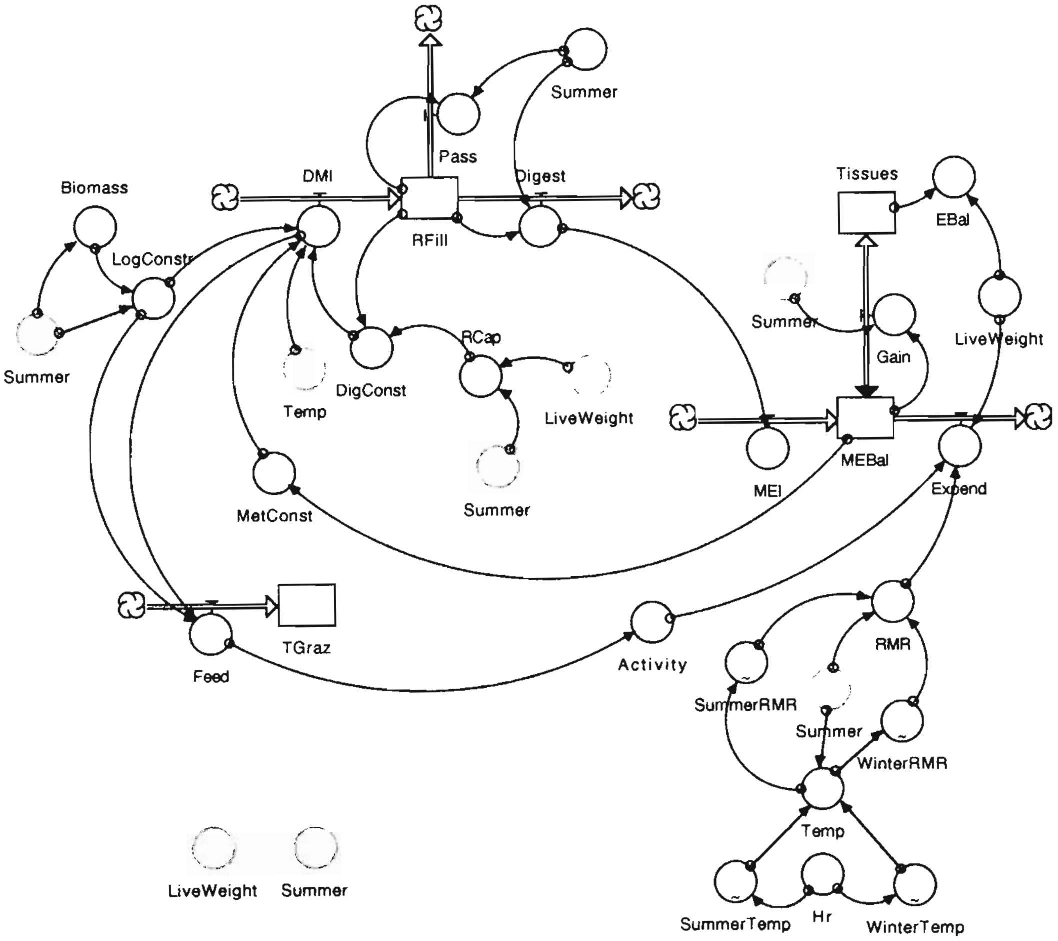

Fig. 1. Model of activities and energetics of moose, where, Feed = feeding rate; Feed Bout = feeding bout; LogConstr = logistical constraints; MetConstr = metabolic constraints; DigConstr = digestive constraints; DMI = dry matter intake; Pass = passage rate; Digest = digestion rate; RFill = rumen fill; MEI = metabolizable energy intake; MEBAL = surplus metabolizable energy; Expend = energy expenditures; RMR = resting metabolic rate; Temp = ambient temperature; and Hr = hour of the day; TGRAZ = cumulative time spent feeding.

needs for maintenance, thermoregulation, activity, and productive functions (growth in this example). Thus, when the pool of surplus metabolizable energy (ME) was positive, the animal was considered satiated, otherwise the animal tried to make up the shortfall by feeding. Although given units of energy, ME can be thought of as the concentration of metabolites involved in metabolic regulation of feed intake.

Resting metabolic rate was calculated from ambient temperature using curves for winter and summer in Renecker and Hudson (1986a). Thermoneutral basal metabolic rate was 16 kJ/W$^{0.75}$/hr throughout the year but rose exponentially above the upper critical temperature of 0°C in winter and 15°C in summer. The lower critical temperature of moose (Renecker *et al* 1978, Renecker and Hudson 1986a) is below that usually encountered (< 30°C) near Edmonton where the experimental work was conducted.

Only two active states (resting and feeding) were considered since they normally account for up to 90% of the daily energy budget (Risenhoover 1987, Renecker and Hudson 1989a, Van Ballenberghe and Miquelle 1990). Costs of feeding were taken as 1.18 times the resting metabolic rate (Renecker and Hudson 1989b).

Seasonal demands for growth (or reproduction) were set at zero for the winter simulation and 1,500 kJ/hr for summer assuming a target growth rate of 1 kg/d, an equal proportion of lean and fat tissue, and an efficiency of ME coversion for growth of 0.45 (ARC 1980).

The pool of surplus metabolizable energy was replenished with digested dry matter (*vide infra*), assuming a ME content of 18.6 kJ/g (Hudson and White 1985b).

Digestive Fill

Gut fill is considered a major constraint on food intake of ruminants although there is some debate about whether dry matter or fresh weight is most important (Hobbs 1990). We have taken Hobbs recommendation and used dry matter.

The dry matter pool (RFILL) is incremented by dry matter intake (DMI) and depleted by the competitive process of passage (PASS) and digestion (DIGEST). Initial rumen pool size and rate constants for passage of digesta were taken from Renecker and Hudson (1990a). Winter values were for an aspen (*Populus tremuloides*) browse/alfalfa (*Medicago sativa*) diet and summer values were for an aspen foliage/alfalfa diet.

The impulse to feed was considered proportional to the disparity between gut fill and gut capacity (RCAP), which was considered to be the dry matter content determined in moose on seasonal diets (Renecker and Hudson 1990a). However, since ruminants organize activities into discrete bouts rather than continuously "topping-up", we introduced a time lag for this feedback signal.

Logistics of Feeding

The final constraint on feeding rate was imposed by the biomass, structure, and perhaps quality of forages. Estimates of maximum feeding rates (MAXRATE) and forage biomass at which feeding rates were reduced 50% (BIOM50) were taken from Renecker and Hudson (1986b) using the following relationship for saturation kinetics:

$$Y\ (g/min) = MAXRATE \times BIOMASS/(BIOM50 + BIOMASS).$$

Seasonal parameters were taken from July when moose strip foliage and in January when the diet is largely of browse.

RESULTS

Seasonal Diel Patterns

Undisturbed free-ranging moose in the aspen-dominated boreal forest of western Canada, show marked seasonal cycles of time spent ruminating but, surprisingly, not time spent feeding, which varied little from 10 hr/day (Fig. 2). They organize feeding time into about 5 bouts/day without any apparent

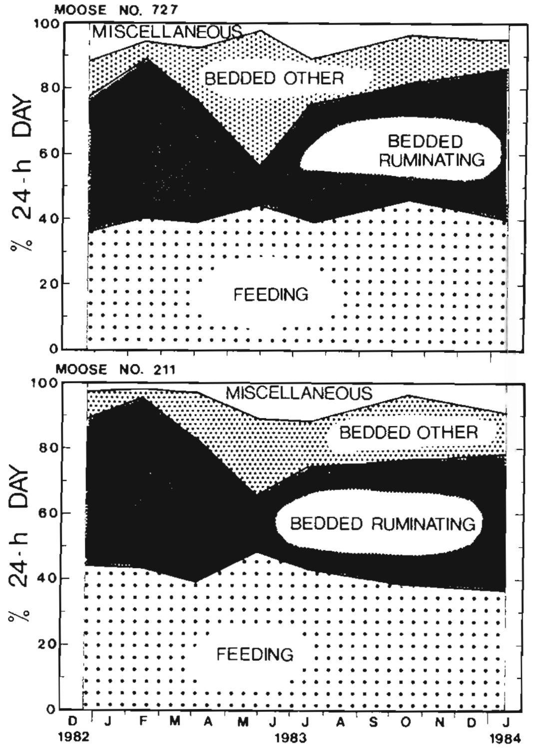

Fig. 2. Seasonal activity budgets of two free-ranging moose cows in the aspen-dominated boreal forest, central Alberta.

synchrony with daylight (Fig. 3). In contrast, Van Ballenberghe and Miquelle (1990) observed a change in daily summer feeding time of moose in Interior Alaska that varied from about 6.2 hr in early May to 9.5 hr in July. In the same Alaska study area, Risenhoover (1986) recorded an average daily feeding time of 4.9 hr for moose during winter.

Simulated activity patterns for winter and summer days reproduced observed patterns faithfully (Fig. 4). Total time spent feeding approached 12 hr in winter and 11 hr in summer for model 350 kg non-pregnant moose cows.

The tendency of model moose to feed more often in summer for digestive and metabolic reasons was countered by suppression of feeding during the heat of the day. Feeding bouts in winter tended to be longer than in summer, presumably because of lower feeding rates. These seasonal values averaged 107 min/bout recorded for real moose (Renecker and Hudson 1989a).

Sensitivity

Activity and energy budgets of moose are influenced by ambient temperature, forage biomass, and forage quality. Ambient temperature, specifically heat stress, reduces dry matter intake and increases energy expenditures (Renecker and Hudson 1990b). Although the relationship between heat load and suppression of feeding has not been precisely quantified, available information used in our model implied that a diet/temperature profile which reduced feeding to 6 hr/day, when followed by a cool day, would increase feeding time to over 12 hr/day the next diel cycle (Fig. 5). The energy deficit of 34 MJ which accumulated on the first day increased further to only 38 MJ by the end of the second.

We also explored the sensitivity of moose to forage biomass (Fig. 6). A 300 kg model moose in a thermal neutral environment was relatively unresponsive to change in forage biomass ranging from 500 to 2,500 kg/ha. However, below 500 kg/ha, foraging times had to increase dramatically and energy balance declined sharply. Since preemption of feeding by other activities seems to limit feeding to about 13 hr/day, the energy budget apparently became precarious at this level.

Energy balance was even more strongly influenced by forage quality measured as fractional rates of passage and digestion (Fig. 6). Since digestion rates are about 65% of fractional passage rates in moose on winter and summer forages (Renecker and Hudson 1990a), we examined simultaneous changes in both. For a 300 kg model moose, energy balance increased from -35 $kJ/W^{0.75}$ at values typical for winter forages to about 20 $kJ/W^{0.75}$ for typical summer forages. Over the same range, predicted feeding times declined slightly from 14 to 13 hr/day.

Consequences of Body Size

Although the model does not consider possible effects of body size on feeding efficiency and thermoregulation, the consequence of size on the interactions of metabolic requirements and digestive capacity can be explored (Fig. 7). The model predicted negative energy balance for moose of any size, but indicated an energy optimum weight of 350 kg. The energetic penalty at higher weights is underestimated since moose do not increase feeding times to such levels.

On cool summer days, moose of all weights maintained positive energy balance with a relatively short feeding time but the greatest advantage accrued to smaller-bodied moose. Heat stress forced the energy budget strongly negative largely by increasing energy expenditures. Although temperatures preempted midday feeding bouts compensation at other times of the day was possible under the combination of conditions used in this analysis. Although small moose enjoyed the greatest energetic advantage on both hot and cool summer days, the interaction of metabolic, digestive, and logistic constraints created particularly unfavorable energy balance for moose weighing about 450 kg.

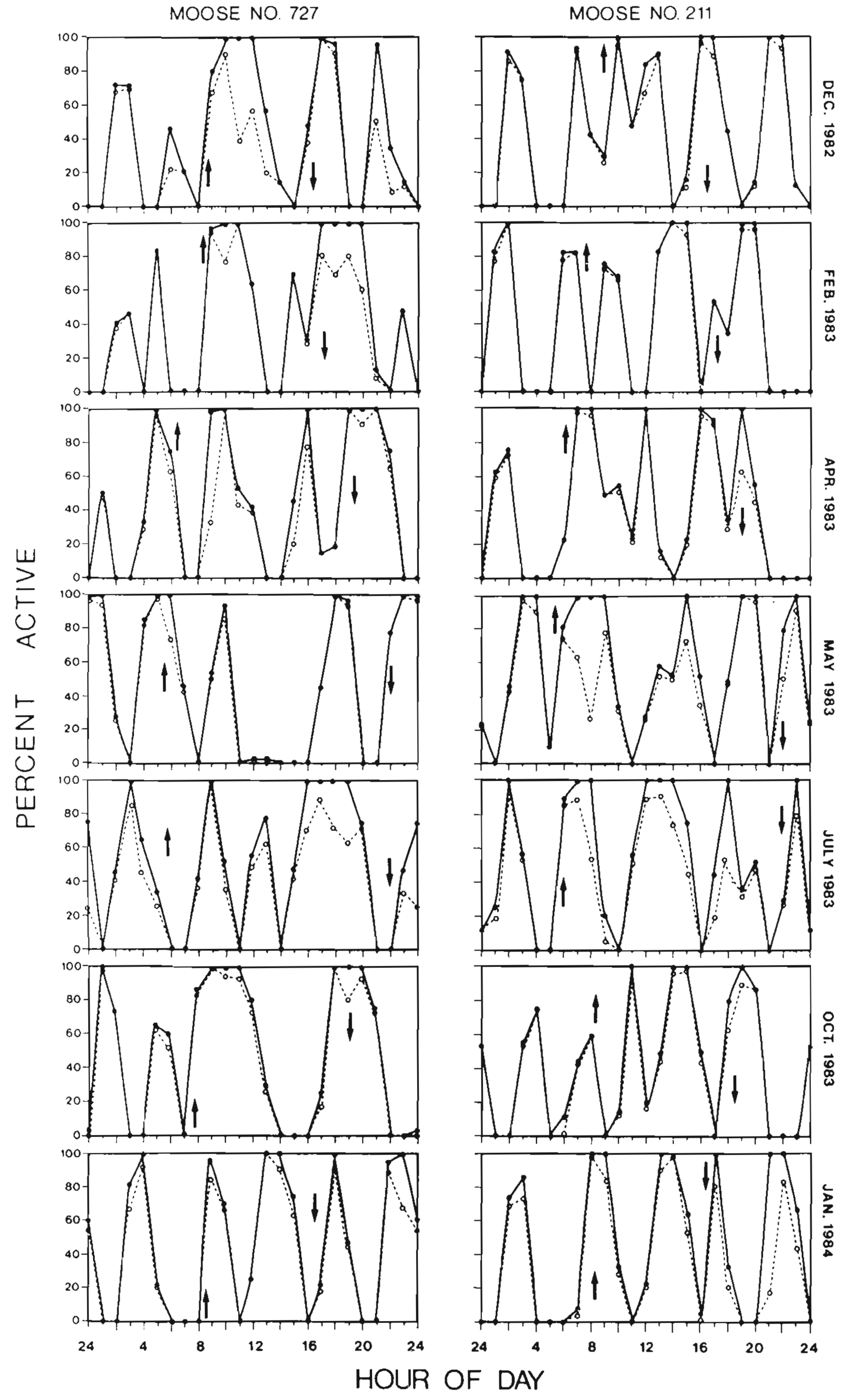

Fig. 3. Diel activity patterns of two free-ranging moose cows in the aspen-dominated boreal forest, central Alberta. Solid and broken lines indicate total active and feeding times, respectively. Upward and downward arrows indicate sunrise and sunset, respectively.

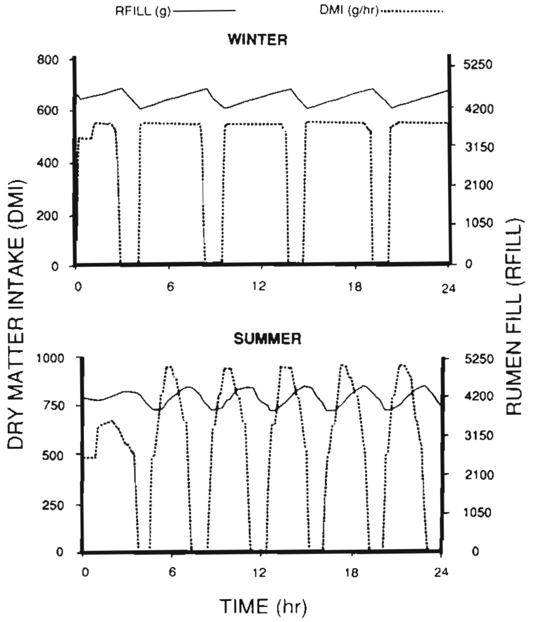

Fig. 4. Predicted activity bouts of moose in winter (top) and summer (below) where, RFILL is rumen fill and DMI is dry matter intake.

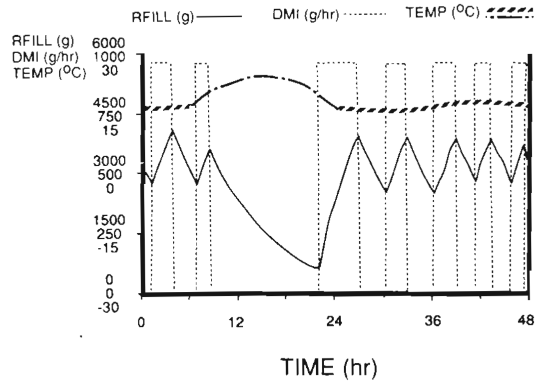

Fig. 5. Compensation of feeding time in moose following preemption of feeding by hot weather (RFILL = rumen fill; DMI = dry matter intake; TEMP = ambient temperature in °C).

DISCUSSION

Although the activities of ruminants are largely directed to forage acquisition, they must satisfy their nutritional needs within the constraints of security, thermal comfort, and social obligations. Animals are faced with optimizing trade-offs related to habitat and food selection, and daily budgets. In this paper, we examined constraints operating on daily activity and energy budgets in an attempt to unravel the day to day trade-offs and understand the energetic implications of resource-use behavior.

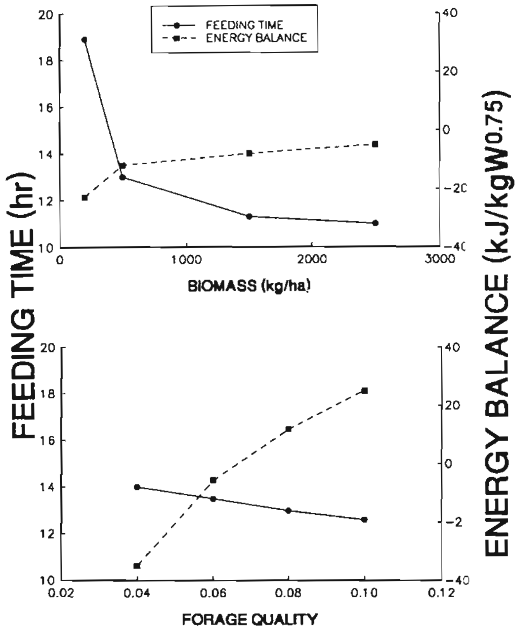

Fig. 6. Daily feeding time (hr) and energy balance (kJ/$W^{0.75}$) of a 300 kg moose in relation to forage biomass (top) and forage quality measured at hourly fractional passage rate (below).

There is little doubt that the larger body size of a moose and other large northern ungulates is favored in cold boreal environments (Irving 1966, Parker and Robbins 1985, Renecker *et al.* 1978, Renecker and Hudson 1986a,). Large runimants, such as moose, minimize heat loss by the low surface area to volume ratios. Due to a larger relative surface area, smaller ungulates, such as deer, disipate heat more rapidly than the larger moose who faces substantial effects of heat loading because of body size. Warm temperatures influence thermoregulatory mechanisms of moose and can tax respiratory cooling in all seasons (Renecker and Hudson 1986a, 1989b, 1990b, Welch 1988). Heat stress leads to higher energy expenditures (Renecker and Hudson 1986a) and suppression of activity (Renecker and Hudson 1989b,1990b). In attempt to

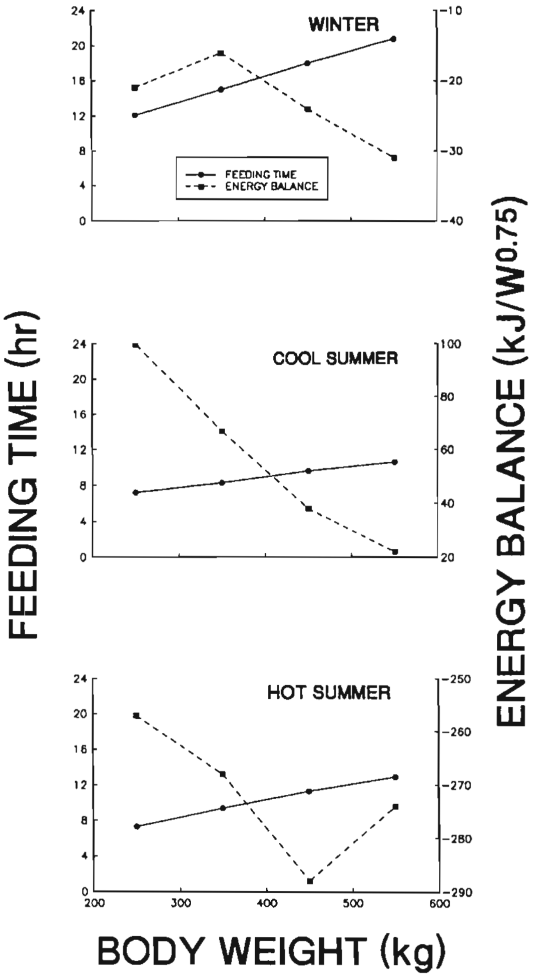

Fig. 7. Daily feeding time (hr) and energy balance (kJ/W$^{0.75}$) in relation to body size of model moose in winter and on cool or hot summer days.

balance these higher expenditures, moose must make decisions and balance trade-offs between the need to feed and thermoregulate.

On the basis of the relationship between metabolic requirements (W$^{0.75}$) and body weight, moose appear to be energetically as large in body size as possible rather than striving for an energetic optimum. It would appear that the "Bell-Jarman Principle" is not place and functional in morphological development of the moose. However, predictions from our model suggest that there may be an attempt by the selection forces of bioenergetics and foraging behavior to hold back the size of moose. But moose probably must strive to become as large as possible to withstand other forces, such as predators, cold, snow, etc. and to ensure the social commitments of mating occur within a narrow window of their temperate environment.

The daily energy cycle of moose appears adequately explained by the interplay of three hierarchical constraints: rumen repletion-depletion cycles, metabolic demands, and logistics of feeding. Thermal stress and security are additional but as yet poorly defined factors in some environments.

High ambient temperatures appear to influence the "decision rules" of moose and may drive them to either choose open, aquatic habitats or suppress of feeding activity. In wetlands, foraging returns may be lower in terms of quality in comparison to other habitats, however, this strategy may allow moose to tolerate greater extremes in ambient temperature and thereby increase their energy economy. It also appears that when feeding activity is suppressed there are potentially critical implications on the precarious energy budget of the moose.

In summer, moose balance energy costs of foraging during periods of high temperature by choice of open acquatic habitats (Flook 1955, Knorre 1959, Kelsall and Telfer 1974, Telfer 1984, Renecker and Hudson 1989b, Renecker and Hudson 1990b). Forage returns in these habitats may be lower relative to other habitats (Renecker 1987, Renecker and Hudson 1988), however, wetlands or cool valleys (Telfer 1988) allow moose to tolerate high extremes in ambient temperature and thereby increase their energy economy. It appears, that apportioned time to a habitat is strongly influenced by thermal environments. This is an important criteria for moose managers to consider when critical habitat requirements are defined and the consequences of alteration of food and cover are considered. Management decisions must consider both the need for thermal cover to shelter moose from extreme cold but must acknowledge and implement a plan to provide suitable habitat to buffer heat loading both in summer and winter. On the basis of this theoretical assumption, it appears that apportioned time to habitat use by this large northern browser is strongly influenced by thermal environments.

We do not have information on the effects of size on thermal insulation, energy costs of locomotion in snow, nor feeding efficiency. However, on the basis of differential scaling of metabolic rate and digestive capacity, we can predict that, in the face of logistic constraints on foraging, large body size implies longer feeding times and more precarious energy budgets for northern browsers. This is contrary to the benefits of large size purported for efficient grazers with an abundant low quality forage resource.

The theory known as the "Bell-Jarman Principle" has been proposed to explain how body size effects social behavior and diet selection in ruminant species (Bell 1969, 1971, Jarman 1974). While it explains distributions in ruminant body size relative to available forage resources, it fails to clearly explain exceptions. For example, the reedbuck (*Redunca* spp.) and sheep (*Ovis aries*) are small in body size, yet are not especially selective for high quality forage (Hudson 1985). Conversely, two extremely large ruminants, the giraffe and moose, have adapted to niche of the concentrate selector. It is evident that for the giraffe and moose to exist, food resources must be clumped. In such a case, long legs facilitate travel through the niche in search of new patches of browse which may be widely dispersed. Although the "Bell-Jarman Principle" is justifiable in most instances and has been argued by others (Geist 1974), it is a generalization which oversimplifies and fails to explain many of the exceptions, such as the large browser, the moose.

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