Use of aquatic plants by moose: sodium hunger or foraging efficiency?

JAMES G. MACCRACKEN[1]
Department of Fish and Wildlife Resources, University of Idaho, Moscow, ID 83844-1136, U.S.A.

VICTOR VAN BALLENBERGHE
USDA, Forest Service, Pacific Northwest Research Station, Institute of Northern Forestry, 3301 C Street, Suite 200, Anchorage, AK 99503-3954, U.S.A.

AND

JAMES M. PEEK
Department of Fish and Wildlife Resources, University of Idaho, Moscow, ID 83844-1136, U.S.A.

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Use of submergent aquatic plants by North American moose (*Alces alces*) has been linked to sodium hunger. Habitat preferences, seasonal diets, forage abundance and quality, and population surveys indicated that emergent plants in small shallow ponds were important to moose on the Copper River Delta, Alaska. However, sodium was abundant in terrestrial browse. We propose that foraging in aquatic habitats, particularaly on emergent species, may be highly efficient based on the following habitat attributes and behavioral observations: (*i*) ponds dominated by either emergent or submergent species produced about 4 times more forage than terrestrial habitats, (*ii*) emergent and submergent plants were more digestible and had higher concentrations of minerals than browse, (*iii*) use of aquatic habitats followed trends in forage production over the growing season, (*iv*) indirect evidence suggested that forage intake rates were greater in aquatic habitats, and (*v*) use of aquatic habitats by male and female moose was in proportion to the sex structure of the population. These data provide consistent circumstantial evidence that use of emergent species, and possibly submergents, may maximize the intake of nutrients and also reduce conflicts between cropping forage and vigilance during a foraging bout.

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Chez l'Orignal (*Alces alces*), la consommation de plantes aquatiques submergées a toujours été attribuée au besoin de sodium. Le choix de l'habitat, le régime alimentaire saisonnier, l'abondance et la qualité de la nourriture, et des inventaires de la population ont démontré que les plantes émergentes des petits étangs peu profonds ont une grande importance pour les orignaux du delta de la rivière Copper en Alaska. Cependant, le sodium abonde dans le brout terrestre. Nous posons en hypothèse que la recherche de nourriture en milieu aquatique, particulièrement la consommation d'espèces émergentes, est une stratégie très efficace si l'on tient compte des attribute du milieu et des divers comportements suivants: (*i*) les étangs dominés par des espèces émergentes ou submergées peuvent fournir environ quatre fois plus de nourriture que les habitats terrestres, (*ii*) les plantes émergentes et les plantes submergées sont plus digestibles et comptent des concentrations plus élevées de minéraux que le brout, (*iii*) l'utilisation des habitats aquatiques suit les tendances de la production de nourriture au cours de la saison de croissance, (*iv*) des preuves indirectes permettent de croire que les taux de consommation de nourriture sont plus élevés dans les habitats aquatiques et (*v*) l'utilisation des milieux aquatiques par les mâles et les femelles se fait selon des proportions comparables aux proportions de mâles et de femelles dans la population. Ces données constituent des preuves circonstantielles faibles que la consommation de plantes émergentes, et peut-être aussi de plantes submergées, peut maximiser l'absorption de matières nutritives et également réduire les conflits entre le broutage et la surveillance au cours d'une période d'alimentation.

[Traduit par la rédaction]

Introduction

Seasonal variation in forage abundance and quality, activity patterns, metabolism, body mass, and social behavior (Schwartz 1992) requires that moose (*Alces alces*) maximize their net intake of energy. Adequate fat reserves need to be accrued during summer, and premature depletion of reserves must be avoided during winter.

Moose in North America frequently consume submergent aquatic vegetation during spring and summer (Murie 1934; Botkin et al. 1973; Fraser et al. 1982). Some studies have emphasized sodium (Na) acquisition as the impetus for aquatic foraging by moose (Botkin et al. 1973; Jordan et al. 1973; Belovsky 1981; Belovsky and Jordan 1981; Fraser et al. 1982, 1984). The Na hypothesis is based on strong circumstantial evidence (Jordan 1987), but continues to be debated and investigated (Risenhoover and Peterson 1986). In addition, Faber et al. (1988) did not find a link between moose foraging on emergent aquatics in Sweden and Na in terrestrial forages.

In this paper we propose that the use of aquatic plants, particularly emergents, by moose is efficient in terms of maximizing the net intake of nutrients (Hanley 1984) and reducing competition between cropping forage and scanning for predators during a foraging bout (Berger et al. 1983). We analyze new data from Alaska and data in the published literature as the foundation for this hypothesis. We do not test this hypothesis, but provide evidence of its potential validity from a number of studies conducted in a variety of areas.

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[1] Present address: Policy Analysis Group, College of Forestry, Wildlife, and Range Sciences, University of Idaho, Moscow, ID 83844-1134, U.S.A.

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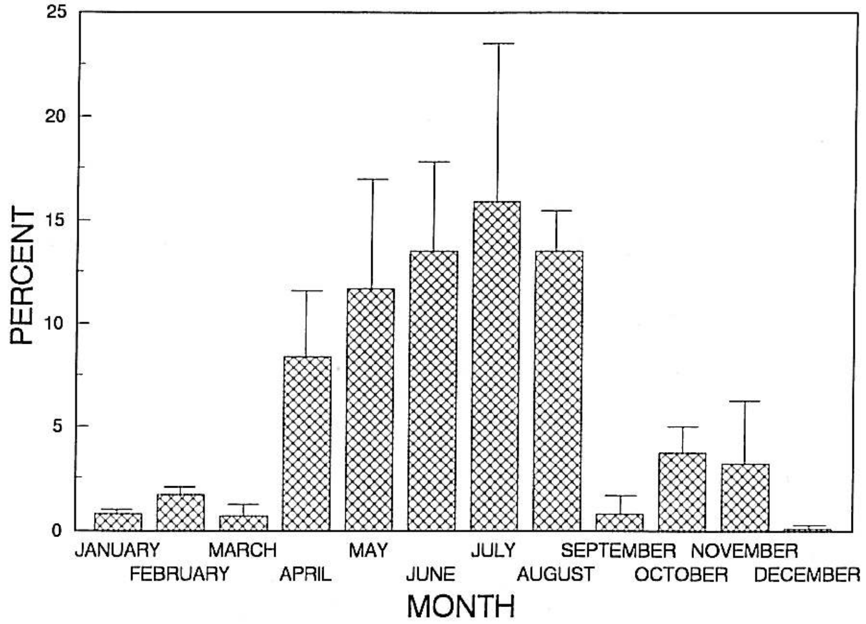

FIG. 1. Mean (SE) proportion of moose observed in aquatic habitats during flights over the west Copper River Delta, Alaska. Data were collected from March 1987 to July 1989.

Study area and methods

Data on moose habitat use and seasonal diets, and forage production, digestibility, and mineral composition, were collected from the west Copper River Delta, Alaska (WCRD, ≈700 km^2), from March 1987 to July 1989 (MacCracken 1992). The Copper River Delta (≈3200 km^2) is the largest wetland remaining on the Pacific Coast of North America and contains a variety of terrestrial and aquatic habitats used by moose.

The importance of aquatic habitats to moose on the WCRD was evaluated by determining whether moose preferentially selected for aquatic habitats, and by estimating the proportion of the population that used those habitats. We fitted 22 moose (6 ♂♂, 16 ♀♀; about 10% of the population) with radio collars and regularly relocated them with a fixed-wing aircraft year round between 08:00 and 17:00. Second-order habitat selection (Johnson 1980) was estimated by comparing the proportion of habitats within home ranges of radio-collared moose with the proportion of habitats available on the study area (Marcum and Loftsgaarden 1980). The proportion of the population that used aquatic habitats was estimated by comparing moose seen in aquatic habitats with all moose observed. The later data included moose with and without collars.

When moose were seen in aquatic habitats, the category (pond, creek, deep-water lake, river, slough, etc.) was noted. The origin (lateral levee, glacial, oxbow, dune, beaver (*Castor canadensis*), etc.) of ponds, size, and the vegetation zone occupied (anchored or floating mat, emergent, submergent, deep water, etc.) were also recorded. In addition, the activity (feeding, bedded, moving, social), and sex- and age-class (male, female, female with calf, etc.) of the animals were recorded.

During July 1988 and 1989, aquatic habitats were sampled for annual forage production (kg/ha) by clipping plots within a replicated sampling scheme (MacCracken 1992). Over-winter forage mass in aquatic habitats was estimated based on the annual production of species that were available during intermittent midwinter thaws. Four terrestrial habitat types were also sampled for annual production of leaves and twigs of browse and over-winter twig mass using a double sampling technique (MacCracken and Van Ballenberghe 1993*b*) and a replicated sampling scheme.

The seasonal diets of moose on the WCRD were estimated from fecal and rumen samples, estimates of browse consumption from vegetation sampling, and observations of foraging moose (MacCracken and Van Ballenberghe 1993*a*). Estimates were pooled by month, and seasonal changes in diets were identified with complete-linkage cluster analysis.

Forage quality was assessed for winter, spring, and summer periods. Digestible protein and digestible dry matter were estimated following procedures outlined by Hanley et al. (1992). Mineral content was estimated with standard atomic absorption spectrophotometry. Samples analyzed included individual species and parts as well as forage mixes simulating diet composition (MacCracken 1992).

Hypothesis criteria

At least 1 of 2 habitat characteristics was considered necessary to facilitate efficient foraging by moose: (1) annual production of aquatic forages should be greater than that of terrestrial browse, and (2) aquatic plants should be higher in nutritional quality than browse. These conditions should promote the following responses: (*i*) maximum use of aquatic forage by moose should correspond to peak production, (*ii*) forage intake rates should be greater when feeding in aquatic habitats, and (*iii*) use of aquatic habitats by males and females should be in proportion to the sex structure of the population. Data from this study and from the literature addressing the above criteria were analyzed.

Statistical comparisons among the data from the WCRD were made with factorial univariate or multivariate analysis of variance. Comparisons between aquatic and terrestrial habitats, summarized from this study and the literature, were made with *t* tests. Mean values reported in the text are followed by the standard error in parentheses.

Results and discussion

On the WCRD, more than 90% of all observations of radio-collared moose occurred in 5 habitat types, with aquatic habitats used the least. More than 90% of moose in aquatic habitats were in small (≤1 ha) ponds resulting from lateral levee formation. Approximately 14% of the WCRD was occupied by these ponds, which were classified as palustrine emergent wetlands (Cowardin et al. 1979). Moose selected home ranges where the proportion of these ponds, as well as sweetgale–

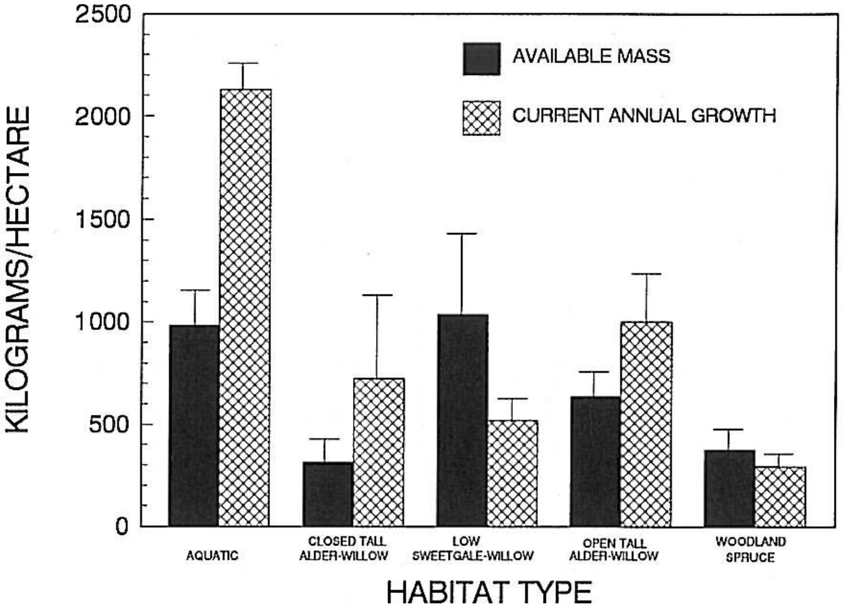

FIG. 2. Mean (SE) mass of forage plants in five habitat types used by moose on the west Copper River Delta, Alaska. Available mass was forage available during winter.

willow (*Myrica gale—Salix* spp.) habitat, was greater than over the entire WCRD.

Moose were observed using aquatic habitats year-round (Fig. 1). However, the greatest use ($F = 39.1$, $P = 0.001$) occurred from May to August, peaking in July. While in these ponds, >90% of the moose observed were feeding in the emergent-vegetation zone, which was dominated by horsetails (*Equisetum fluviatile, E. palustre, E. variegatum*), buckbean (*Menyanthes trifoliata*), sedges (*Carex* spp.), and marsh five-finger (*Potentilla palustre*). Water depth was generally ≤1 m in this zone, and submergent species averaged only 0.3(0.2)% of the total annual production of the ponds sampled (MacCracken 1992).

Annual forage production was approximately 4 times greater ($F = 29.8$, $P = 0.001$) in the ponds than in terrestrial habitats (Fig. 2). However, over-winter available mass in two terrestrial habitats was similar ($P > 0.05$) to that of the aquatic habitat. This equality may explain why the aquatic habitat was not used more extensively during winter thaws.

The diets of moose on the WCRD were dominated by the twigs and leaves of willows (*S. barclayi, S. sitchensis*) year-round. However, corresponding to the peak in use of aquatic habitats, the percentage of buckbean and horsetails was greatest in ($F = 2.9$, $P = 0.04$) the spring/early summer diet of moose (MacCracken 1992).

In general, the leaves of browse were higher ($F = 3.5$, $P = 0.002$) in digestible protein than aquatic herbs, however, buckbean had the highest estimates (Table 1). In contrast, digestible dry matter was consistently greater ($F = 8.6$, $P = 0.0004$) in aquatic herbs than in terrestrial browse. Digestible dry matter and digestible energy of forages are closely related (Schwartz et al. 1987). Additionally, the ash content of these forage classes followed the same pattern as digestible dry matter (Table 1).

Significant differences ($F = 3.5$, $P = 0.0001$) among forage species in mineral estimates were attributed to higher levels of calcium (Ca), iron (Fe), potassium (K), and fluoride (Fl) in aquatic herbs than in terrestrial browse, but not Na (Table 2). However, when species were pooled by habitat type, the aquatic habitat had greater ($F = 3.7$, $P = 0.02$) levels of Na as well as magnesium (Mg), manganese (Mn), K, and phosphorous (P).

Weeks and Kirkpatrick (1976) proposed that Na hunger in white-tailed deer (*Odocoileus virginianus*) was related to high levels of K in spring forages, which resulted in a loss of Na due to wet feces. Fraser et al. (1984) and Risenhoover and Peterson (1986) suggested that Na hunger in moose also appeared to fit that hypothesis. On the WCRD, K:Na ratios were not significantly different ($F = 0.13$, $P = 0.72$) between aquatic herbs (22(6)) and browse (28(8)), indicating that aquatic plants would not be useful in alleviating a Na deficit

TABLE 1. Percent digestible protein (DP), digestible dry matter (DDM), and ash for aquatic herbs and terrestrial browse (leaves and twigs) used by moose on the west Copper River Delta, Alaska

Category and species	DP[a]	DDM[a]	Ash
Aquatics			
Equisetum spp.	7.7(2.7)	77.5(4.8)	12.2(0.5)
Carex spp.	4.4(3.7)	63.0(8.5)	5.7(0.5)
Menyanthes trifoliata	9.2(3.9)	75.9(3.4)	6.6(0.5)
Potentilla palustre	2.8(1.6)	63.0(7.5)	4.9(0.7)
Browse			
Alnus sinuata	6.8(0.1)	47.2(5.8)	3.7(1.1)
Myrica gale	9.1(0.7)	38.7(3.6)	2.5(0.5)
Populus trichocarpa	6.3(1.7)	54.1(0.5)	5.1(1.5)
Salix alaxensis	6.4(2.5)	52.6(7.0)	5.3(1.9)
S. barclayi	6.6(2.1)	47.6(5.2)	4.8(1.8)
S. sitchensis	6.4(1.8)	48.3(6.9)	4.6(1.2)

NOTE: Values are given as means with standard error in parentheses. Samples were collected during July 1988 and 1989.

[a] Based on procedures of Robbins et al. (1987*a*, or 1987*b*) and Hanley et al. (1992).

TABLE 2. Mean concentration (ppm) of some minerals in aquatic herbs and terrestrial browse (leaves and twigs) used by moose on the Copper River Delta, Alaska

Category and species	Ca	Fe	Fl	K	Mg	Mn	Na	P
Aquatics								
Equisetum spp.	7139	37	4	18 003	1802	72	927	1601
Carex spp.	3501	87	2	9 319	818	115	349	1153
Menyanthes trifoliata	4566	10	2	15 432	1500	14	867	2189
Potentilla palustre	6017	24	3	6 819	2016	20	588	866
Browse								
Alnus sinuata	4539	7	2	6 701	1420	26	263	1643
Myrica gale	2659	8	2	3 501	931	26	520	788
Populus trichocarpa	4095	20	8	6 748	1247	8	164	1167
Salix alaxensis	5730	18	3	4 211	1048	24	280	1332
S. barclayi	1434	8	2	9 252	1530	23	227	1222
S. sitchensis	4798	6	1	11 498	1767	24	288	1401

NOTE: Samples were collected in July 1988 and 1989.

TABLE 3. Estimates of annual production, forage quality, and foraging efficiency measures for aquatic and terrestrial habitats used by moose from North American studies

	Habitat		
Characteristic	Aquatic	Terrestrial	Reference
Annual production (kg/ha)	1290(15)	337(13)	Belovsky and Jordan 1978
	2130(185)	490(138)	MacCracken 1992
Forage quality			
Crude protein (% dry matter)	16(1)	13(1)	Fraser et al. 1984
	17(1)	13(1)	MacCracken 1992
Gross energy (kcal/g)	4.2(0.1)	4.8(0.1)	Fraser et al. 1984
Ash (% dry matter)	12(1)	5(0.3)	Fraser et al. 1984
	8(1)	5(1)	MacCracken 1992
In vitro digestion	47(14)	36(11)	Belovsky and Jordan 1978
	83(10)	52(4)	Oldemeyer et al. 1977
In vivo digestion	94	72	Belovsky and Jordan 1978
Digestible dry matter (%)	68(3)	48(3)	MacCracken 1992
Digestible protein (%)	11(1)	6(1)	Fraser et al. 1984*
	6.8(1.9)	6.4(0.1)	MacCracken 1992
Digestible energy (kcal/g)	2.8(0.1)	2.2(0.04)	Fraser et al. 1984*
(% dry matter)	68.2(2.5)	47.6(2.3)	MacCracken 1992
Foraging efficiency			
Intake rate (g/min)	20(1)	17(2)	Belovsky and Jordan 1978
Foraging bout length (min)	60		De Vos 1958
	54		Joyal and Scherrer 1978
	58(9)		Fraser et al. 1982
		115(10)	Renecker and Hudson 1989
		73(1)	Van Ballenberghe and Miquelle 1990
		81(7)	Bevins et al. 1990

NOTE: Values are means with standard error in parenthesis.
*Estimated by adjusting values for mean digestibility that was calculated from the values presented in this table.

resulting from this mechanism. However, K:Na ratios were greater ($F = 4.31$, $P = 0.02$) in summer (33(12)) than in winter (15(4)) and spring (26(7)), coinciding with peak use of aquatic habitats by moose. Additionally, K:Na ratios of moose diets were correlated ($r = 1.0$, $P = 0.01$) with the Na content of moose feces (MacCracken 1992). Weeks and Kirkpatrick (1976; p. 616) reported K:Na ratios that were 1 order of magnitude greater (112–549) than WCRD forages (11–43), and K:Na ratios calculated from Fraser et al. (1984; p. 85) ranged from 183–314. These comparisons indicated that K:Na ratios in WCRD browse should not produce a strong Na drive. Furthermore, feeding experiments conducted by Christian (1989) with captive voles (*Microtus pennsylvanicus*) cast doubt on the validity of the high K–Na hunger hypothesis.

The moose – aquatic habitat relationship on the WCRD clearly differed from that at Isle Royale, Michigan and Sibley Park, Ontario (Jordan 1987). On the WCRD, emergent species dominated the flora of the ponds and were eaten by moose. Na was abundant in aquatic and terrestrial forage, and no clear link between Na hunger and feeding on aquatic plants was apparent. In contrast to inland areas (Fraser et al. 1982; Tankersley and Gasaway 1983; Risenhoover and Peterson

1986), moose on the WCRD were never observed using mineral licks, and even anecdotal accounts of lick use were lacking. We conclude that moose on the WCRD do not experience Na deficiencies, yet use of aquatic plants was significant. Faber et al. (1988) reached a similar conclusion for a study in Sweden where aquatic habitats and forage species were more similar to the WCRD than to those of other North American studies. They were the first to suggest that use of aquatic plants by moose may be for other reasons than Na acquisition.

Support for the foraging efficiency hypothesis

Data from this study and that in the literature addressing the criteria that would facilitate efficient foraging by moose are summarized in Table 3. Estimates of annual forage production in habitats dominated by submergent or emergent species were, on average, 4 times greater ($t = 5.9$, $P = 0.003$) than those for terrestrial habitats.

The nutritional quality of both submergent and emergent macrophytes was greater than that of terrestrial browse (Table 3). Crude protein ($t = 5.5$, $P = 0.001$), gross energy ($t = 17.4$, $P < 0.001$), and ash content ($t = 8.6$, $P < 0.001$) were greater in aquatic plants. All measures of dry-matter digestibility were higher ($t = 2.74$, $P = 0.03$) for aquatic plants (73(10)%) than for browse (52(7)%). The same was true for digestible protein ($t = 6.9$, $P < 0.001$, 9(2)%, and 6(0.2)%, respectively) as well as digestible energy for submergents from Sibley Park ($t = 5.2$, $P = 0.003$) and emergents from the WCRD ($t = 6.3$, $P = 0.001$).

Constraints on rumen fill imposed by the water content of aquatic plants (i.e., bulk) may reduce their nutritional value (Jordan 1987). However, bulk is not a significant problem when moose forage on emergent vegetation. The 3 aquatic plants eaten by moose on the WCRD averaged 78(1)% moisture, compared with 69(6)% for Sitka alder (*Alnus sinuata*) and Sitka willow (*S. sitchensis*) ($t = 1.53$, $P = 0.3$; T. Stephenson, unpublished data). In addition, Hobbs (1990) and Holand (1992; p. 1332) argued that moisture content does not significantly restrict ingesta fill.

Use of aquatic habitats by moose peaked in July on the WCRD, in late June – early July at 2 sites in Ontario (Fraser et al. 1980, 1982), mid-July in Sweden (Faber et al. 1988), and midsummer on Isle Royale (Belovsky et al. 1973). In addition, other studies have also reported heaviest use of aquatic habitats by moose in mid–late summer (De Vos 1958; Joyal and Scherer 1978). Production of aquatic forage over the growing season was not estimated in any of the studies reviewed. Auclair et al. (1976) reported that maximum standing crop and net productivity of *E. fluviatile* occurred in early July for a *Scirpus–Equisetum* wetland in southern Quebec. In general, production of aquatic macrophytes peaks during July–September, depending on the species (Wetzel 1975).

Belovsky and Jordan (1978) reported a slightly greater forage intake rate by moose when feeding on submergent plants versus browse. However, their intake estimate was based on investigators using their hands to simulate moose cropping. No other studies have made this comparison.

Data on foraging bout lengths largely support the classification of moose as energy maximizers (Belovsky and Jordan 1981) and concentrate selectors (Hofmann 1986). The length of foraging bouts varies with forage abundance, forage quality, and searching and handling times. Both Cederlund et al. (1989) and Van Ballenberghe and Miquelle (1990) reported a significant increase in foraging bout lengths of moose as forage quality and abundance increased. Presumably, moose spent more time seeking preferred species or plant parts in order to select the highest quality diet possible. However, the length of foraging bouts of moose on the WCRD declined significantly from winter to summer (MacCracken 1992). A notable difference between these studies was that moose used aquatic habitats only on the WCRD. The emergent wetlands on the WCRD were a concentrated source of high quality forage dominated by two or three species that were uniformly distributed throughout a patch. In addition, aquatic plants are less variable in nutritional quality than browse because of lower variation in fiber and, presumably, tannin content among plant parts. These conditions decrease the importance of searching for preferred species or plant parts while foraging on aquatics, resulting in relatively rapid rumen fill. Belovsky and Jordan (1978; p. 87) also opined that moose were not selecting for plant parts or species when feeding in ponds. These conclusions suggest that once moose select a foraging site in aquatic habitats, they may switch from an energy-maximizing to a time-minimizing strategy. Additional support for this contention is also supplied by other studies that have estimated the length of foraging bouts for either aquatic or terrestrial habitats (Table 3). Feeding bouts in aquatic habitats dominated by submergents averaged 56(2) min compared with 90(13) min in terrestrial habitats ($t = 2.2$, $P = 0.08$).

Energy expenditures associated with moving through water and the soft substrates of ponds may reduce the advantages of foraging on aquatic plants. Belovsky and Jordan (1978) estimated that foraging in aquatic habitats on Isle Royale was 3 times more costly than in terrestrial habitats. However, Risenhoover (1987) and Miquelle (1990) reported a negative exponential relationship between forage abundance and movement rates by moose in terrestrial habitats. The fact that aquatic habitats are about 4 times more productive than terrestrial habitats should result in less distance traveled per unit of forage mass consumed. Also, the greater nutritional quality of aquatic plants further offsets the greater costs associated with movement in those habitats.

On the WCRD, females (61%) were observed foraging in aquatic habitats more often than males (25%). However, the sex ratio of the WCRD population was maintained at approximately 30 males : 100 females, and moose used aquatic habitats in proportion ($\chi^2 = 2.03$, $P = 0.15$) to the sex structure of the population.

Fraser et al. (1982) reported that more males than females visited aquatic habitats during spring, with a reversal of that relationship in mid-August to September. Less frequent use of aquatic habitats by females in spring could be related to constraints imposed by young calves (Fraser et al. 1980), and no information on the sex structure of the population was given. None of the other studies we reviewed differentiated moose use of aquatic habitats by sex or presented data on the sex structure of the population.

Foraging efficiency has also been related to the time an animal spends scanning its surroundings during a foraging bout (Berger et al. 1983; Stockwell et al. 1991). Cervids use aquatic habitats to escape predators (Mech 1966, 1970; Gasaway et al. 1983), and moose are presumably more secure while foraging in aquatic habitats, and may be able to devote more time to cropping forage versus vigilant, scanning behavior. This contention is supported by the fact that moose often completely submerge their heads for extended periods while in aquatic habitats (Belovsky and Jordan 1978).

Conclusions

Moose forage in two different types of aquatic habitats; shallow ponds dominated by emergent species (Faber et al. 1988; this study), and deeper ponds dominated by submergents (reviewed by Jordan 1987). The energetics of foraging in these habitats probably differ. Researchers at Isle Royale concluded that moose incurred a Na deficit over the winter that was alleviated by the use of submergent aquatic plants (Belovsky and Jordan 1981; Jordan 1987). Fraser et al. (1982) suggested that the use of submergents at Sibley Provincial Park was most closely related to Na hunger because of high levels of K in browse during the spring. Many other studies also support the high K–Na hunger mechanism (Weeks and Kirkpatrick 1976; Fraser et al. 1982; Tankersley and Gasaway 1983; Risenhoover and Peterson 1986); but see Christian (1989) for conflicting evidence. In contrast, this study and Faber et al. (1988) did not find a relationship between the use of emergent aquatic plants and Na. On the WCRD, moose may use aquatic habitats because they permit efficient foraging. In addition, data presented in studies of moose using submergent species are also consistent with the criteria supporting this perspective.

Our study was unique in directly estimating the use of aquatic habitats by a moose population. During July, about 25% of the moose observed were using aquatic habitats at any one time. This was probably an underestimate, since feeding bouts were relatively short and moose moved to other habitat types to rest and ruminate. The fact that second-order habitat selection emphasized the role of aquatic habitats implies greater importance than can be construed from population surveys alone.

The hypothesis that foraging in aquatic habitats may be highly efficient deserves testing. The development and testing of foraging theory generally occurs at a relatively fine-grained scale, i.e., choices made by individuals. The data supporting the foraging efficiency hypothesis were from studies focused on both individuals and at coarser scales, i.e., populations and landscapes. Consistencies among these cross-scale comparisons lend additional strength to the potential validity of the foraging efficiency viewpoint.

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