

## 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, thermo-regulation, 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.* (1987c) 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.* (1987c) 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.



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

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

<sup>a</sup>The number of species comprising >90% diet, or the number of species which represented at least 5% of the diet.

<sup>b</sup>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

<sup>c</sup>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.

<sup>d</sup>Winter diets were listed for both early and late winter.

<sup>e</sup>Winter foods were listed for 3 different years, 1945, 1948, and 1950.

<sup>f</sup>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.

<sup>g</sup>Food habits were listed for 7 different habitats.

<sup>h</sup>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.

<sup>i</sup>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.

<sup>j</sup>Diets were October and November.

<sup>k</sup>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.

<sup>l</sup>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.

<sup>m</sup>Winter diets contained 0.4% "other" items, I listed them as forbs, although some were undoubtedly browse



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

Winter			Spring			Summer			Reference	Location
%	%	%	%	%	%	%	%	%		
protein	DMD <sup>a</sup>	CWC <sup>a</sup>	protein	DMD <sup>a</sup>	CWC <sup>a</sup>	protein	DMD <sup>a</sup>	CWC <sup>a</sup>		
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) <sup>b</sup>	Alberta
6-7	26-29	65-67				15-18	47-67	29-46	Regelin <i>et al.</i> (1987) <sup>c</sup>	Alaska
5-8									Houston (1968) <sup>d</sup>	Wyoming
						10-14			Crête and Jordan (1982) <sup>e</sup>	Quebec
5-10	28-49								Hjeljord <i>et al.</i> (1982) <sup>f</sup>	Norway
7-8	20-50	56-77							Schwartz <i>et al.</i> (1988c) <sup>g</sup>	Alaska

<sup>a</sup>DMD = dry matter digestion, CWC = cell wall constituents.

<sup>b</sup>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.

<sup>c</sup>Data for winter were from December, February, and April. Data for summer were from June.

<sup>d</sup>Crude protein content was listed for major browse species and does not represent diet protein.

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

<sup>f</sup>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 influence 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<sup>2</sup> 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 virginianus*) (Ozoga and Verme 1970), and



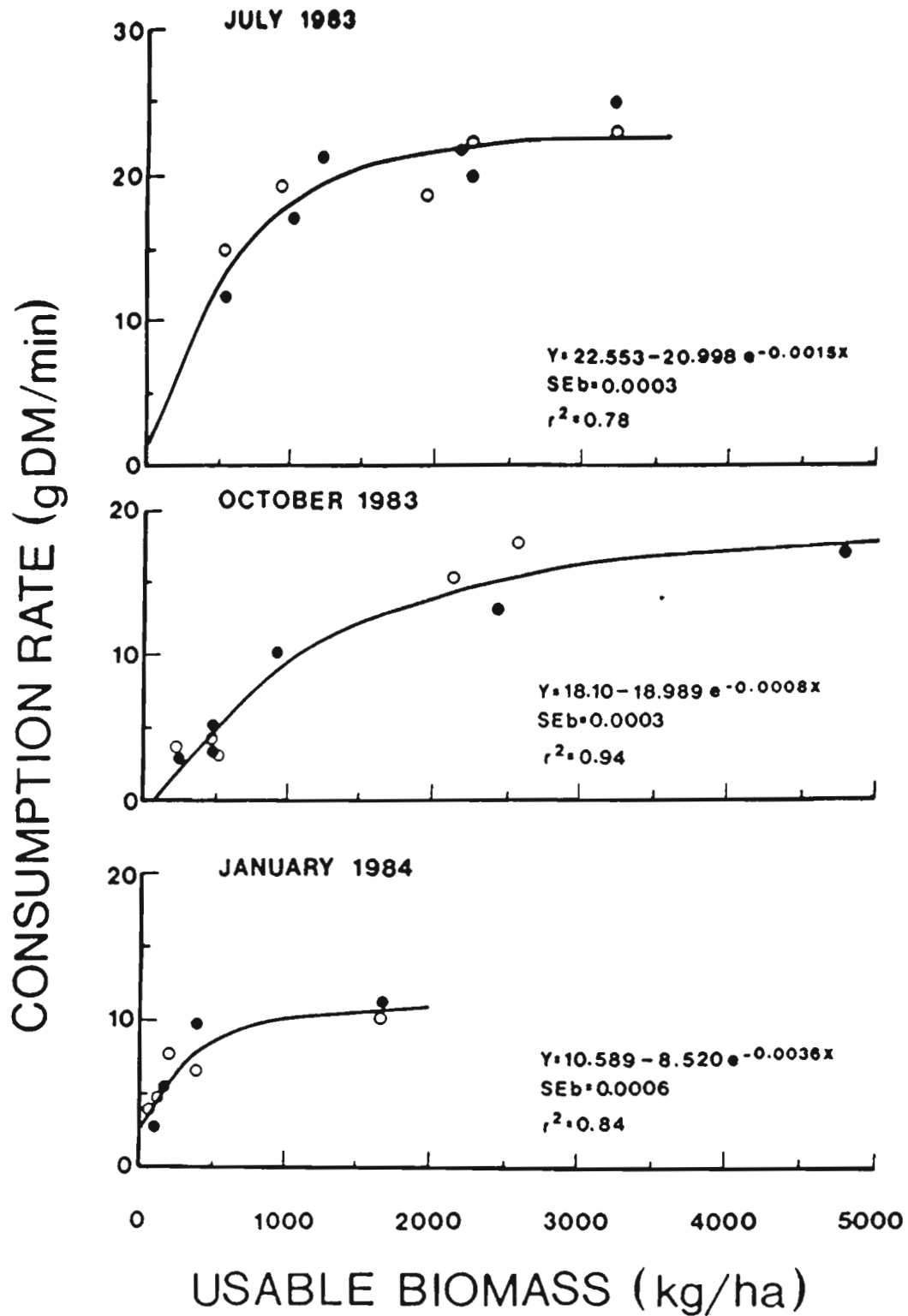


Fig. 1. Relationship between usable forage biomass and consumption rate (g dry matter/min) of free-ranging moose during summer, autumn, and winter. Original data presented by Renecker and Hudson (1986a)





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<sup>2</sup>) is about equal to male white-tailed deer (Kelsall 1969), but greater than roe deer (*Capreolus capreolus*) (300-600 gms/cm<sup>2</sup>), chamois (*Rupicapra rupicapra*) (200 gms/cm<sup>2</sup>), and reindeer

(*Rangifer tarandus* (140-180 gms/cm<sup>2</sup>) (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 1986b), but are intolerant of heat (Renecker *et al.* 1978, Renecker and Hudson 1986b, Chermnykh 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

















