

## HABITAT AND FORAGE SELECTION OF MOOSE IN THE ASPEN-DOMINATED BOREAL FOREST, CENTRAL ALBERTA

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**ABSTRACT:** Forage and habitat selection of tame moose (*Alces alces*) in a 65 ha enclosure were studied for an annual cycle. Although the staple winter foods were woody twigs, moose consumed large amounts of leaf litter and bark under some environmental conditions. Foliage dominated the diet following leaf flush in May. Selectivity of moose for plants high in cell solubles was most pronounced during autumn. Moose used a variety of habitats throughout the year. Although relative use varied with foraging returns on an annual basis, habitat choice during late spring and summer became two-fold: to maximize the intake of foods high in cell solubles, and to mitigate thermal imbalances and insect annoyance.

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Moose are widely distributed throughout the circumboreal zone (Krefting 1974, Telfer 1978, Coady 1983). Patterns of habitat use have been described for populations throughout their North American distribution (Brassard *et al.* 1974, Berg and Phillips 1974, Trottier *et al.* 1983, Pierce and Peek 1984). Within Alberta, several studies have quantified habitat selection and food choice (Barrett 1972, Cairns 1976, Mytton and Keith 1981). Because of the low densities and inaccessible environment in which moose live, patterns of resource-use usually must be documented by indirect means. Few studies are based on direct observation of moose in the aspen-dominated boreal forest.

Most studies about habitat selection of moose have focused on radio-telemetry locations of free-ranging moose (Pierce and Peek 1984, Leptich and Gilbert 1989) and the apparent use of these areas on the basis of their availability. More recently, Van Ballenberghe and Miquelle (1990) used direct observations of moose activity to help interpret seasonal decisions patterns. Comparisons of moose behavioral and habitat use patterns between areas helps the manager in the development of consistent use patterns and what criteria are

apparently important in the various seasons.

Although there may be value in cataloging patterns of resource-use in the hope of extracting some understanding from comparative analyses, relationships are often hopelessly confounded. Resource-use behaviour is strongly influenced by needs to forage efficiently, ameliorate thermal stress or insect annoyance, minimize risk of predation, and interact socially. In this study, we attempted to minimize the effects of social interaction and security by using habituated, adult, non-reproductive females isolated from bulls and predators in a 65 ha enclosure. Under these circumstances, resource-use behaviour should largely reflect the trade-off between foraging efficiency and comfort (protection from thermal stress and insect annoyance).

Our main objective was to determine if resource-use behaviour could be interpreted in such simple terms. Specifically, we attempted to answer the following questions: a) do moose select forages on the basis of nutritional quality, b) do moose use different habitats for resting and feeding, and c) are foraging times in each habitat related to foraging returns?

## METHODS

### Study Area

The study was conducted 48 km south-east of Edmonton at the Ministik Wildlife Research Station, Alberta, Canada. The area is located on the Cooking Lake glacial moraine within the aspen-dominated boreal forest zone (Rowe 1972), although a history of fire and clearing has left little coniferous cover. Surface till deposited by the most recent glacial advance has formed an undulating complex of hills and closed depressions. These are numerous seasonal and permanent bodies of water. These wetlands form incomplete drainage systems throughout the area. The level of water in the sloughs represents the local water table where the soil till is impervious.

Most of the area is forested by trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*). The main understory shrub is beaked hazel (*Corylus cornuta*) whereas willow (*Salix* spp.) dominates the perimeter of wetlands. Plant communities and nutritional quality (nitrogen, cell solubles, cell wall fraction, and *in situ* digestibility) of forages were previously described in more detail by Renecker and Hudson (1985, 1986a, 1988).

Although winters are typically cold and dry, summers are generally warm with a mean June to September temperature of 15°C with extreme day time maximums of >30°C (Olson 1985). Black-globe temperatures ranged from -31°C in winter to an extreme of 42°C in summer (Renecker and Hudson 1989). Annual precipitation averages 500 mm with 25% occurring as snow (Anon. 1980).

### Animals

Two adult female moose (2.5 years old at the beginning of the study) were hand-reared and maintained on a pelleted aspen-concentrate ration (Schwartz *et al.* 1985) in a 2 ha pasture. They were released into a 65 ha enclosure every 6-8 weeks from December,

1982 to January, 1984. Before each trial, they were allowed an average of 4 weeks for digestive and spatial adjustment to natural habitats and forage. The two cows were distinguished by ear tag numbers 211 and 727.

### Analysis

Food choice was determined by the bite-count technique (Renecker and Hudson 1986a). Intake of each forage was calculated on a dry weight basis as the product of number of bites and bite size. Relative use was expressed as percentage of aggregate daily intake. Diameters at the point of browsing of several woody species were measured with calipers during autumn, winter, and spring.

Habitat use was determined by 24-hr continuous time-sampling. Relative use of habitats occupied by each moose was calculated as a percentage of a 24-hr day and related to available area of habitats within the enclosure. A habitat selection index, based on a ratio between observed and expected frequencies of use (Gates and Hudson 1981), was applied to observations in each season (for example, a value of 1.0 implied that animals selected habitats in proportion to their abundance). Proportional habitat use was related to relative foraging returns published by Renecker and Hudson (1986a).

Statistical comparisons were made by analysis of variance (Snedecor and Cochran 1967). Means are reported with their standard errors ( $\pm$  S.E.).

## RESULTS

### Food Habits

Moose in this study consumed 5 major forage categories throughout the year (Tables 1 and 2) with shrubs and leaf litter contributing the largest proportion. Forbs were important only during summer and autumn. During winter, willow, balsam poplar, beaked hazel, and leaf litter comprised an average of  $95 \pm 2\%$  of daily intake. Diameters at the point of browsing increased as winter progressed (Ta-

Table 1. Diet of free-ranging moose no. 727 from December, 1982 to January, 1984 expressed as the percent of total dry matter intake.

Plant Species	Percentage <sup>1</sup>						
	Dec	Feb	Apr	May	July	Oct	Jan
<b>Shrubs</b>							
Willow	6.9	11.1	1.0	12.0	2.2		3.8
Balsam Poplar	19.5	20.0	7.1	4.8	11.4		6.6
Trembling Aspen	6.1		0.6	0.5	3.1	6.6	42.9
Beaked Hazel	1.6		3.2	68.5	8.8	0.2	14.8
Red-Osier Dogwood		0.6			0.1	0.2	
Rose				2.4	1.2	0.4	
Snowberry				15.5	4.8	77.3	
Saskatoon				0.2		0.8	
Chokecherry				3.4			
Soapberry				0.8			
Red Raspberry					1.1	1.1	
White Birch					0.6		
Cranberry						1.6	
Gooseberry						0.3	
Bark				38.6	0.2		27.0
Leaf Litter	65.8	67.8	49.8			2.7	4.9
<b>Forbs</b>							
Cattails					46.7		
Stinging Nettle					0.1		
Canada Thistle						0.3	
<b>Sedge</b>							
				0.1	1.2	11.9	
<b>Grass</b>							
			0.8				

<sup>1</sup>Percentage values less than 0.1% were omitted. Percentages calculated as percent of dry weight of forage intake when estimated by bite-count technique (Renecker and Hudson 1985).

ble 3) to a peak in April. Twigs of balsam poplar and willow measured during January, 1984 were significantly ( $P < 0.05$ ) larger than recorded the previous winter as animals reverted to large sprout growth in old field succession because of the dense snow crust.

Although moose began stripping bark from trembling aspen in early April, use of

other plants changed little from winter. Foliage dominated diets after leaf flush in early May; the most important species, beaked hazel, accounted for 39-69% of the diet. Willow, balsam poplar, and western snowberry (*Symphoricarpos occidentalis*) were frequently selected. Raspberry (*Rubus idaeus* var. *strigosus*) leaves exceeded 19% of the

Table 2. Diet of free-ranging moose no. 211 from December, 1982 to January, 1984 expressed as the percent of total dry matter intake.

Plant Species	Percentage <sup>1</sup>						
	Dec	Feb	Apr	May	July	Oct	Jan
<b>Shrubs</b>							
Willow		58.5		11.1	56.7	8.8	12.7
Balsam Poplar	19.5	26.1	28.2	14.3	14.0	13.0	22.0
Trembling Aspen	5.9			2.1	1.8		53.3
Beaked Hazel	67.8		39.2	18.3			
Red-Osier Dogwood	0.3				0.2	0.2	
Rose				0.8	0.2	0.1	0.1
Snowberry				0.3		4.2	0.7
Saskatoon	0.8			1.5	0.7		
Chokecherry				0.6			
Soapberry	0.4	2.6			0.1		
Red Raspberry				12.3	1.8	8.9	0.1
Honeysuckle			9.4	1.2	0.4		
White Birch				0.8	1.3		
Cranberry			1.9				
Gooseberry				3.8		1.0	
Bark			38.5				
<b>Leaf Litter</b>	4.3	12.8	32.2			55.6	7.1
<b>Forbs</b>							
Pea Vine				0.6			
Cattails					3.1		
Alsike Clover					0.2		
Canada Thistle						19.8	3.0
Yarrow							1.1
<b>Sedge</b>				0.8	0.2		
<b>Grass</b>	0.8		1.1				

<sup>1</sup>Percentage values less than 0.1% were omitted. Percentages calculated as percent of dry weight of forage intake when estimated by bite-count technique (Renecker and Hudson, 1985).

daily intake of moose no. 211. The remaining shrubs constituted 10-11% of the late spring diet. Sedge and grass did not exceed 10% of the diet and the only forb consumed was pea vine (*Lathyrus* spp.).

By mid July, willow, balsam poplar, and beaked hazel accounted for 9-57% of the diet. Cattails (*Typha latifolia*) were consumed by breaking the stalk above the roots and slowly consuming the entire plant. On other occa-

sions, animals would only feed on the thick white portion of stems below water level.

During autumn, moose foraged selectively on available green plant material. Snowberry and Canada thistle (*Cirsium arvense*) remained green and were favoured by moose. In several cases, moose stripped only fruits from snowberry when green leaves were not present. Leaf litter was a dominant food for animal no. 211 accounting for over 55% of the diet. Fallen leaves remained partially green, had not been subject to leaching, and were abundant. Along with fallen leaves, this animal selected stems of willow and balsam poplar which contributed 32.7% of the use. Sedge (*Carex* spp.) comprised > 11% of the autumn diet of moose no. 727. Sedge was consumed largely during one feeding bout in an area which supported green plant material.

Moose appeared to select their winter and summer diets from the forage classes of twigs, leaves, sedges, grasses, and forbs according to plant quality. Proportion of the forage class in the diet was significantly correlated with *in*

*situ* digestibility reported by Renecker and Hudson (1988) (for winter:  $Y=0.046X + 29.153$ ;  $SEb = 0.0183$ ;  $r^2=0.26$ ;  $P<0.05$ ; for summer:  $Y=0.0126X + 55.96$ ;  $SEb=0.048$ ;  $r^2=0.43$ ;  $P<0.05$ ). Diet proportions were not significantly ( $P>0.05$ ) related to protein or cell wall content of the seasonal diet.

### Habitat Selection

During the first winter, moose selected habitats which provided canopy cover or were close to nearby tall shrubs (Fig. 1). Forest and willow habitats yielded a selection index (ratio between observed and expected frequencies of use) of 1.2 and 2.5, respectively. This indicated that moose selected these habitats more frequently than would be expected from their relative abundance. In the second winter, they spent more time in open habitats and forest edge. Frequent freeze-thaw cycles restricted access to leaf litter except near dead-falls and the base of trees, probably forcing moose into open areas in search of food. The selection index rose to 5.12 for old-field suc-

Table 3. Mean diameter ( $\pm$ SE) at point of browsing for several browse species consumed by free-ranging moose from December, 1982 to January, 1984 at the Ministik Wildlife Research Station, Alberta, Canada.

Plant Species	Mean Diameter $\pm$ SE (mm)				
	Dec	Feb	Apr	Oct	Jan
Balsam Poplar	2.86 $\pm$ 0.06	3.09 $\pm$ 0.07	3.67 $\pm$ 0.08	2.78 $\pm$ 0.11	3.42 $\pm$ 0.13
Trembling Aspen	2.50 $\pm$ 0.13				3.03 $\pm$ 0.10
Willow	2.23 $\pm$ 0.08	2.44 $\pm$ 0.07	3.15 $\pm$ 0.18	2.18 $\pm$ 0.06	2.75 $\pm$ 0.14
Hazel	2.13 $\pm$ 0.04		2.31 $\pm$ 0.05	2.10 $\pm$ 0.08	2.20 $\pm$ 0.09
Saskatoon	2.10 $\pm$ 0.09			1.57 $\pm$ 0.11	
Red-Osier Dogwood	2.13 $\pm$ 0.12	2.17 $\pm$ 0.17	1.64 $\pm$ 0.08		
Snowberry				1.17 $\pm$ 0.06	
Cranberry				2.43 $\pm$ 0.49	
Red Raspberry					2.00 $\pm$ 0.03
Soapberry	1.74 $\pm$ 0.08	2.55 $\pm$ 0.19		1.64 $\pm$ 0.12	
Honeysuckle				2.22 $\pm$ 0.21	

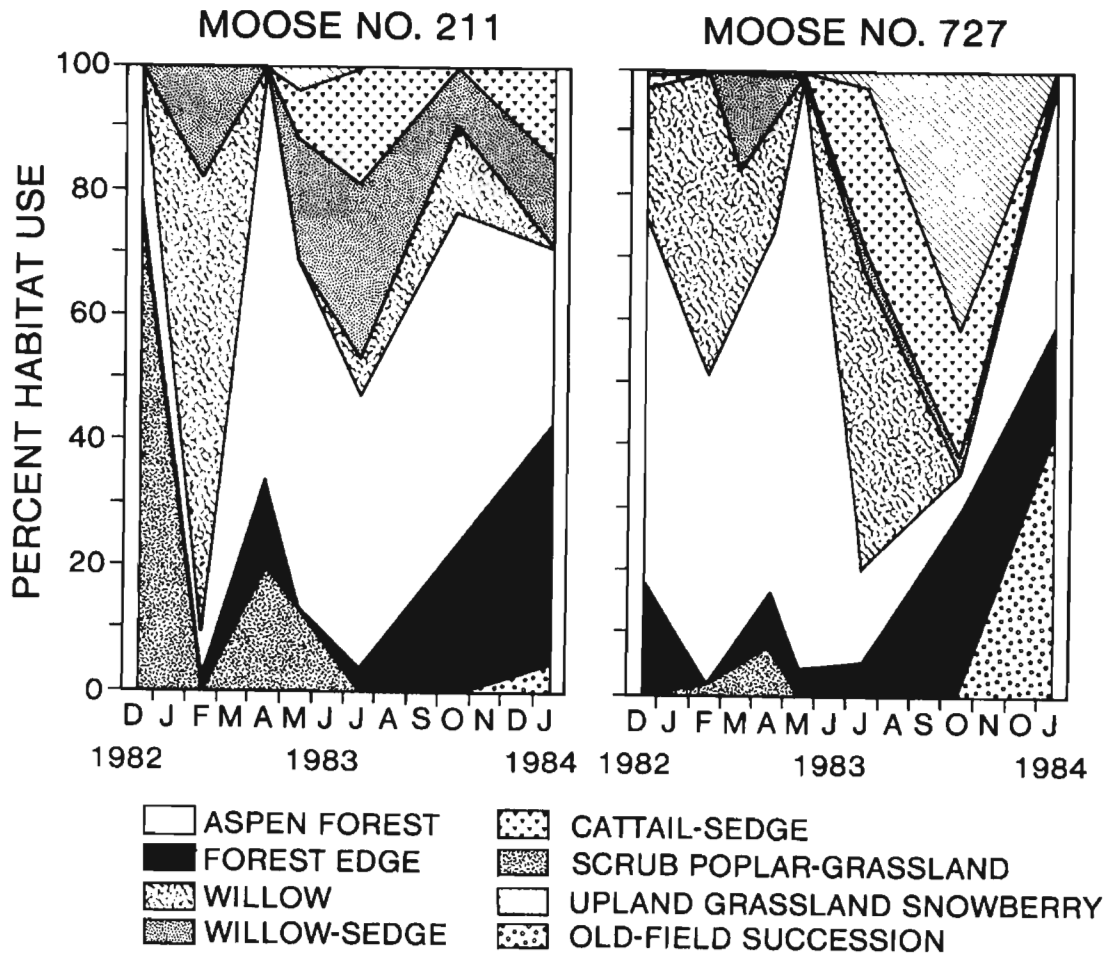


Fig. 1. Use of major habitats by 2 moose cows in aspen-dominated boreal habitats from December 1982 to 1984 at the Ministik Wildlife Research Station, Alberta, Canada.

cession.

During winter, aspen, poplar, or willow cover was important for both feeding and bedding. The advantage of overhead cover was reflected by a black-globe temperature averaging  $0.7 \pm 0.2^{\circ}\text{C}$  higher than the comparable ambient temperature in that microclimate. Similarly, the change from clear to cloud covered skies resulted in a  $7^{\circ}\text{C}$  rise in black-globe temperature.

Although use of aspen forest continued into early spring, open areas such as willow-sedge, forest edge, and scrub-poplar grassland habitats became increasingly important from mid-winter to April. Nevertheless, animals returned to the aspen forest to bed.

During late spring, use of the aspen forest increased markedly (selection index of 1.8) as animals stripped leaves from shrubs. Use of cattail-sedge and willow habitats (selection indices of 3.08 and 2.44, respectively) progressively increased into summer whereas use of the forest habitats declined (selection index of 0.3). Animals foraged on cattails only during midday when black-globe temperatures exceeded  $29^{\circ}\text{C}$  and insect activity was extreme. These wet meadows were often used as bedding sites since they provided cool water and access to wind which ameliorated heat stress and insect activity.

Variation in habitat selection between individuals was greatest during autumn. Moose

no. 211 spent 52% of her time in aspen forest selecting Canada thistle and raspberry whereas no. 727 spent 41% of her time in more open habitats (selection index of 2.0) consuming green leaves and fruits of western snowberry. There also was notable shift to the forest edge and willow communities where woody stems and fallen leaves were consumed.

While foraging, moose appeared to select habitats on the basis of relative foraging returns (efficiency) and availability of dietary species expressed either as rates of intake of protein or digestible dry matter (Figs. 2 and 3). But under thermal stress or severe insect annoyance, foraging opportunities were sacrificed for comfort and energy economy in wetland communities.

**DISCUSSION**

**Forage Selection**

Forage selection by moose seems to be dictated largely by forage availability and quality as shown in Figs. 2 and 3. When available food is of generally high quality and abundant, moose need not be selective. As quality declines but variance among forages is high as in autumn, moose become more selective and compensate for a reduced intake by maximizing nutrient capture. In winter, forages are uniformly low quality so selection is based largely on availability.

Few studies have reported extensive use of fallen leaves by moose during autumn, winter, and spring. Investigations have demonstrated the importance of leaf litter to free-ranging wapiti (*Cervus elaphus nelsoni*) (Gates 1980, Nietfeld 1983) and quantified the con-

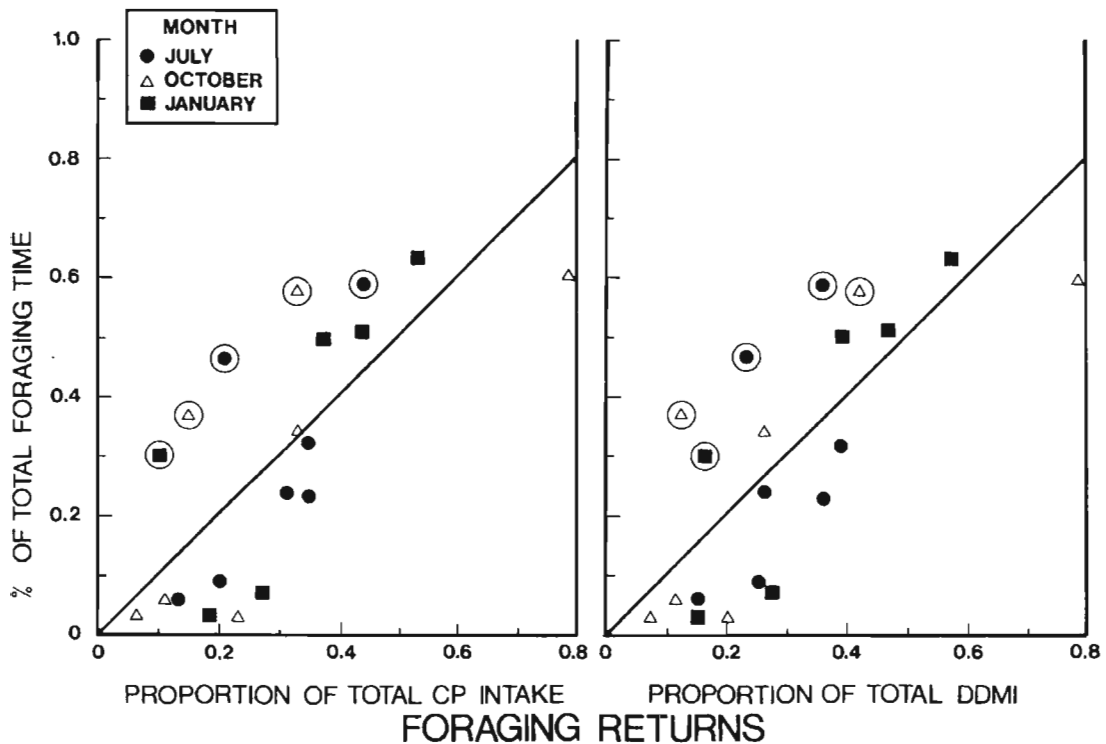


Fig. 2. Relative foraging time spent in major habitats in relation to relative foraging returns expressed as g crude protein consumed/min and g digestible dry matter intake (DDMI/min). Large circles denote habitat use during high ambient temperatures, insect harassment, selective foraging or snow crusts. The solid line represents the isometric line.

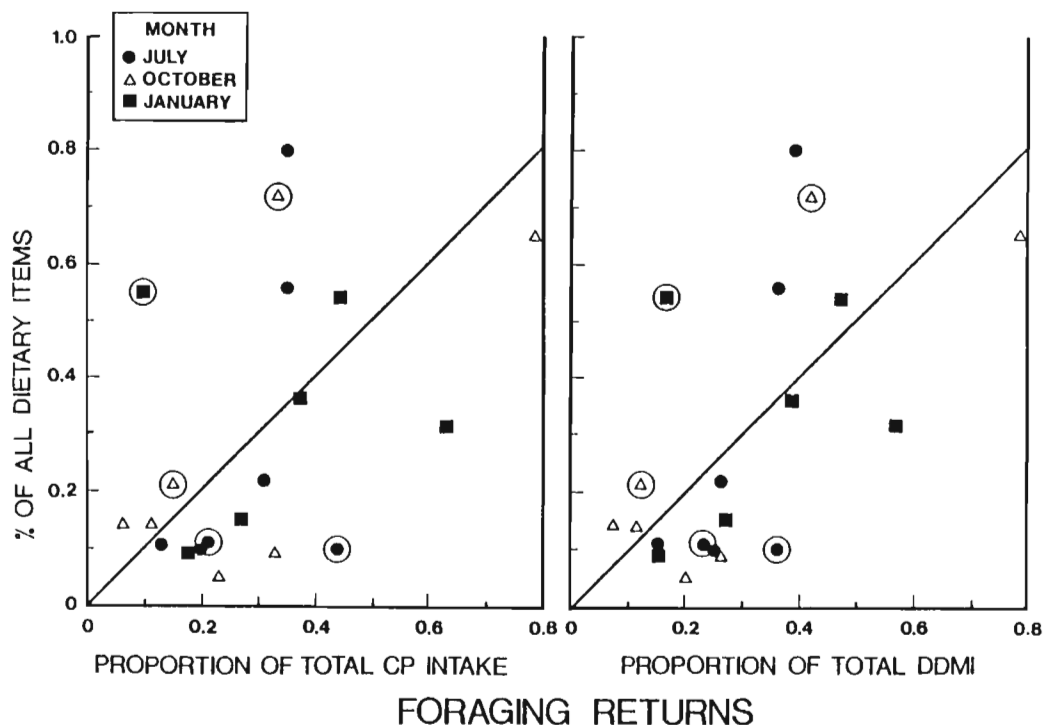


Fig. 3. Relative percent of total number of useable dietary items found in major habitats in relation to relative foraging returns expressed as g crude protein consumed/min and g digestible dry matter intake (DDMI/min). Large circles denote habitat use during high ambient temperatures, insect harassment, selective foraging, or snow crusts. The solid line represents the isometric line.

siderable biomass it provided (Renecker and Hudson 1986a). Although the crude protein content of fallen leaves decreases with leaching from autumn precipitation and spring thaws, digestibility remains higher than for woody stems (Renecker and Hudson 1988). If time and energy available to moose is limited, then the higher digestible dry matter content and reduction in travel costs involved with each feeding bout should improve the energy benefit of this forage resource in comparison to other foods during winter and early spring.

Snow crusts strongly influenced winter forage selection. Freeze-thaw cycles prevented access to leaf litter forcing moose into old field succession for sprout growth. The larger stem diameters of consumed twigs suggest a reduction in choice and selection concurrently with a decline in voluntary intake from the previous winter (Renecker and Hudson 1985).

Woody browse was a winter staple as in

other studies. Moderate intake of balsam poplar may reflect its availability and association with frequently-used willow communities. Woody stems from balsam poplar did not exceed 26% of the daily intake, possibly because of secondary metabolites (Palo 1984, Risenhoover *et al.* 1985) or the larger, more bulky twigs are more restrictive on the rate of passage of digesta through the ruminoreticulum. Extensive use was made of beaked hazel during December by one moose. Cairns (1976) reported heavy use of beaked hazel in nearby Elk Island National Park (EINP). In Riding Mountain National Park, beaked hazel was the dominant food species of moose throughout the year (Trottier 1981, Trottier *et al.* 1983). Because the understory vegetation is similar at EINP and Ministik Wildlife Research Station, moose should exhibit similar dietary preferences. The absence of beaked hazel from February diets of moose in this





study may be related to forage quality. During midwinter, stems of beaked hazel were lower in digestibility, cell solubles, and crude protein than either willow or leaf litter.

Bark was an important food in early spring. Peterson (1981) identified similar use of aspen bark during winter. Murie (1934) concluded that bark stripping indicated food shortage. Miquelle and Van Ballenberghe (1989) have suggested that moose consumed bark from aspen, balsam poplar, and willow when browse in Denali National Park was in short supply or range was limited by the animal's mobility. During winter, quality of bark declines due to dormancy (Oldemeyer 1974). However, during the spring nutrient flush, bark is highly digestible (Renecker and Hudson 1985) probably from the movement of cell solubles through the bark cambium (Chapin 1980). Differences in relative intake of bark in the diets of moose between ranges may be related to habitat interspersion. For example, the range in Denali National Park is abundant with riparian willow areas that offer aspen and associated shrub components that are more important. Mature aspen stands may provide more diverse but less concentrated food resources for moose and potentially longer pursuit times between patches. Given these conditions, there may be a lower cost-benefit through the trade-off of a reduction in browse intake for a higher consumption of more digestible aspen bark.

Following leaf flush, foliage emerged as the major dietary item. Trottier *et al.* (1983) reported similar use of the shrub layer by moose in southwestern Manitoba where leaves stripped from shrubs comprised 75% of the diet. Consumption of cattails and use of aquatic habitats by moose probably reflect the animal's response to extreme heat and insect harassment. Although cattails were lower in digestibility and crude protein and higher in fiber content than leaves of shrubs during summer (Renecker and Hudson 1985, 1988), the energetic advantages of cool water may

have enabled the moose to feed longer (Renecker and Hudson 1989). Crête and Jordan (1981) also reported cattails as a summer food of moose. In terms of quality, when cattails are the most available wetland plant, it would be important that moose utilize them. Consumption of this food source with a crude protein content of 13.9% *in situ* digestibility of 64%, and probably high starch content (Renecker 1987) reduces the even greater energy disparity that would occur if moose would choose to skip a meal because of oppressively high ambient temperatures (Renecker and Hudson 1992).

Quality of forage was an important factor in the choice of autumn foods. Areas protected from early frost supported green, succulent forage. Selective use of western snowberry, Canada thistle, and fallen leaves permitted these moose to maintain a more digestible diet in autumn than in summer, although intake was reduced (Renecker and Hudson 1985). Other studies have reported the winter use of elk thistle (*Cirsium foliosum*) (Knowlton 1959) and bull thistle (*Cirsium vulgare*) (Stone 1971) by moose. In the same study area, Canada thistle was observed as an preferred autumn food of wapiti (*Cervus elaphus nelsoni*) (Nietfeld 1983). *In situ* digestibility of Canada thistle (69.4%) was on average about two times more digestible than aspen, hazel, and willow twigs (32.7%) in autumn (Renecker and Hudson 1988). If the goal of this browser, the moose, is to maximize the net rate of nutrient capture then the optimal solution would be to consume Canada thistle that was abundant in the same food patch as browse species such as honeysuckle (*Lonicera* spp.), raspberry, western snowberry, and gooseberry (*Ribes* spp.) which supported nutritious green leaves into October.

Sedge was consumed in relatively small quantities by moose in this study during spring, summer, and autumn observation periods. Other workers have reported similar limited use of sedge by moose in British Columbia

(Eastman and Ritcey 1987), Alaska (Regelin *et al.* 1987), Isle Royale (Krefting 1951), Newfoundland (Dodds 1960), and several locations in western Canada and the Northwest Territories (Thomas 1990).

### Habitat Selection

Since our moose used in this study were habituated, protected from predation, and non-reproductive, these factors should be minimized and habitat selection should largely reflect the trade-off between foraging efficiency and comfort. On an annual basis, foraging efficiency emerged as the dominant effect. Moose seemed to apportion their time in different habitats according to relative foraging rates. This "proportional rule" allowed moose to acquire large absolute quantities of fibrous food that was high in digestible nutrients by choosing habitat types that offered maximum opportunities for efficient foraging. However, other factors such as heat stress, summer insect harassment, winter melt-freeze cycles, and spatial change in the distribution of forage appeared to influence the "decision rules" of moose and resulted in deviations from an isometric response between foraging returns and either diet or foraging time.

In summer, there are relatively small differences in food quality among patches in comparison to other seasons and generally, moose were nonselective feeders during this period (see foraging returns in Figs. 2 and 3). As food quality declines, moose become more selective choosing patches which reduce foraging efficiency but increase nutrient capture. As a consequence, they compensate for the lower intakes by maximizing diet quality. This strategy resulted in no penalty of overall diet quality or possibly retention time in the rumen. In winter, moose continue to apportion time in habitats according to quality and biomass. However, selectivity was less important as a compensatory mechanism for limited food resources.

During winter, deviations in the use of habitats in proportion to foraging efficiency can be explained in terms of forage availability and snow conditions. The relative use of these areas varies markedly with winter severity and snow conditions (Cairns 1976; Peek *et al.* 1982). Generally, moose minimize daily movements during winter and utilize readily available food items, such as leaf litter or dense stands of riparian willow. However, snow crusting results in a decline in the availability of forage biomass and a shift in habitat use and food selection. Moose must increase their search times as a trade-off for reduced foraging efficiency and use a variety of different habitats with usable food items.

Although selection of habitats reflects both food resources and security, the consequences of canopy cover is modified meteorological conditions and relaxed energetic constraints. The benefits of these habitat options in terms of the operational environment would only become prominent factors during severe winters because moose are extremely cold tolerant (Renecker *et al.*, 1978, Renecker and Hudson 1986b).

Several studies in central Alberta have also reported heavy use of poplar and mixed poplar cover types for both feeding and nonfeeding activities (Nowlin 1976, Penner, 1971). The presence of moose in aspen forest and willow habitats is probably related to availability of food (Telfer 1967). Closed canopy forest provided moose with abundant high quality food. The shade provided by these habitats was probably attractive with higher ambient temperatures of May. Since moose spent between 22% and 43% of the 24-hr day bedded under an aspen canopy during the daylight hours.

During summer, moose selected more open habitats associated with water. Standing and lying in sedge meadows or cattail stands reduced thermal stress (Renecker and Hudson 1989) and annoyance from swarms of mosquitoes (*Culicidae* spp.). Use of ponds and

streams for relief from heat has been reported previously by Flook (1959) and Kelsall and Telfer (1974). Moose are susceptible to heat stress at lower ambient temperatures than other ungulates (Renecker and Hudson 1986b).

Upland grassland snowberry and forest edge habitats were used more than expected during autumn. Most activities in these areas were carried out during darkness to avoid solar radiation and black-globe temperatures exceeding 20°C. Nevertheless, the use of these communities in relation to forested areas probably reflects the selectivity and mix of forages.

### CONCLUSIONS

We speculate that moose acquire large absolute quantities of highly digestible but lignified food by selection of habitat types that offer maximum opportunities for efficient foraging of a variety of dietary items. Moose probably perceive food patches similar to deer (Hanley 1982) in terms of the breadth of quality in forage species (crude protein content) and biomass (digestible dry matter intake). However, thermoregulatory needs, high insect activity, and snow conditions can alter the decision-making process in moose.

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### REFERENCES

- ANON. 1980. Canadian Climate Normals. 1951-1980. Temperature and Precipitation. Pub. Canadian Climate Program, Environment Canada, Ottawa p. 126.
- BARRETT, M. W. 1972. A review of the diet, condition, disease and parasites of the Cypress Hills moose. Proc. N. Am. Moose Conf. Workshop. 8:60-79.
- BERG, N. E., and R. L. PHILLIPS. 1974. Habitat use by moose in northwestern Minnesota with reference to other heavily willowed areas. Nat. can. 101: 101-116.
- BRASSARD, J. M., E. AUDY, M. CRETE, and P. GRENIER. 1974. Distribution and winter habitat of moose in Quebec. Nat. can. 101:67-80.
- CAIRNS, A.L. 1976. Distribution and food habits of moose, wapiti, deer, bison and snowshoe hare in Elk Island National Park, Alberta. M.Sc. Thesis, University of Calgary, Calgary 167 pp.
- CHAPIN, F. S., III. 1980. The mineral nutrition of wild plants. Ann. Rev. Ecol. Syst. 11:233-260.
- COADY, J. W. 1983. Moose. Pages 902-922 in J. A. Chapman, and G. A. Feldhamer, eds. Wild mammals of North America: Biology, Management, and Economics. The John Hopkins University Press, Baltimore.
- CRETE, M., and A. JORDAN. 1981. Regime alimentaire des orignaux du sud-ouest quebecois pour les mois d'avril a octobre. Can. Field Nat 95: 50-56.
- DODDS, D. G. 1960. Food competition and range relationships of moose and snowshoe hare in Newfoundland. J. Wildl. Manage. 24:52-60.
- EASTMAN, D. S., and R. RITCEY. 1987. Moose habitat relationships and management in British Columbia. Swedish Wildl. Res Suppl. 1:101-117.
- FLOOK, D. R. 1959. Moose using water as a refuge from flies. J. Mammal. 40: 455.

- GATES, C. C. 1980. Patterns of behavior and performance of wapiti (*Cervus elaphus nelsoni*) in the boreal mixed wood forest. Ph.D. Thesis, University of Alberta, Edmonton, 240 pp.
- GATES, C.C., and R. J. HUDSON. 1981. Habitat selection by wapiti in a boreal forest enclosure. *Nat. can.* 108: 153-166.
- HANLEY, T. A. 1982. The nutritional basis for food selection by ungulates. *J. Range Manage.* 35: 146-151.
- KELSALL, J. P., and E. S. TELFER. 1974. Biogeography of moose with particular reference to western North America. *Nat. can.* 101: 117-130.
- KNOWLTON, F. F. 1960. Food habits, movement and populations of moose in the Gravelly Mountains, Montana. *J. Wildl. Manage.* 24: 162-170.
- KREFTING, L. W. 1951. What is the future of the Isle Royal moose herd? *Trans. N. Am. Wildl. Conf.* 16: 461-470.
- \_\_\_\_\_. 1974. Moose distribution and habitat selection in North Central North America. *Nat. can.* 101:81-100.
- LEPTICH, D. J. and J. R. GILBERT. 1989. Summer home range and habitat use by moose in northern Maine. *J. Wildl. Manage.* 53:880-885.
- MIQUELLE, D. G. and V. VAN BALLEMBERGHE. 1989. Impact of bark stripping by moose on aspen-spruce communities. *J. Wildl. Manage.* 53: 577-586.
- MURIE, A. 1934. The moose of Isle Royale. Misc. Pub. No. 25, Mus. Zool., University of Michigan.
- MYTTON, W. R., and L. B. KEITH. 1981. Dynamics of moose populations near Rochester, Alberta, 1975-1978. *Can. Field-Nat.* 95: 39-49.
- NIETFELD, M. T. 1983. Foraging behavior of wapiti in the boreal mixed-wood forest, Central Alberta. M.Sc. Thesis, University of Alberta, Edmonton 187 pp.
- NOWLIN, R.A. 1976. Relationships between habitats, forages and carrying capacity of moose range in northern Alberta. Part 1: Moose preferences for habitat strata and forages (A final report from Ministik Lake, Alberta). Alberta Oil Sands Environ. Res Prog. Rep. T.F.1.2. 18 pp.
- OLDEMEYER, J.L. 1974. Nutritive value of moose forage. *Nat. can.* 101:217-226.
- OLSON, R. 1985. The climate of Edmonton - Climatological studies No. 37, The climate of Canadian cities. No. 2, Environment Canada, Ottawa 54 pp.
- PALO, R.T. 1984. Distribution of birch (*Betula* spp.), willow (*Salix* spp.), and poplar (*Populus* spp.) secondary metabolites and their potential role as chemical defense against herbivores. *J. Chem. Ecol.* 10: 499-520.
- PEEK, J.M., M., SCOTT, L.J. NELSON, D.J. PIERCE, and L.I. IRWIN. 1982. Role of cover in habitat management for big game in northwestern United States. *Trans. North Am. Wildl. Nat. Resource Conf.* 47:363-373.
- PENNER, D.F. 1981. Range ecology and the influence of agriculture on moose and deer range on the Smoky River breaks, Alberta. Alberta Fish Wildl. Div. Rep., Edmonton 50 pp.
- PETERSON, R.L. 1981. North American moose. University of Toronto Press, Toronto 280 pp.
- PIERCE, D.J., and J.M. PEEK. 1984. Moose habitat use and selection patterns in north-central Idaho. *J. Wildl. Manage.* 48:1335-1343.
- REGELIN, W.L., C.C. SCHWARTZ, and A.L. FRANZMANN. 1987. Effects of forest succession on nutritional dynamics of moose forage. *Swedish Wildl. Res Suppl* 1:247-163.
- RENECKER, L.A. 1987. Bioenergetics and behavior of moose (*Alces alces*) in the aspen-dominated boreal forest. Ph.D. Thesis. University of Alberta, Edmonton 265 pp.
- \_\_\_\_\_, R.J. HUDSON, M.K. CHRISTO-

- PHERSEN, and C. ARELIS. 1978. Effect of posture, feeding, low temperature and wind on energy expenditures of moose calves. *N. Am. Moose Conf. Workshop.* 14:126-140.
- \_\_\_\_\_, and \_\_\_\_\_. 1985. Estimation of dry matter intake of free-ranging moose. *J. Wildl. Manage.* 49:126-140.
- \_\_\_\_\_, and \_\_\_\_\_. 1986a. Seasonal foraging rates of free-ranging moose. *J. Wildl. Manage.* 50:143-147.
- \_\_\_\_\_, and \_\_\_\_\_. 1986b. Seasonal energy expenditures and thermoregulatory responses of moose. *Can. J. Zool.* 64:322-327.
- \_\_\_\_\_, and \_\_\_\_\_. 1988. Seasonal quality of forages used by moose in the aspen boreal forest, central Alberta. *Holarctic Ecology* 11:111-118.
- \_\_\_\_\_, and \_\_\_\_\_. 1989. Ecological metabolism of moose in aspen-dominated boreal forests, central Alberta, *Can J. Zool.* 67:1923-1928.
- \_\_\_\_\_, and \_\_\_\_\_. 1992. Theroregulatory and behavioral response of moose: Is large body size an adaptation or constraint? *Alces* 28 Suppl 1:52-64.
- RISENHOOVER, K.L. L.A. RENECKER, and L.E. MORGANTINI. 1985. Effects of secondary metabolites from balsam poplar and paper birch on cellulose digestion. *J. Range Manage.* 38:370-372.
- ROWE, J.S. 1972. Forest regions of Canada. - Dept. Environ. Can. Forest Serv. Pub. No. 130. 172 pp.
- SCHWARTZ, C.C., W.C. REGELIN, and A.W. FRANZMANN. 1985. Suitability of a formulated ration for moose. *J. Wildl. Manage.* 49: 137-141.
- SNEDECORE, G.W., and W.G. COCHRANE. 1967. *Statistical methods.* Iowa Univ. Press, Ames 593 pp.
- STONE, J.L. 1971. Winter movements and distribution of moose in upper Rock Creek drainage, Granite County, Montana. M.Sc. Thesis. University of Montana, Missoula 80 pp.
- TELFER, E.S. 1967. Comparison of moose and deer winter range in Nova Scotia. *J. Wildl. Manage.* 31: 418-425.
- \_\_\_\_\_. 1978. Habitat requirements of moose, the principal taiga range animal. *Proc. Int. Rangeland Cong.* 1:462-465.
- THOMAS, D.C. 1990. Moose diet and use of successional forest in the Canadian taiga. *Alces* 26: 24-29.
- TROTTIER, G.C. 1981. Beaked hazelnut - a key browse species for moose in the boreal forest region of Western Canada? *Alces* 17:257-281.
- \_\_\_\_\_, S.R. ROLLINS, and R.C. HUTCHINSON. 1983. Range, habitat and foraging relationships of ungulates in Riding Mountain National Park. Canadian Wildlife Service, Large Mammal System Studies Rep. No. 14. 224 pp.
- VAN BALLEMBERGHE, V., and D.G. MIQUELLE. 1990. Activity of moose during spring and summer in interior Alaska. *J. Wildl. Manage.* 54:391-396.