PHYSIOLOGICAL AND NUTRITIONAL ADAPTATIONS OF MOOSE TO NORTHERN ENVIRONMENTS

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ABSTRACT: Moose (*Alces alces*) exploit the boreal forest where food resources have high nutritive value during brief summers, and low quality and availability during long winters. To accommodate to this fluctuating environment, moose store large quantities of fat during summer and fall which helps to offset their winter energy deficit. Annual rhythms are keyed to this cycle. Intake rates vary seasonally and correspond with nutrient quality and forage availability. Moose are hyperphagic in summer and reduce food intake during winter. Activity budgets vary among environments and seasons with foraging and resting/ruminating occupying most of their time. Metabolism follows a circannual cycle that peaks in mid-summer with a nadir in late-winter; peak metabolism corresponds to maximum energy intake and storage. Moose are classified as seasonally adaptable concentrate selectors that choose a diet primarily of browse foliage and twigs. This diet is high in lignin as well as readily digestible nutrients. Energy and protein requirements are similar to other cervidae. Body composition, like metabolism and intake, is dynamic seasonally. Nutritional adaptations stabilize energy balance and allow moose to withstand energy shortages in a fluctuating environment.

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The ultimate goal of any wild ruminant is to efficiently acquire energy from a dynamic environment and maintain productivity. However, needs for food are often at odds with requirements for security, thermoregulation, and mating. There are over 176 species (Morris 1965) of extant ruminants inhabiting most biomes in the world. Although the distribution of these mammals is largely constrained by climate and vegetation, physiological adaptations play a major role. Ruminants possess a vast array of morphological, physiological, and behavioral adaptations which makes each species efficient at capturing and processing energy. Understanding how ruminants balance energy flows helps unravel trophic strategies.

Moose are the largest cervid (Peterson 1952) and generally the most abundant wild ruminant of the extensive boreal forests of North America, the Soviet Union, and Scandinavia (Flerov, 1952, Peterson 1955, Danilov 1987). Moose possess a unique set of ecological and physiological adaptations which allow them to successfully occupy one of the coldest regions on earth.

The International Moose Symposia have served as a forum for information exchange between moose biologist throughout the world. A major function of each conference includes invited reviews of selected topics about moose; this paper is a review of moose nutrition and physiology. Gasaway and Coady (1974) presented the first of such reviews at the symposium held in Quebec City in 1973. By necessity, much of their review contained information gathered on other ruminant species, primarily domestic livestock; existing information about moose nutrition was very limited. Schwartz *et al.* (1987*c*) presented the 2nd review at the symposium held in Uppsala, Sweden in 1984. Their review reflected the dramatic increase in the information base about the nutritional requirements of moose. It has been 6 years since Schwartz *et al.* (1987*c*) prepared their review, and the extent of our knowledge about moose nutrition has advanced. I will synthesize much of the information about moose nutrition and use these data to show how moose flourish in the northern environment.

Diet Choices and Diversity

There is a great diversity in plant species eaten by moose through their circumpolar range (Peek 1974, Bergstrom and Hjeljord 1987, Eastman and Ritcey 1987, Joyal 1987, Kuznetsov 1987, Lavsund 1987, Thompson and Euler 1987) but these species do possess one common attribute. Food habits studies clearly demonstrate that moose choose diets primarily of leaves and/or stems of woody vegetation (Table 1). Except for aquatic plants and forbs in summer diets, deciduous or coniferous browse in the form of twigs and leaves represents almost 100% of the diet in winter and >60% in spring and summer. Grasses rarely comprise more than 1% of the diet.

Moose diets in specific areas are not diverse; most studies indicate that >90% of diet contains fewer than 7 different plant species (Table 1). Similarly, the number of plant species comprising at least 5% of the diet rarely exceeds 7. Grasses and sedges, although available in most habitats are seldom consumed during seasons other than spring when their nutrient content and digestibility are high (Peek 1974). Only 1 study in spring (Houston 1968) and 2 studies in summer (Houston 1968, LeResche and Davis 1973) documented grasses comprising >1% of the diet (Table 1).

Food Availability

Abundance of moose foods (generally measured as current annual growth) varies seasonally and among habitats (Table 2). For example, in Quebec, estimates of forage biomass ($\bar{x}$ = 73-321 kg/ha) in summer varied among years and forest types; winter forage averaged only about 20% of summer biomass (Crete and Jordan 1982). In the aspen (*Populus tremuloides*) dominated forest of Alberta, browse biomass ranged from 530-2,230 kg/ha in summer to 17-105 kg/ha during winter in different forest type (Renecker 1987). Winter biomass averaged 33% of summer estimates. Risenhoover (1987) measured woody plant biomass in various habitats in both Isle Royale National Park and Denali National Park, during winter. Estimates ranged from 16-266 kg/ha at Isle Royale and 23-222 kg/ha in Denali. Biomass estimates varied with habitats; riparian willow (*Salix* spp) was most productive, whereas an old burn was least productive.

Forage biomass also varies with seral age of forests. Parker and Morton (1978) demonstrated that in Newfoundland woody biomass (primarily balsam fir) increased from around 200 kg/ha in 2 year old clearcuts to over 2,000 kg/ha by 8 years where it peaked and gradually declined. On the Kenai Peninsula, Alaska, important browse species (mainly paper birch [*Betula papyrifera*], but some aspen and willow) tend to peak about 15 years after a fire (Spencer and Hakala 1964). Oldemeyer and Regelin (1987) estimated the biomass of important browse species in seral stands of forest. Browse production measured at 3, 10, 30, and 90 years post burn were at 37, 1399, 397, and 4 kg/ha, respectively. Similarly, in interior Alaska, aspen forage was most abundant 1-5 years post burn (198 kg/ha in 1-year old stand), whereas birch (167 kg/ha in 11 year old stand) and willow (66 kg/ha in 16 year old stands) provided the most browse 10-16 years post burn (Wolf and Zasada 1979) in winter. Stands >25 years of age generally had <10 kg/ha of forage. Moose density is often associated with food abundance (Eastman and Ritcey 1987, Joyal 1987, Oldemeyer and Regelin 1987, Thompson and Euler 1987, Schwartz *et al.* 1989), unless other forms of mortality (i.e., hunting, predation, disease and parasites) limit density.

Diet Quality

The nutritional quality of moose diets varies seasonally, but in general, spring and summer diets are 1.5 to 3 times more nutritious than winter diets (Table 3), depending upon which constituent is examined. Summer diets

Table 1. Percentage of the major food classes consumed by moose by season in North America.

Winter					Spring					Summer/fall						
% browse	% forbs	% grass	90% diet[a]	>5% diet[a]	% browse	% forbs	% grass	90% diet[a]	>5% diet[a]	% browse	% forbs	% grass	90% diet[a]	>5% diet[a]	Reference	Location
99	<1	<1			55	34	11			79	17	4			Houston (1968)	Wyoming
100	0	0	2-4[b]	2-4											Harry (1957)	Wyoming
100	0	0	1-3[c]	2-4											Spencer and Chatelain (1953)	Alaska
100	0	0	1												Wilson (1971)	Utah
100	0	0	6-7[d]	4-6											Thompson and Vukelich (1981)	Ontario
100	0	0	11-18[e]	6-7											Krefting (1951)	Michigan
100	0	0	3	2	89	5	<1	5	5	90	8	<1[f]	4	4	Regelin *et al.* (1987)	Alaska
100	0	0	2-5[g]	2-5											Risenhoover (1989)	Alaska
99	<1	<1	5[h]	5	99	<1	<1	5[h]	5	73	26	<1	4[h]	4	Renecker (1987)	Alberta
100	0	0	2	2						61	25	7	4[i]		LeResche and Davis (1973)	Alaska
99	1	0	9	9	94	6	<1	10	6	88	11	<1	7[j]	7	Stevens (1970)	Montana
100	0	0	4	5											Barrett (1972)	Alberta
97[k]	3	0	4	3						29	71	<1	3[k]	3	Knowlton (1960)	Montana
100	0	0	5	5						100	0[l]	0	2	3	Joyal (1976)	Quebec
100	01	0	2	3											Joyal and Scherrer (1974, 1976)	Quebec
99	<1[m]	0	6	7											Zach *et al.* (1982)	Manitoba
100	0	0	3	3											Ludewig and Bowyer (1985)	Maine
100	0	0	6-7												Risenhoover (1987)	Michigan

[a] The number of species comprising >90% diet, or the number of species which represented at least 5% of the diet.

[b] Three techniques were used to determine food habits. Stomach analysis and tracking indicated 2 species, while direct observations indicated 4 species made up >90% diet, respectively

[c] Winter diets from 3 different areas are listed. Three species predominated in diets from Kasilof, 2 species from Kenai, and the Chickaloon Bay area, and only one species from the 1947 burn.

[d] Winter diets were listed for both early and late winter.

[e] Winter foods were listed for 3 different years, 1945, 1948, and 1950.

[f] Summer diets were listed for July-August and September. July-August diets were data from LeResche and Davis (1973), which are listed separately here. Therefore summer diets listed for Regelin *et al.* (1987) are September diets only.

[g] Food habits were listed for 7 different habitats.

[h] Food habits were presented for 2 moose during winter (Dec, Jan, and Feb). I combined all the data into a single unweighted estimate for winter. Leaf litter comprised 26.5% of this winter diet. Spring diets were from April and May; bark and leaf litter made up 19 and 20% of the diet, respectively. Summer diets were from July: cattail comprised >95% of the forbs consumed.

[i] Lowbush cranberry (*Vaccinium vitis-idaea*) comprised 21 and 51% of the browse from normal and depleted ranges. There were 25 different forbs eaten in summer, but only 2 were of eaten in major quantities.

[j] Diets were October and November.

[k] Early winter diets are presented. Late winter diets were 100% browse. Summer diets are presented. Fall diets were comprised of 92% browse, 7% forbs, and 1% grass.

[l] Diets were determined by browse surveys; aquatic plants eaten were not listed as part of the diet. Moose spent an average of 54 + 18 minutes feeding on aquatic plants between June and August.

[m] Winter diets contained 0.4% "other" items, I listed them as forbs, although some were undoubtly browse

Table 2. Biomass estimates of moose forages in North America.

Habitat type	Biomass estimate (kg/ha) summer	winter	Location	Comments	Reference
Tolerant hardwoods	217-321	49- 89	Quebec	1977 data, heavy and light hunting	Crête and Jordan (1982)
Open forest	73-289	19-242	Quebec	1978-79 data, heavy and light hunting blocks	Crête and Jordan (1982)
Intolerant hardwoods open forest	237-289	58-72	Quebec	1977 data, heavy and light hunting blocks	Crête and Jordan (1982)
Tolerant hardwoods closed forest	117-248	24-99	Quebec	1978-79 data, heavy and light hunting blocks	Crête and Jordan (1982)
Intolerant hardwoods closed forest	78-202	152-28	Quebec	1977-79 data, heavy and light hunting blocks	Crête and Jordan (1982)
Decidious -maple		16	Isle Royale	SE ± 2	Risenhoover (1987)
Deciduous-aspen		94	Isle Royale	SE ± 24	Risenhoover (1987)
1936 burn		3	Isle Royale	SE ± 0.4	Risenhoover (1987)
Mixed forest		72	Isle Royale	SE ± 6	Risenhoover (1987)
Coniferous forest		266	Isle Royale	SE ± 30	Risenhoover (1987)
Spruce		23	Denali	SE ± 9	Risenhoover (1987)
Spruce riparian		169	Denali	SE ± 44	Risenhoover (1987)
Open spruce-willow		130	Denali	SE ± 28	Risenhoover (1987)
Willow riparian-lowland		222	Denali	SE ± 42	Risenhoover (1987)
Willow riparian-upland		54	Denali	SE ± 13	Risenhoover (1987)
Upland willow		80	Denali	SE ± 25	Risenhoover (1987)
Upland birch		26	Denali	SE ± 9	Risenhoover (1987)
Upland aspen	697-856	97	Alberta	Browse biomass only	Renecker (1987)
Forest edge	1,948	54	Alberta		Renecker (1987)
Willow scrub	2,232	105	Alberta		Renecker (1987)
Willow-sedge meadow	530		Alberta		Renecker (1987)

contain excess digestible energy and protein, whereas winter diets are generally insufficient in nutrient quality to meet maintenance requirement (Schwartz *et al.* 1987*a*, 1988*a*; Renecker and Hudson 1989). Woody and herbaceous materials eaten have a high lignin to cell wall constituent ratio (Schwartz *et al.* 1980).

Diet quality also can vary with intensity of range use. Crude protein content of moose browse receiving no versus heavy use declined from 6.1 to 5.8% in willows and 8.8 to 7.4% in paper birch (Spencer and Chatelain 1953). Similarly, nutrient content of browse declined with age of twigs. Cowan *et al.* (1950) showed a marked decline in crude protein content from 8.0, to 5.1, and 4.1 in hazel (*Corylus californica*) browse that was 1-, 2-, and 3-year-old growth. Nutrient content also declined with diameter at point of browsing (Hjeljord *et al* 1982). Respective estimates of digestibility of twigs cut at 2, 4, 6, 8, and 10 mm ranged from 50.4 to 29.3% for great willow (*Salix caprea*), from 45.5 to 27.7% in European mountain ash (*Sorbus aucuparia*), and from 21.8 to 8.8% for silver birch (*Betula pendula*) (Hjeljord *et al.* 1982). Similarly, the crude protein content (8.3 to 5.1) and digest-

Table 3. Nutrient composition of diets consumed by moose by season.

Winter			Spring			Summer				
% protein	% DMD[a]	% CWC[a]	% protein	% DMD[a]	% CWC[a]	% protein	% DMD[a]	% CWC[a]	Reference	Location
6-7	32-41	55-57							Risenhoover (1989)	Alaska
5-7	31-38	56-68							Risenhoover (1987)	Michigan
5-7	44-52	49-52	19-20	65-69	31-34	13-14	64-65	35-43	Renecker and Hudson (1985)[b]	Alberta
6-7	26-29	65-67				15-18	47-67	29-46	Regelin *et al.* (1987)[c]	Alaska
5-8									Houston (1968)[d]	Wyoming
						10-14			Crête and Jordan (1982)[e]	Quebec
5-10	28-49								Hjeljord *et al.* (1982)[f]	Norway
7-8	20-50	56-77							Schwartz *et al.* (1988*c*)[f]	Alaska

[a] DMD = dry matter digestion, CWC = cell wall constituents.

[b] Estimates of dry matter digestion were determined with nylon bag and the data were presented in a bar graph. Therefore values were estimated from this chart. Winter values were the range for December, January, and February. Spring values were from May whereas Summer values were for July.

[c] Data for winter were from December, February, and April. Data for summer were from June.

[d] Crude protein content was listed for major browse species and does not represent diet protein.

[e] Samples were collected at the end of the growing season. Values presented are for leaves of major browse species and do not represent diets.

[f] Winter samples of common browse species. Values presented do not represent diets.

ibility (18.9 to 12.6) declined in paper birch twigs cut in 1 mm diameters from 2 to 9 mm (Hubbert 1987).

Mean diameter at point of browsing can vary among individual animals (Crete and Audy 1974), plant species, and habitats (Peek *et al.* 1971, Joyal 1976, Hubbert 1987, Risenhoover 1987); all of these can influences diet quality. Preferred species tend to be browsed to a greater diameter (Peek *et al.* 1971, Joyal 1976), and moose demonstrate a clear preference for the largest available twigs (Risenhoover 1987). On most browse species, twigs from 2.5 to 5.5 mm were browsed more frequently than expected based on their availability (Risenhoover 1987).

Variation in point of browsing between areas within a species is common as suggested by diameter of browsing of balsam fir (*Abies balsamea*) which was 3.2-11.1 mm (des Meules 1962) versus 1.8-7.8 mm (Telfer 1969). Point of browsing is more likely influenced by twig morphology than feeding behavior by moose towards a plant species. Point of browsing of paper birch did not vary as moose stocking rates increased from 1.7 to 4.8 moose/km^2 and level of utilization increased from 23 to 66% of the current annual growth (Hubbert 1987). Moose adjusted to greater density by browsing each plant at a greater intensity (i.e., they removed more current annual growth stems), but not by eating poorer quality food (Hubbert 1987). At extremely high stocking rates or when moose are confined to a winter range for long periods by deep snow, browse diameter (Renecker 1987) and utilization increase, bark stripping becomes more common (pers. observation), and diet quality declines.

Seasonal Intake Rates

Seasonal fluctuation in intake of dry matter appears to be an inherent rhythm of northern ungulates. Studies with moose (Schwartz *et al.* 1984), white-tailed deer (*Odocoileus viriginianus*) (Ozoga and Verme 1970), and caribou (*Rangifer tarandus*) (McEwan and Whitehead 1970) all show that these species regulate seasonal intake of dry matter and digestible energy even when offered high quality food ad libitum.

Intake of dry matter is influenced by the digestible energy content of the diet. Captive moose eating diets of varying energy content consumed different amounts of dry matter, but similar amounts of digestible energy. These moose consumed enough food to meet a seasonal caloric requirement rather than maximizing dry matter fill (Schwartz *et al.* 1988*a*).

Food intake in moose peaks in summer with a nadir in late winter (Schwartz *et al.* 1984, Renecker and Hudson 1985, Schwartz *et al.* 1987*c*). Changes in voluntary intake coincide with changes in forage quality and availability (i.e., summer vs. winter). Moose eat approximately 2.6-3.5% of their body weight (BW) per day in dry matter during summer but only 0.5-1.3% in winter (Schwartz *et al.* 1984, Renecker and Hudson 1985). This equates to approximately 116-142 g/kg $BW^{0.75}$/day in summer and 30-51 g/kg $BW^{0.75}$/day in winter.

Two recent studies (Renecker 1987, Risenhoover 1987) provide valuable insight into foraging strategies of moose, and improve our understanding of the dynamics of forage intake. Renecker (1987) observed moose in one habitat during different seasons, whereas Risenhoover (1987) observed moose during winter in two different environments; both observed moose during daylight hours.

Seasonal intake rate (g dry matter/min) is a function of available forage biomass (g/m^2), bite rate (bites/min) and bite size (g dry matter/bite). Renecker and Hudson (1986*a*) established a significant ($P < 0.001$) curvilinear relationship between intake rate and forage availability (Fig. 1). There were 3 different response curves corresponding to differences in forage quality among seasons. Maximum foraging rates of dry matter were predicted at 23 g/min in July, 18 g/min in October, and 11 g/min in January.

Risenhoover (1987), on the other hand, found no relationships ($P > 0.05$) between intake rates of moose and both total plant biomass and diet species biomass (Fig 2.). Intake rates of dry matter varied greatly between foraging periods ranging from 1.2 to 25 g/min. The biomass of moose food varied from 0 to 65 g/m^2; this was about 50% of biomass estimates of Renecker (1987) in January.

The discrepancy between these two studies is difficult to explain. The functional response curve of Renecker (1987) is similar to curves for wapiti (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), reindeer, and caribou (see Wickstrom *et al.* 1984, Fig. 2). A curvilinear response is the appropriate function when describing such a relationship. It is logical that intake of dry matter beyond some maximum (asymptote) is not influenced by availability. Renecker's curve was based on observations made with 2 animals. Risenhoover, on the other hand, observed at least 32 different moose in his 2 study areas. The lack of a curvilinear fit demonstrates the high variability between individual moose and limits using abundance of forage biomass to predict intake, particularly at lower ranges (0 to 100 g/m^2). Also as Risenhoover (1987:74) suggested "the failure to detect a functional response in moose intake rates suggests that diet species biomass provides a poor indictor of moose encounter rates with acceptable forage." It is difficult to define what is moose food. A lack of a relationship could also be a function of the diversity of shrub habitats which by their nature require intensive sampling.

Intake of food is also related to bite size and rate which vary seasonally, among plant species, and among study areas (Renecker 1987, Risenhoover 1987). Risenhoover found no relationship between mean bite size (g/bite) or mean harvest rate (bites/min) and diet

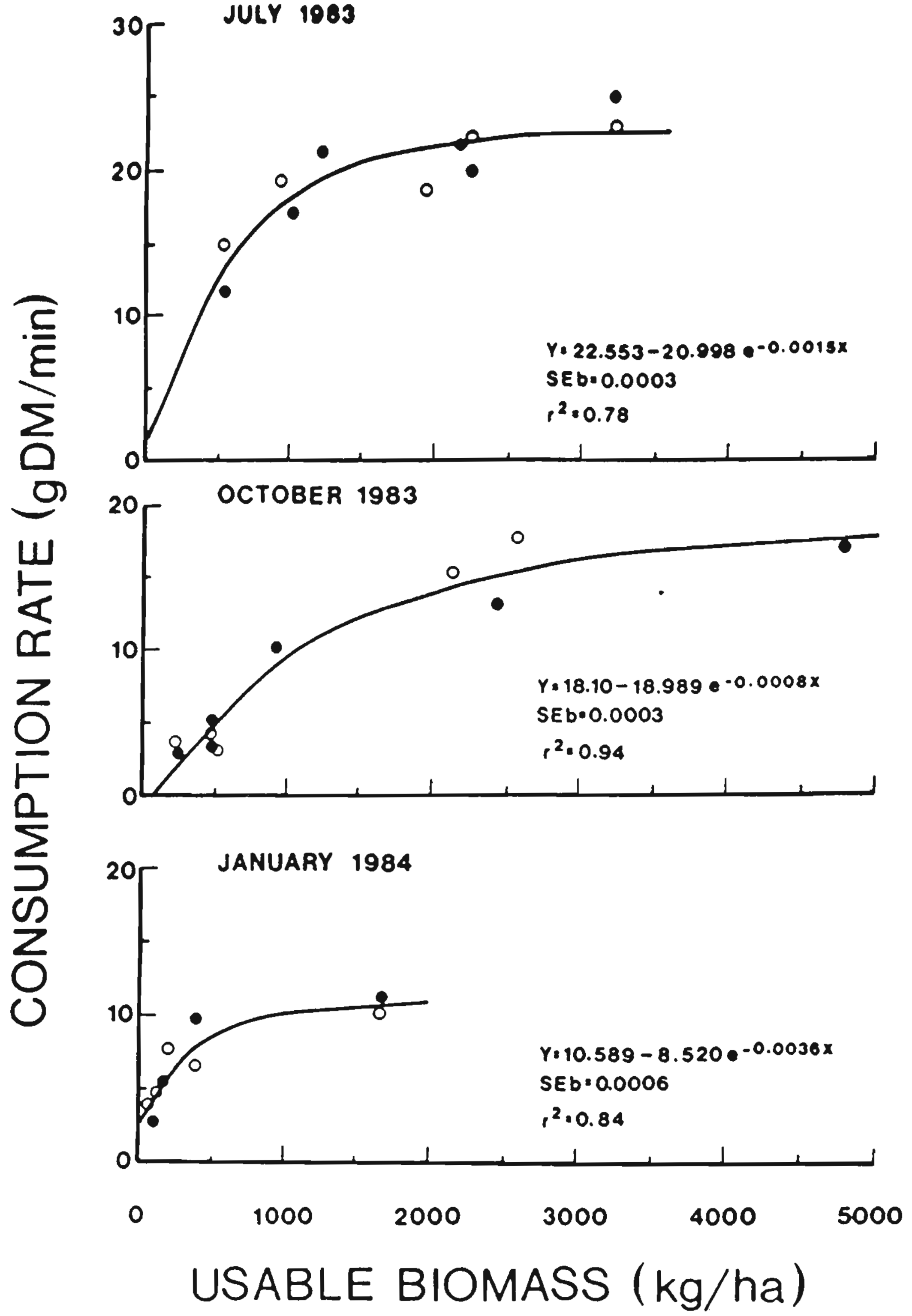

Fig. 1. Relationship between usable forage biomass and consumption rate (g dry matter/min) of free-ranging moose during summer, autumn, and winter. Original data presented by Renecker and Hudson (1986*a*)

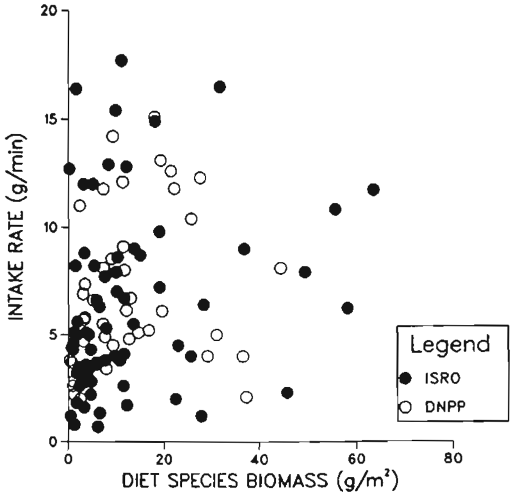

Fig. 2. Mean intake rates of moose in relation to diet species biomass. Original data presented by Risenhoover (1987). ISRO = Isle Royal National Park, DNPP = Denali National Park.

species biomass during winter. Renecker (1987), on the other hand, showed significant differences in both bite rate and bite size among seasons. Risenhoover (1989) concluded that bite size was the major factor determining the harvest rate and subsequent intake rate for individual browse species. But as bite size increased, animals required more handling time in order to ingest forage, and bite rates declined. However, the amount of handling time required per gram declined as bite size increased, and thus, intake rate could be maximized by maximizing bite size (Fig. 3). Renecker concluded that during summer, moose had little difficulty meeting their daily forage requirements for maintenance and production. During winter, low quality food imposed logistic constraints on foraging behavior; opportunity for selection decreased and time required for rumination increased.

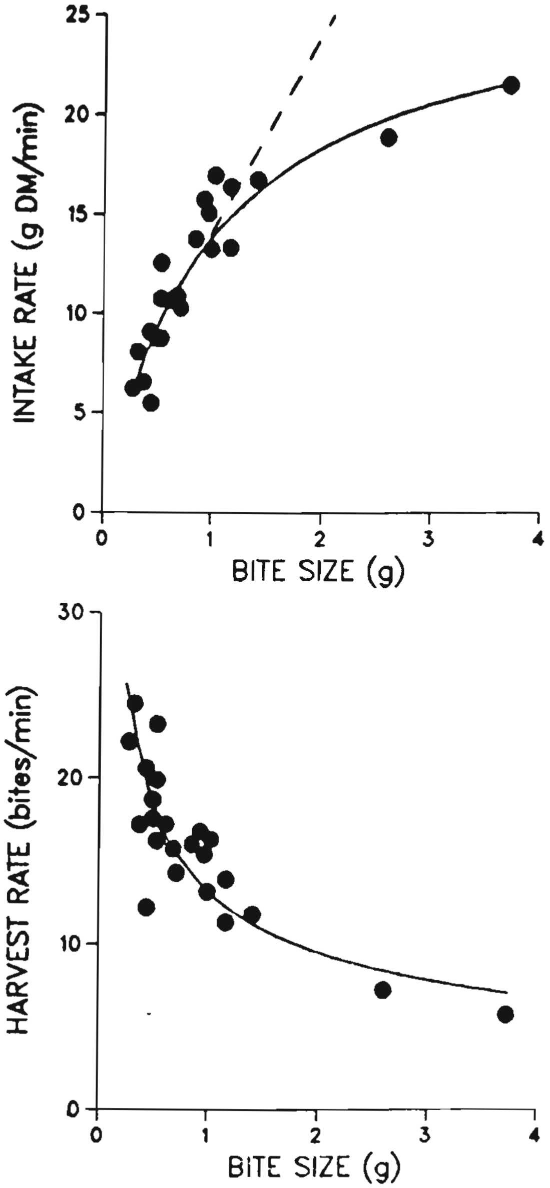

Fig. 3. Species-specific intake rates (top) and harvest rates (bottom) in relation to bite size for 23 woody plant species browsed by moose. Original data presented by Risenhoover (1987).

Morphological Adaptations

The digestive anatomy of the moose is well suited to their diet choices. Kay *et al.* (1980) and more recently Hofmann (1985, 1989) classified the moose as a seasonally adaptive concentrate selector. Hofmann (1989) discussed the development of a flexible system of overlapping ruminant feeding types. The poles of this classification system are represented by concentrate selectors and grass/roughage eaters. The two are vastly different. Details are amply characterized by

Hofmann and Nygren 1992.

The Bell-Jarman principle (Bell 1969, 1971, Jarman 1974) states that small bodied animals tend to be selective in their diet choices (concentrate selectors) while large bodied ruminants are non-selective (roughage eaters). This principle, developed in Africa, was based on the relationship of body size and energy requirements. In general, energy requirements scale to body weight (BW) at approximately $BW^{0.75}$ (Kleiber 1975). Expressed allometrically, large animals require less energy per unit of body weight but more absolute energy than small animals. This simply means small bodied ruminants can be more selective in diet choices, but those choices must be of high quality. Hofmann's classification contains at least 3 large species of concentrate selectors, the giraffe (*Giraffa camelopardalis*), moose, and greater kudu (*Tragelaphus strepsiceros*).

Moose do not conform entirely to Hofmann's classification as a concentrate selector, since foods eaten in winter are not that nutritious (Table 3). Similarly, it may be difficult to make pure anatomical and morphological comparisons between African bovines (Pliocene origin) and North American cervids (Pleistocene origin). This is especially true because of the necessary seasonal and dietary adaptations of moose.

Moose are morphologically adapted to the northern environments where they live. Winter is especially critical since there may be snow on the ground from 4-8 months/year. The ability of moose to travel in snow is governed by the snow's depth, density, and hardness. The long legs and small hooves of moose facilitate mobility in deep soft snow. Their chest height is 64% greater than white-tailed deer (82-105 vs. 50-64 cm), although the foot loading of moose (600-800 gms/cm^2) is about equal to male white-tailed deer (Kelsall 1969), but greater than roe deer (*Capreolus capreolus*) (300-600 gms/cm^2), chamois (*Rupicapra rupicapra* (200 gms/cm^2), and reindeer (*Rangifer tarandus* (140-180 gms/cm^2) (Nasimovich 1955). Therefore, moose have an advantage over other forest browsers like the white-tailed deer since they can move and freely exploit areas with relatively deep snow.

The large body size of moose, which minimizes heat loss helps with survival in a cold climate. Adult moose are capable of tolerating extreme cold (Renecker and Hudson 1986*b*), but are intolerant of heat (Renecker *et al.* 1978, Renecker and Hudson 1986*b*, Chernnykh 1987).

Forage Digestion and Passage

To extract maximum metabolizable energy from ingested foods, ruminants must optimize the trade off between retention and passage (Foose 1982). Retention of food in the rumen allows for more complete digestion whereas rapid passage allows for more food to be processed. Schwartz *et al.* (1980) speculated that moose, as concentrate selectors, confronted this problem by propelling digesta rapidly, fermenting mainly soluble components. Rapid passage was possible because highly lignified browse when masticated, shattered into large cuboidal particles (Mertens 1973, Milchunas *et al.* 1978) suitable for passage.

In a comparative study of cattle (a grazer), wapiti (a mixed feeder), and moose (a concentrate selector), Renecker and Hudson (1990) substantiated the earlier speculation of Schwartz *et al.* (1980). Renecker and Hudson (1990) fed aspen browse, alfalfa hay (*Medicago sativa*) and grass hay to these three ruminant species. They concluded that the ability of browsing moose to extract adequate energy from forages of low asymptotic digestibility depended on rapid passage rate. Moose were most sensitive to diet, propelling browse diets more rapidly than cattle, but retaining grass hay and lucerne longer than either wapiti or cattle. Rapid passage of browse was achieved by propelling large particles through the rumen. Based on critical particle-size theory, threshold range of particles was highest for moose (4.4-6.9 mm) with the probability of passage increasing for high lignin ratios.

In a similar study, Renecker *et al.* (1983) compared the digestive kinetics of grass/alfalfa, alfalfa, and alfalfa/browse mixtures in cattle, wapiti, and moose using the nylon bag technique. They demonstrated only slight differences in digestion of dry matter, suggesting that the fermentation environment in the three ruminants species was basically the same. Disappearance curves and asymptotes were nearly identical for all three forages among all three ruminants. Digestive efficiency appears to be regulated more by forage selection, rumination, gut morphology, and mechanisms controlling rate of passage than by the digestive kinetics of rumen fermentation.

There is a close association between the flow of liquid and solid phases from the rumen of moose (Hubbert 1987, Renecker and Hudson 1990). Hubbert (1987:49-55) discussed the rumen turnover times (RTT) of liquids and solids in cattle, domestic sheep and moose. His liquid-to-solid RTT ratios were 0.964 for moose, 0.788 for sheep, and 0.395 for cattle. Therefore, the liquid digesta phase in the grazer (cattle) flowed at a faster rate than the solids, whereas in the browser (moose) the differences were small; sheep are considered mixed feeders. Grazers retain solids longer because cellulose and hemicellulose require long digestion times whereas retention of highly lignified fiber contained in browse would be inefficient and costly.

Moose have an adaptive digestive strategy to optimize energy intake. Diets are more digestible in spring and summer than in winter (Table 3). Summer diets are composed mainly of highly digestible leaves of deciduous browse, forbs, and aquatic plants. Intake rates are high and moose catabolize large quantities of fat. Winter diets are almost exclusively woody browse (Table 1), and low in digestibility; moose must metabolize fat to meet an energy deficit. Although summer and winter diets have different rates of digestion (Table 3), both contain undigestible lignin. Woody browse has a highly lignified cortex and most of the digestible components are contained in the outer bark and buds. Moose digest this outer material efficiently and propel the indigestible cortex rapidly. However if forage is limited, as in winter, slowing the rate of passage may be beneficial by allowing for some digestion of the woody browse cortex (Hubbert 1987).

Seasonal Metabolism

Seasonal metabolic rhythms occur in a number of northern wild ruminants including caribou (McEwan and Whitehead 1970), roe deer (Weiner 1977), white-tailed deer (Silver *et al.* 1969), mule deer (Freddy 1984, Parker and Robbins 1984), and wapiti (Lieb and Marcum 1979, Parker and Robbins 1984). Moose, like other northern ruminants, have a cyclical metabolic rate, with a peak in summer and a nadir in winter (Regelin *et al.* 1985, Renecker and Hudson 1986b). Changes in seasonal metabolism are related to changes in feed intake and body weight (Schwartz *et al.* 1984, Renecker and Hudson 1985, Hubbert 1987), which probably reflects changes in mass of metabolically active tissues like the liver and digestive system (Arnold 1985). Body condition, particularly fat reserves, may also affect metabolism independent of plane of nutrition and endogenous rhythms (Reid and Robb 1971, Byers *et al.* 1989).

Estimates of theoretical basal metabolism (68.3 kcal/kg $BW^{0.75}$, Renecker and Hudson 1983), (68.8 kcal/kg $BW^{0.75}$, Hubbert 1987), and (72.7 kcal/kg $BW^{0.75}$, Schwartz *et al.* 1988*a*) are close to the interspecific mean of 70 kcal/kg $BW^{0.75}$ provided by Kleiber (1975).

Seasonal Activity

Like most ruminants, moose spend most

of the day eating and ruminating (Risenhoover 1986, Renecker and Hudson 1989, Van Ballenberghe and Miquelle 1990). These activities vary seasonally (Renecker and Hudson 1989) with forage abundance, quality, digestibility, and passage rate. Feeding bouts are shorter during summer when forage availability and digestibility are high (Risenhoover 1986, Renecker and Hudson 1989, Van BallenBerghe and Miquelle 1990) than during winter. Moose in Denali National park were active 12.8 hours/day in summer (Van Ballenberghe and Miquelle 1990) but only 5.8 hours/day in winter (Risenhoover 1986); this represents a 2.2-fold increase in the daily activity period from winter to summer.

The duration of rumination bouts and total daily rumination time is significantly related to both cell wall constituents in the diet and digestible dry matter intake (Renecker and Hudson 1989). Moose ruminate longer and more intensively in winter when forage fiber is high (Renecker and Husdon 1989), which may limit food intake (Risenhoover 1986). Because lignin is resistant to digestion, intensive rumination is the means by which moose breakdown forage to a size capable of passage.

The spatial arrangement of forage has a strong effect on time spent feeding. Intake of dry matter is positively related to forage density and inversely related to search time (Risenhoover 1986, Renecker 1987). On an annual basis search effort appeared to be an important component of foraging (Renecker 1987). Moose tend to increase forage intake by selecting habitats rich in food (Risenhoover 1987).

Body Composition

Changes in body composition and fat metabolism in moose are a dynamic process. Large gains and depletions are associated with the summer flush of forage and winter declines in food availability and quality, respectively. Seasonal weight dynamics of moose have been associated with reduced diet quality and forage availability (Renecker and Hudson 1986*b*, Schwartz *et al.* 1987*b*). Estimates of body composition of moose (Schwartz *et al.* 1988*b*) suggest that moose enter winter with large amounts of body fat (20-26%). There are vast differences between males and females (Schwartz *et al* 1988b). Males lose large amounts of body fat during the rut (Sep. - Oct.) because they quit eating (Schwartz *et al.* 1984). Females continue to improve body composition until early winter (Schwartz *et al.* 1984, 1988*b*, Renecker and Hudson 1986*b*) and then loose body mass and fat.

Stored body fat and protein represent the currencies that allow moose to survive a winter energy deficit. Fat and protein are metabolized during winter and used to supplement the energy deficit associated with reduced intakes. Energy balance then influences survival. Summer ranges govern fattening whereas winter ranges dictate depletions. Excesses in energy during summer influence reproduction; animals on high quality range breed earlier and tend to produce more twins (Peterson 1955, Franzmann 1978, Franzmann and Schwartz 1985).

Protein and Energy Requirements

Protein and energy are considered by many people to be the major limiting nutrients within the environment (Moen 1973, Wallmo *et al.* 1977). Estimates of energy requirements for maintenance of moose during winter (131 kcal/kg $BW^{0.75}$/day of metabolizable energy) (Schwartz *et al.* 1988*a*) are similar to those of white-tailed deer (Ullrey *et al* 1969, 1970). Similarly, the nitrogen requirement for maintenance (0.627 g/kg $BW^{0.75}$/day) for moose (Schwartz *et al.* 1987*a*) was within the range reported by Robbins (1983:159) for several species of wild ruminants. These data suggest that moose nutrient requirements are similar to other ruminants.

Strategies for Survival

Selective processes operating on the moose have resulted in an organism that is adapted to the northern environment. Some of these adaptations are reflected in the nutritional strategies that the animal employs to survive and reproduce.

Diet choices are mainly leaves and stems of woody browse. These foods predominate in the boreal forest. Moose are selective feeders spending most of their time eating and ruminating in habitats rich in available forage. Their digestive system is adapted to process the woody browse diet they consume. By taking large bites and chewing their foods for long periods the material is broken down into particles capable of passing quickly out of the rumen. Diet fiber is high in lignin and is not retained in the rumen.

Moose have high metabolic rates and are hyperphagic in summer when food quality and availability are high. The opposite is true in winter. Energy and protein requirements are similar to other ruminants.

Fat reserves are cyclic and reflect seasonal rhythms of intake and metabolism. These rhythms appear to be controlled by feedback mechanisms linking body condition and fat reserves (Arnold 1985). Arnold (1985:82) reviewed the mechanics of intake control and stated that "long term stability of energy balance is thought to be controlled by the size of the fat reserves", and that "many species in temperate and arctic areas appear not to have stability in energy balance even in a constant nutritional environment." Arnold (1985:97-98) further stated that "the regulation of forage intake by free-ranging wild herbivores is through both internal controls concerned with digestion, rate of passage of digesta through the digestive system, and set points probably including energy balance and body condition."

Schwartz *et al.* (1988*a*) proposed the following for moose, based on their observations with captive animals. When available, moose consume large quantities of high quality food during summer. Body condition peaks in early fall prior to the rut for bulls. Peak body condition for females occurs latter and is associated with natural declines in forage quality and availability. Peaks in body condition activate mechanisms (set point) which depress intake. Depressed intake occurs in captivity even when animals are offered high quality food ad libitum. Reductions in intake occur in the wild concomitantly with natural declines in food quality and availability. Decreased intake results in a lower metabolic rate (Hubbert 1987) and a shift to a negative energy balance. Body stores are depleted to a low in body condition (set point) in spring. The process then reverses. Set points, which result in metabolic shifts, correspond with environmental changes in food quality and availability (Regelin *et al.* 1987, Renecker 1987, Renecker and Hudson 1988). Set points vary with individuals and level of intake. Body condition likely influences intake during winter. If the lower set point is reached prior to change in food availability (i.e., green-up), animals in the wild starved to death. However under confined conditions where food is available, moose that reached the lower set point prior to spring increase intake, while moose in good condition (above the set point) do not (Schwartz *et al.* 1988*a*). These mechanisms are not rigidly fixed and exhibit plasticity when animals are stressed.

The annual cycle of food intake, fat metabolism, metabolic rate, and body mass dynamics is not driven simply by food quality and availability in the environment. It represents a complex interaction between internal physiological regulators and the external environment. Physical condition of moose is keyed to environmental quality, but deeply rooted in physiological and morphological adaptations of the species. Nutritional energetics plays an important role in the survival of individual moose which ultimately influences population dynamics and survival of the species.

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