

NUTRITIONAL QUALITY OF WILLOWS FOR MOOSE: EFFECTS OF TWIG AGE AND DIAMETER

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ABSTRACT: Alaskan moose (*Alces alces gigas*) consume willow (*Salix* spp.) as a fundamental component of their winter diet. We collected Barclay willow (*S. barclayi*) from 5 nearby sites (15-80 m apart) on the Kenai Peninsula, Alaska, USA, during winter 1999-2000. We tested effects of diameter and age of twigs on nutritional quality of willows for moose. Smaller-diameter twigs had higher in vitro dry matter digestibility (IVDMD), and protein content, but lower fiber content ($P < 0.001$) than larger twigs. An inverse relationship occurred between the age of twigs and protein content ($P < 0.001$), with older-aged twigs containing less protein. Accordingly, age of twigs was negatively related to fiber content ($P = 0.002$). Conversely, no relation existed between age of twigs and IVDMD ($P = 0.34$). Tannin content ($P < 0.001$) and age of twigs ($P = 0.04$) varied among sites, with older twigs possessing more tannins than younger ones. No difference in tannins, however, occurred between diameter categories of twigs ($P = 0.48$). Digestible energy differed between diameter categories ($P = 0.02$) and among ages of twigs ($P = 0.02$), as well as among collection sites ($P < 0.001$). Thus, structural components of the twig to support growth were more important in affecting digestibility, whereas age of the twig was more influential in determining nitrogen and tannin content. The relation between twig age and tannin content, however, was the inverse of that expected. More research is needed to understand how quality of winter browse interacts with additional factors, such as predation risk, population density, and allometric differences between sexes, to affect diet selection and foraging behavior of moose and other large herbivores.

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Browse is an important element in the winter diet of moose (*Alces alces*) inhabiting boreal forests (Peek 1974, 1998; Ludewig and Bowyer 1985; Renecker and Schwartz 1998). Indeed, the diet of Alaskan moose (*A. a. gigas*) is composed principally of willows (*Salix* spp.), which may be eaten throughout the year (Van Ballenberghe et al. 1989; Miquelle et al. 1992; Van

Ballenberghe 1992; Bowyer et al. 1998, 1999a). Further, diameter of twigs available to moose for consumption may be a crucial aspect of diet selection by this large browser (Vivas et al. 1991, Bowyer and Bowyer 1997).

Most nutrients used by moose are contained in the surface of woody twigs, with hard-to-digest carbohydrates (cellulose and

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hemicellulose) composing the core (Schwartz and Renecker 1998). Therefore, as twig diameter of browse increases (i.e., the diameter at the point of browsing), the ratio of surface nutrients to the core declines, as does the nutritional value of such forage for moose (Hjeljord et al. 1982, Schwartz and Renecker 1998). In winter, adult moose eat forage that contains levels of crude protein below maintenance, and dry-matter intake necessary to meet nitrogen requirements is difficult to attain (Schwartz and Renecker 1998). Further, the role that tannins play in forage selection is complex, and may affect foraging by herbivores (Reid et al. 1974, Bryant and Kuropat 1980, Leslie and Starkey 1987, Robbins et al. 1987, Bryant et al. 1991). For instance, leaders of new growth in birch (*Betula* sp.) were heavily defended by secondary compounds, which altered foraging behavior by snowshoe hares (*Lepus americanus*; Bryant et al. 1994).

During winter, moose may be protein as well as energy limited; hence, forage selection should favor young twigs with smaller diameters. Moose eat twigs older than first-year growth, but data on the nutritive value of those older twigs are sparse (Cowan et al. 1950). Indeed, diet quality for herbivores likely involves a preference for species of plants, as well as specific parts of plants (Janzen 1979).

There is increasing evidence that moose play a fundamental role in the structure and function of boreal ecosystems (Pastor and Naiman 1992, Molvar et al. 1993, Bowyer et al. 1997, Berger et al. 2001, Kie et al. 2003); however, much remains to be learned about their foraging ecology. Gaining insights into why moose forage on a particular plant or select specific twigs, or diameters of twigs, from that plant is critical to understanding the mechanisms controlling foraging behavior.

We tested for differences in forage quality as affected by diameter of twigs,

age of twigs, tannin content, collection site, and their interactions. We also examined the digestible energy content (DE) of willows, and tested for differences between age classes and diameter categories of twigs. We hypothesized that larger twigs would have a lower nitrogen content, be less digestible, have more fiber, and have a lower tannin content than smaller twigs. Likewise, we also predicted that older twigs would have lower nitrogen content, be less digestible, have more fiber, and possess lower tannin content than younger twigs. Further, we hypothesized that dietary energy and protein would change with size and age of browse, and that small changes in browse chemistry might alter availability of protein and energy for moose.

STUDY AREA

We sampled twigs of willow (*Salix barclayi*) at an elevation of 275 m along a roadside located on the Kenai Peninsula, near Ninilchik, Alaska, USA, (60° N, 149° W) during winter 1999-2000. The Kenai Peninsula is characterized by a maritime climate influenced by its proximity to the Pacific Ocean (Weixelman et al. 1998). Annual precipitation ranges from 40 to 50 cm with most falling as snow in winter and rain in spring or autumn (Schwartz and Franzmann 1991). Annual snowfall ranges from 140 to 165 cm (Oldemeyer and Regelin 1987). Mean annual temperature is 1° C, and mean monthly temperatures range from - 30 to 21° C (Schwartz and Franzmann 1991).

We began sampling in early December after willows had become dormant and lost their leaves. Moose migrated from higher elevations across our study site to lower-elevation valleys as winter snowfall accumulated. Thus, moose use of the study area was limited, and much of the willow in this area was unbrowsed, or only lightly browsed. Sampling was completed in late

February, and samples were stored between 0 and -25° C until analyzed.

Our study area was a plateau along the sides of an unpaved road that ran east from Ninilchik for approximately 21 km. The roadside was surrounded by boreal forest dominated by white spruce (*Picea glauca*). Willows ranged in size from 1-3 m in height. Our sampling site was located adjacent to the road (3-20 m from the snowburm) about 16 km from Ninilchik. There was no overstory cover, and patches of dense growth of willows characterized the understory. Shading affects nutritional quality of willows (Hjeljord et al. 1990, Bø and Hjeljord 1991, Molvar et al. 1993); however, willows we selected were shaded only slightly by a few trees, thereby minimizing that complication. Likewise, this area exhibited little variation in slope, exposure, or drainage. Finally, easy access allowed us to sample large quantities of willow in a relatively small area.

METHODS

We sampled an area along a roadside that encompassed 155 m, which included 5 distinct patches of willows located 15-80 m apart ($\bar{X} \pm SD = 38.8 \pm 28.69$ m). All stems with abundant twigs (> 15 leaders) were cut from a plant at snow level, labeled, and transported to the laboratory for subsequent analyses. Three stems (containing numerous leaders) from each of 5 sites were selected haphazardly for nutritional analyses; the remainder of branches was withheld for a related experiment on feeding behavior of moose. Current annual growth (1-year-old), 2-year-old growth, and 3-year-old growth were measured with dial calipers to the nearest 0.1 mm at the bud scale scar, and pooled according to diameter and age classes. Twigs were categorized according to diameter: small (0.8 - 2.9 mm) and large (3.0 - 4.9 mm). This classification was based on previous studies of

twig selection by foraging moose (Molvar and Bowyer 1994, Bowyer and Bowyer 1997, Stephenson et al. 1998, Weixelman et al. 1998), diameter and age classes of twigs available to us for sampling, and the need to obtain sufficient material in a particular age and diameter category for nutritional analyses.

Samples of twigs from each site were pooled by age class and diameter category, oven dried to constant mass at 55° C, and then ground with a Wiley mill (1-mm screen). All nutrients were assayed on the basis of dry mass (DM). In vitro dry matter digestibility (IVDMD; Tilley and Terry 1963) was determined for each sample. Fresh rumen inoculum for the digestion trial was obtained from 1 captive reindeer (*Rangifer tarandus*) that was fistulated, and held at the Robert G. White Large Animal Research Station of the University of Alaska Fairbanks (UAF). We conditioned the reindeer to a diet of willow by adding a mixture of approximately 12 g ground willow and 500 ml water directly into the rumen (via canula) every 2-3 days for 18 days. The Forage Quality Analysis Laboratory at UAF performed IVDMD, nutrient analyses, and tannin assays, with duplicates for selected samples. Detergent analysis (Van Soest et al. 1991) was used to determine structural composition of plant cells (percentage dry weight of neutral-detergent fiber [NDF], acid detergent fiber [ADF]), ash of acid extracted fiber, and lignin). Fiber fractions were used to derive estimates of cell contents (DM - NDF), hemicellulose (NDF - ADF), and cellulose (ADF - lignin). Nitrogen was determined with an elemental analyzer (Model # CNS 2000, Leco, St. Joseph, MI, USA) and expressed as crude protein based on the assumption of 6.25 g protein per 1 g nitrogen (Robbins 1993). Soluble carbohydrates such as starch were estimated as the difference between cell contents and crude protein, with the as-

sumption that lipid content of winter browse was negligible (Robbins 1993). Tannins were extracted from willows in ethanol (50 % v/v) at 95° C, and assayed by the method of Folin-Dennis (Martin and Martin 1982).

Differences in nutritional quality of twigs from age classes and diameter categories were compared with multivariate analysis of variance (MANOVA), with measures of forage quality (e.g., IVDMD, N, and tannins) as dependent variables, and age (e.g., 1-, 2-, and 3-years-old) and diameter (e.g., large and small) of twigs, and their interactions as main effects. MANOVA controls for the lack of independence among dependent variables necessary to examine effects of twig diameter and age (Johnson and Wichern 1982, Neter et al. 1996, McGarigal et al. 2000). Our design, which included 2 identical categories of twig diameter for each age class, controlled for bias from an overall correlation between age and diameter of twigs. Moreover, we reduced the overall α to 0.01 for each measure of forage quality to adjust for any remaining lack of independence in our variables (e.g., main effects).

Gross energy available in twigs was calculated with caloric values for protein (24.89 kJ/g), soluble carbohydrates (17.48 kJ/g), hemicellulose (17.82 kJ/g), and cellulose (17.49 kJ/g) from Blaxter (1989). Fractional digestibility of cell wall components (cellulose and hemicellulose) was calculated from IVDMD by assuming that DM of protein and soluble carbohydrate were 60% digestible. Digestible-energy content (DE) of twigs was estimated by combining gross energy and DM digestibilities of each fraction.

RESULTS

Overall, we documented effects of site, twig age, and twig diameter on nitrogen content (MANOVA, $F_{9,69} = 49.86, P < 0.0001$), IVDMD ($F_{9,69} = 7.83, P < 0.0001$), and tannin concentration ($F_{9,69} = 7.01, P <$

0.0001) of willows; no interactions occurred between site or twig characteristics ($P > 0.05$). No difference ($P = 0.45$) occurred for mean nitrogen content of willow twigs among sites (range of means = 5.9-6.2%). Nitrogen content of twigs differed for age classes ($P < 0.001$) and diameter categories ($P < 0.001$) of twigs, with older and larger-diameter twigs possessing lower nitrogen content than younger and smaller twigs (Fig. 1).

There was an effect ($P < 0.001$) of site on IVDMD of willow twigs (range of means = 44.1-47.2%). Likewise, IVDMD was affected by the diameter of twigs, with larger twigs having lower IVDMD than smaller twigs (Fig. 1). Age of twigs, however, was not related to IVDMD (Fig. 1). Little overlap occurred in values when we

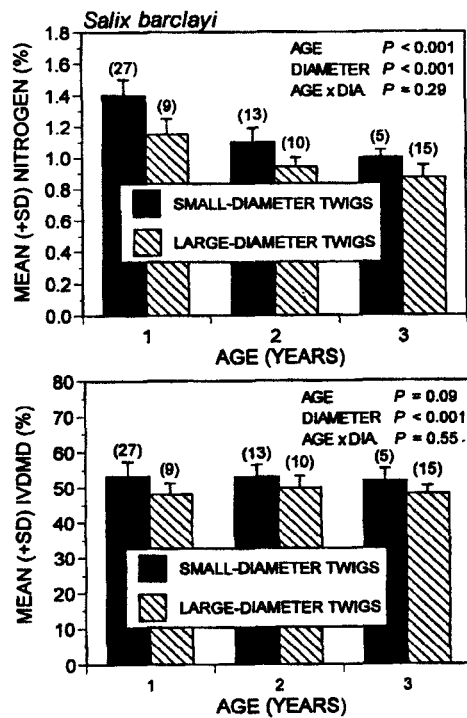


Fig. 1. Nitrogen content (top) and in vitro dry matter digestibility (bottom) of small-diameter (0.8-2.9 mm) and large-diameter (3.0-4.9 mm) twigs in relation to age of Barclay willow (*Salix barclayi*), Kenai Peninsula, Alaska, USA, winter 1999-2000.

compared cellulose and IVDMD between large and small diameter twigs (Fig. 2). Conversely, considerable overlap occurred between ages of twigs when cellulose was examined in relation to IVDMD (Fig. 2). These results confirm that cellulose in the core of stems strongly affected IVDMD. Additional measures of forage quality followed a similar pattern with significant differences occurring among age classes and

diameter categories of willow twigs, except for ash, which differed neither in twig age nor diameter, and lignin, which did not vary with age (Table 1).

Variation in mean tannin concentration of willow twigs among sites ranged from 167.30 mg/g to 209.32 mg/g. Similarly, tannin content ($\bar{X} \pm SD$) varied among ages of twigs (1-year-old = 185.4 ± 41.63 mg/g; 2-year-old = 206.4 ± 42.86 mg/g; 3-year-old

Table 1. Forage quality (% dry mass) of 1-year-old, 2-year-old, and 3-year-old growth, and of small (0.08 – 2.9 mm) and large (3.0 – 4.9 mm) categories of twig diameter for Barclay willow (*Salix barclayi*), Kenai Peninsula, Alaska, USA, winter 1999-2000. Composites of 15-25 twigs were included in each sample. Sample sizes for age and diameter categories were: 1-year-old, small ($n = 27$); 1-year-old, large ($n = 9$); 2-year-old, small ($n = 13$); 2-year-old, large ($n = 10$); 3-year-old, small ($n = 5$); and 3-year-old, large ($n = 15$).

Variable ¹	Age					
	1-year-old		2-year-old		3-year-old	
	\bar{X}	(SD)	\bar{X}	(SD)	\bar{X}	(SD)
Acid-detergent fiber						
Small	39.68	(2.44)	40.60	(2.37)	42.33	(2.24)
Large	32.39	(2.78)	42.60	(3.37)	44.54	(3.00)
Neutral-detergent fiber						
Small	47.98	(2.93)	49.97	(2.16)	52.97	(2.24)
Large	53.54	(3.39)	54.81	(3.98)	55.82	(3.33)
Ash of acid extracted fiber						
Small	0.35	(0.12)	0.30	(0.08)	0.33	(0.05)
Large	0.31	(0.11)	0.30	(0.09)	0.31	(0.09)
Derived lignin						
Small	21.64	(1.57)	21.47	(1.98)	20.98	(1.06)
Large	19.28	(2.01)	18.09	(1.03)	19.56	(1.73)
Derived hemicellulose						
Small	8.31	(1.01)	9.37	(0.67)	10.64	(0.24)
Large	11.15	(1.16)	12.21	(0.60)	11.28	(0.73)
Derived cellulose						
Small	17.68	(1.62)	18.83	(1.05)	21.02	(1.89)
Large	22.79	(2.69)	24.22	(2.79)	24.67	(2.40)

¹MANOVA indicated that significant differences in forage quality occurred among different age classes and between diameter categories ($P < 0.01$) for all variables, except for ash of acid extracted fiber (age: $P = 0.56$; diameter: $P = 0.15$) and derived lignin (age: $P = 0.27$).

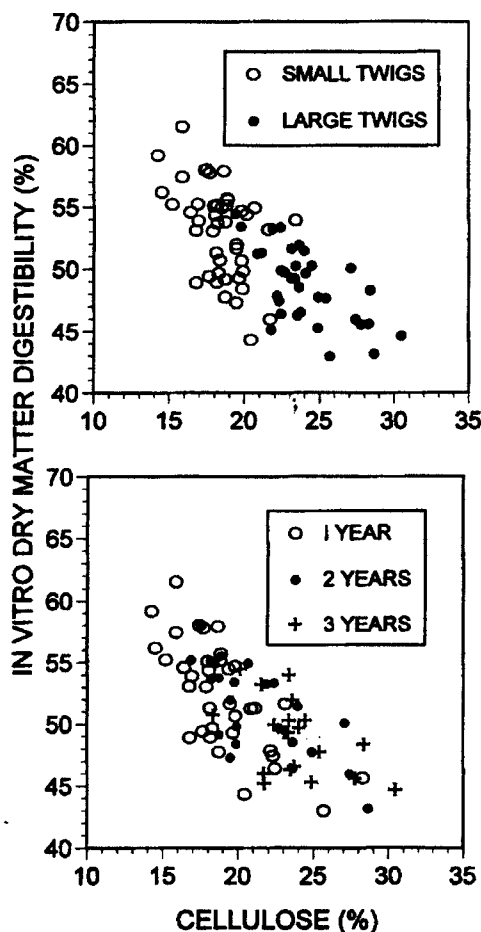


Fig. 2. In vitro dry matter digestibility and cellulose content of small-diameter (0.8–2.9 mm) and large diameter (3.0–4.9 mm) twigs (top), and twigs of different age (bottom), of Barclay willow (*Salix barclayi*), Kenai Peninsula, Alaska, USA, winter 1999-2000.

= 204.8 ± 41.31 mg/g); 1-year-old twigs had less tannin than 2- or 3-year-old twigs ($P = 0.04$). Diameters of twigs, however, did not affect tannin content ($\bar{X} \pm SD$): small diameter = 199.3 ± 40.85 mg/g; large diameter = 192.7 ± 45.15 mg/g ($P = 0.48$).

Estimated gross energy of protein and carbohydrates was similar among all groups and ranged from 13.65 to 15.09 kJ/g. Digestible energy content (DE); however, differed among sites ($P < 0.001$, range of means = 6.99 to 7.65 kJ/g), across ages ($P < 0.001$, range of means = 7.06 to 7.54

kJ/g), and between twig diameters ($P < 0.001$, range of means = 7.12 to 7.60 kJ/g).

DISCUSSION

Our results indicated that forage quality of willow twigs in winter varied on a relatively fine spatial scale, especially IVDMD, tannin concentration, and estimated digestible energy. The cause of that variation, however, is uncertain, but cannot be attributed to previous browsing, aspect, drainage, or shading, because our sampling design precluded marked differences among such variables in those nearby sites (15-80 m apart). Other factors related to plant growth (Chapin et al. 1995) that we could not assess, such as soil temperature, structure, nutrients, and moisture, may have been responsible for differences in quality of twigs we documented (Chapin 1983, Molvar et al. 1993, Post and Stenseth 1999, Lenart et al. 2002). This fine-scale variation in quality of browse warrants further study.

Older twigs of willow had lower nitrogen content than younger twigs. Larger-diameter twigs of willow also had lower nitrogen content than smaller twigs. Protein availability probably declines with absolute content of nitrogen and with tannin concentrations as parts of plants age, for both diameter categories. Surprisingly, older twigs with lower nitrogen content were better defended by tannins than younger twigs with more nitrogen, an unexpected pattern if tannins function primarily to interfere with utilization of nitrogen by ruminants (Robbins et al. 1987). Larger-diameter twigs also were less digestible; however, age of twigs did not affect IVDMD. Although age of twigs was more influential in determining nitrogen content, structural components of twigs to support growth (twig diameter) were more important in affecting IVDMD (Fig. 1), as revealed in the relation between IVDMD and cellulose (Fig. 2). Although some differences in quality of

twigs relative to age and diameter were not large (Fig. 1), such variation may be important to foraging herbivores as they accumulate nutrients over time (White 1983).

Importance of winter forage for moose should be viewed in a broad perspective (Weixelman et al. 1998); several factors likely affect foraging behavior. Browse consumed by moose during winter is composed largely of willow twigs that have a low content of crude protein (5-7%), which will not meet maintenance requirements (Schwartz 1992), or fully support reproduction (Schwartz et al. 1988). Northern ungulates are in a negative energy balance during winter, and foraging activities principally slow the rate of loss of body reserves (Mautz 1978, Barboza and Bowyer 2001). Some losses of body reserves, however, may be physiologically regulated, because moose voluntarily reduce their metabolic rate and food intake during winter to conserve energy (Schwartz et al. 1988). If nitrogen levels are below maintenance requirements, then IVDMD may become increasingly important for survival of moose in winter.

Shorter retention times in the rumen are correlated with higher-quality diets and longer retention times with lower-quality forage (Schwartz et al. 1988). Rumen microbes ferment soluble sugars and cell solubles rapidly; however, cell walls require much longer to process (Spalinger 2000, Russell and Rychlik 2001). Lignin content also reduces digestibility of forages, as can tannins and other plant secondary compounds (Bryant et al. 1991, 1994).

Secondary plant compounds (i.e., tannins) may play a role in food choice, because browsing vertebrates avoid consuming plant tissues that contain high concentrations of secondary metabolites (Bryant and Kuropat 1980, Palo et al. 1985). Further, tannins are thought to negatively affect digestibility of browse for moose

during winter (Bryant and Kuropat 1980, Palo et al. 1985). Estimations of digestibility of woody forage, however, may not need to be adjusted for tannins, because there may be some benefits to ruminants from ingesting forages containing tannins (Kumar and Singh 1984, Leslie and Starkey 1987, Hagerman and Robbins 1993). Reid et al. (1974) postulated that the presence of tannins provided partial protection of proteins from degradation in the rumen, thereby enhancing assimilation of nitrogen. Robbins et al. (1987) suggested that reduction of protein digestion caused by tannins may not result from gastrointestinal adaptations, but may be because of the small amounts of tannins in winter browse. The saliva of moose contains large amounts of proline-rich proteins, which may bind tannins and thereby reduce their effects on moose (Hagerman and Robbins 1993, Juntheikki 1996). Further, many tannins in willow are linear-condensed tannins that moose bind well, in contrast to other tannins in lower-quality foods, which moose saliva does not bind (Barry and McNabb 1999).

Weixelman et al. (1998) suggested that reduced food availability, quality, and digestibility, combined with the increased energetic costs of foraging during severe weather, should force animals to maximize caloric return per unit energy expended. In addition, there may be twigs that are too small, or too widely dispersed to provide sufficient nutritional value for moose. Relationships between forage digestibility, retention time in the rumen, and rate of intake (Owen-Smith 1982, Van Soest et al. 1991), indicate digestibility is likely an important factor in forage selection by ruminants. Those relationships probably affect the size of a bite for moose foraging in winter, because larger bites have poorer nutritional quality (Schwartz et al. 1988, Molvar and Bowyer 1994).

Decreases in digestible-energy content

of willow twigs with age and diameter reflect declining proportions of crude protein and cell contents as the matrix of the plant cell wall increases in concentration. Differences in digestible-energy content of twigs may be directly related to food intake required in winter. Schwartz and Renecker (1998) calculated a daily intake of digestible energy in moose during November as 975 kJ/kg^{0.75}. Based on our calculations, consumption of 1-year-old twigs with small diameters would require a mean (\pm SD) daily intake of 124 ± 9 gDM/kg^{0.75} body mass, whereas intakes of 3-year-old twigs with large diameter subtend intakes that are 15% greater (141 ± 8 gDM/kg^{0.75}). That increment in digestive load would increase gut fill and influence passage rate. Changes in digestive function associated with energy demand may feedback on processes of forage selection at the level of plant and twig.

The pattern of nutrients and secondary metabolites across ages and between diameter classes of willow twigs did not conform to some of our initial predictions, especially a lack or variation in IVDMD with increasing age. Nonetheless, our results support the hypothesis that moose should alter their foraging behavior to respond to variation in plant nutrients (and perhaps secondary compounds), at fine scales that include nearby foraging sites and differences among twigs on the same plant. The forgoing arguments clearly indicate that quality of forage should be a critical component in diet selection by large herbivores, but such relationships have been notoriously difficult to demonstrate in free-ranging moose (Weixelman et al. 1998). Those difficulties likely relate to effects of predation risk, including influences of group size, distance from concealment cover, and differential vulnerability of sex and age classes to predators, on foraging behavior and diet selection by moose (Edwards 1983, Molvar and Bowyer 1994, Weixelman et al.

1998, White et al. 2001). In addition, variation in population density with respect to carrying capacity (K) of the environment (Bowyer et al. 1999b, Kie 1999, Kie et al. 2003) undoubtedly alters foraging behavior of large mammals. Likewise, allometric differences between sexes of ruminants may also affect assimilation of nutrients and consequently foraging behavior (Schwartz et al. 1987; Barboza and Bowyer 2000, 2001; Spaeth et al. 2001). Moreover, the propensity of sexes to partition space outside the mating season in heterogeneous habitats (Miquelle et al. 1992, Bowyer et al. 2001) has a strong influence on habitats selected and, in consequence, the manner in which moose forage. We believe our descriptions of nutrients in willows and how they varied with respect to site, as well as age and diameter of twigs, is an important first step in clarifying diet selection by moose. We contend, however, that a more complete understanding of foraging dynamics in this large herbivore ultimately will require a better integration of the life-history characteristics of moose with nutritional composition and abundance of their forage.

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REFERENCES

- BARBOZA, P. S., and R. T. BOWYER. 2000. Sexual segregation in dimorphic deer: a new gastrocentric hypothesis. *Journal of Mammalogy* 81:473-489.
- _____, and _____. 2001. Seasonality of sexual segregation in dimorphic deer: extending the gastrocentric model. *Alces* 37:275-292.
- BARRY, T. N., and W. C. McNABB. 1999. The implications of condensed tannins on the nutritive value of temperate forages fed to ruminants. *British Journal of Nutrition* 81:263-272.
- BERGER, J., P. B. STACEY, L. BELLIS, and M. P. JOHNSON. 2001. A mammalian predator-prey imbalance: grizzly bear and wolf extinction affect avian Neotropical migrants. *Ecological Applications* 11:229-240.
- BLAXTER, K. L. 1989. *Energy metabolism in animals and man*. Cambridge University Press, Cambridge, UK.
- BØ, S., and O. HJELJORD. 1991. Do continental moose ranges improve during cloudy summers? *Canadian Journal of Zoology* 69:1875-1879.
- BOWYER, J. W., and R. T. BOWYER. 1997. Effects of previous browsing on the selection of willow stems by Alaskan moose. *Alces* 33:11-18.
- BOWYER, R. T., M. C. NICHOLSON, E. M. MOLVAR, and J. B. FARO. 1999b. Moose on Kalgin Island: are density-dependent processes related to harvest? *Alces* 35:73-89.
- _____, B. M. PIERCE, L. K. DUFFY, and D. A. HAGGSTROM. 2001. Sexual segregation in moose: effects of habitat manipulation. *Alces* 37:109-122.
- _____, V. VAN BALLENGERGHE, and J. G. KIE. 1997. The role of moose in landscape processes: effects of biogeography, population dynamics, and predation. Pages 265-287 in J. A. Bissonnette, editor. *Wildlife and landscape ecology: effects of pattern and scale*. Springer-Verlag, New York, New York, USA.
- _____, _____, and _____. 1998. Timing and synchrony of parturition in Alaskan moose: long-term versus proximal effects of climate. *Journal of Mammalogy* 79:1332-1344.
- _____, _____, _____, and J. A. K. MAIER. 1999a. Birth-site selection in Alaskan moose: maternal strategies for coping with a risky environment. *Journal of Mammalogy* 80:1070-1083.
- BRYANT, J. P., and P. J. KUROPAT. 1980. Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. *Annual Review of Ecology and Systematics* 11:261-285.
- _____, F. D. PROVENZA, J. PASTOR, P. B. REICHARDT, T. P. CLAUSEN, and J. T. DE TOIT. 1991. Interactions between woody plants and browsing mammals mediated by secondary metabolites. *Annual Review of Ecology and Systematics* 22:431-436.
- _____, R. K. SWIHART, P. B. REICHARDT, and L. NEWTON. 1994. Biogeography of woody plant chemical defense against snowshoe hare browsing: comparison of Alaska and eastern North America. *Oikos* 51:385-394.
- CHAPIN, F. S., III. 1983. Direct and indirect effects of temperature on arctic plants. *Polar Biology* 2:47-52.
- _____, G. R. SHAVERS, A. E. GIBLIN, K. J. NADELHOFFER, and J. A. LAUNDRE. 1995. Responses of arctic tundra to experimental and observed changes in climate. *Ecology* 76:694-711.
- COWAN, I. MCT., W. S. HOAR, and J. HATTER. 1950. The effect of forest succession upon the quantity and upon the nutritive values of woody plants used as food by moose. *Canadian Journal of Research D* 28:249-271.
- EDWARDS, J. 1983. Diet shifts of moose due to predator avoidance. *Oecologia*

- 60:185-189.
- HAGERMAN, A. E., and C. T. ROBBINS. 1993. Specificity of tannin-binding salivary proteins relative to diet selection by mammals. *Canadian Journal of Zoology* 71:628-633.
- HJELJORD, O., N. HOVIK, and H. B. PEDERSEN. 1990. Choice of feeding sites by moose during summer: the influence of forest structure and plant phenology. *Holarctic Ecology* 13:333-343.
- _____, F. SUNDSTOL, and H. HAAGENRUD. 1982. The nutritional value of browse to moose. *Journal of Wildlife Management* 46:333-343.
- JANZEN, D. H. 1979. New horizons in the biology of plant defenses. Pages 331-348 in G. A. Rosenthal and D. H. Janzen, editors. *Herbivores: their interactions with secondary plant metabolites*. Academic Press, New York, New York, USA.
- JOHNSON, R. A., and D. W. WICHERN. 1982. *Applied multivariate statistical analysis*. Second edition. Prentice Hall, Englewood Cliffs, New Jersey, USA.
- JUNTHEIKKI, M.-R. 1996. Comparison of tannin-binding proteins in saliva of Scandinavian and North American moose (*Alces alces*). *Biochemical Systematics and Ecology* 24:595-601.
- KIE, J. G. 1999. Optimal foraging and risk of predation: effects on behavior and social structure in ungulates. *Journal of Mammalogy* 80:1114-1129.
- _____, R. T. BOWYER, and K. M. STEWART. 2003. Ungulates in western forests: habitat requirements, population dynamics, and ecosystem processes. Pages 296-340 in C. J. Zabel and R. G. Anthony, editors. *Mammal community dynamics: management and conservation in the coniferous forests of western North America*. The Johns Hopkins University Press, Baltimore, Maryland, USA.
- KUMAR, R., and M. SINGH. 1984. Tannins: their adverse role in ruminant nutrition. *Journal of Agricultural Food Chemistry* 32:447-453.
- LENART, E. A., R. T. BOWYER, J. VER HOEF, and R. W. RUESS. 2002. Climate change and caribou: effects of summer weather on forage. *Canadian Journal of Zoology* 80:664-678.
- LESLIE, D. M., JR., and E. S. STARKEY. 1987. Fecal indices to dietary quality: a reply. *Journal of Wildlife Management* 51:321-325.
- LUDEWIG, H. A., and R. T. BOWYER. 1985. Overlap in winter diets of sympatric moose and white-tailed deer in Maine. *Journal of Mammalogy* 66:390-392.
- MARTIN, J. S., and M. M. MARTIN. 1982. Tannin assays in ecological studies: lack of correlation between phenolics, proanthocyanidins and protein-precipitating constituents in mature foliage of 6 oak species. *Oecologia* 54:205-211.
- MAUTZ, W. W. 1978. Sledding on a brushy hillside: the fat cycle in deer. *Wildlife Society Bulletin* 6:88-90.
- MCGARIGAL, K., S. CUSHMAN, and S. STAFFORD. 2000. *Multivariate statistics for wildlife and ecology research*. Springer, New York, New York, USA.
- MIQUELLE, D. G., J. M. PEEK, and V. VAN BALLEMBERGHE. 1992. Sexual segregation in Alaskan moose. *Wildlife Monographs* 122.
- MOLVAR, E. M., and R. T. BOWYER. 1994. Costs and benefits of group living in a recently social ungulate: the Alaskan moose. *Journal of Mammalogy* 75:621-630.
- _____, _____, and V. VAN BALLEMBERGHE. 1993. Moose herbivory, browse quality, and nutrient cycling in an Alaskan treeline community. *Oecologia* 94:472-479.
- NETER, J., M. H. KUTNER, C. J. NACHTSHEIM, and W. WASSERMAN. 1996. *Applied*

- analysis of variance and experimental designs. Fourth edition. Irwin, Homewood, Illinois, USA.
- OLDEMEYER, J. L., and W. L. REGELIN. 1987. Forest succession and habitat management, and moose on the Kenai National Wildlife Refuge. Swedish Wildlife Research Supplement 1:163-180.
- OWEN-SMITH, N. 1982. Factors influencing the transfer of plant products into large herbivore populations. Pages 359-404 in B. J. Huntley and B. H. Walker, editors. The ecology of tropical savannas. Springer-Verlag, Berlin, Germany.
- PALO, R. T., K. SUNNERHEIM, and O. THEANDER. 1985. Seasonal variation of phenols, crude proteins and cell wall content of birch (*Betula pendula*) in relation to ruminant in vitro digestibility. *Oecologia* 65:314-318.
- PASTOR, J., and R. J. NAIMAN. 1992. Selective foraging and ecosystem processes in the boreal forests. *American Naturalist* 139:690-705.
- PEEK, J. M. 1974. A review of moose food habit studies in North America. *Naturaliste Canadien* 101:131-141.
- _____. 1998. Habitat relationships. Pages 351-401 in A. W. Franzmann and C. C. Schwartz, editors. Ecology and management of the North American moose. Smithsonian Institution Press, Washington, D.C., USA.
- POST, E., and N. C. STENSETH. 1999. Climate variability, plant phenology, and northern ungulates. *Ecology* 80:1322-1339.
- REID, C. S. W., M. J. ULYATT, and J. M. WILSON. 1974. Plant tannins, bloat and nutritive value. *Proceedings of the New Zealand Society of Animal Production* 34:82-93.
- RENECKER, L. A., and C. C. SCHWARTZ. 1998. Food habits and feeding behavior. Pages 403-440 in A. W. Franzmann and C. C. Schwartz, editors. Ecology and management of the North American moose. Smithsonian Institution Press, Washington, D.C., USA.
- ROBBINS, C. T. 1993. Wildlife feeding and nutrition. Second edition. Academic Press, San Diego, California, USA.
- _____, T. A. HANLEY, A. E. HAGERMAN, O. HJELJORD, D. L. BAKER, C. C. SCHWARTZ, and W. W. MAUTZ. 1987. Role of tannins in defending plants against ruminants: reduction in protein availability. *Ecology* 68:98-107.
- RUSSELL, J. B., and J. L. RYCHLIK. 2001. Factors that alter rumen microbial ecology. *Science* 292:1119-1122.
- SCHWARTZ, C. C. 1992. Physiological and nutritional adaptations of moose to northern environments. *Alces Supplement* 1:139-155.
- _____, and A. W. FRANZMANN. 1991. Interrelationship of black bears to moose and forest succession in the northern coniferous forest. *Wildlife Monographs* 113.
- _____, M. E. HUBBERT, and A. W. FRANZMANN. 1988. Energy requirements of adult moose for winter maintenance. *Journal of Wildlife Management* 52:26-33.
- _____, W. L. REGELIN, and A. W. FRANZMANN. 1987. Seasonal weight dynamics of moose. Swedish Wildlife Research Supplement 1:301-310.
- _____, and L. A. RENECKER. 1998. Nutrition and energetics. Pages 441-478 in A. W. Franzmann and C. C. Schwartz, editors. Ecology and management of the North American moose. Smithsonian Institution Press, Washington, D.C., USA.
- SPAETH, D. F., K. J. HUNDERTMARK, R. T. BOWYER, P. S. BARBOZA, T. R. STEPHENSON, and R. O. PETERSON. 2001. Incisor arcades of Alaskan moose: is dimorphism related to sexual segregation

- tion? *Alces* 37: 217-226.
- SPALINGER, D. E. 2000. Nutritional ecology. Pages 108-139 in S. Demarais and P. R. Krausman, editors. *Ecology and management of large mammals in North America*. Prentice Hall, Upper Saddle River, New Jersey, USA.
- STEPHENSON, T. R., V. VAN BALLEMBERGHE, and J. M. PEEK. 1998. Response of moose forage to mechanical cutting on the Copper River Delta. *Alces* 34:479-494.
- TILLEY, J. M. A., and R. A. TERRY. 1963. A two-stage technique for the in vitro digestion of forage crops. *Journal of the British Grassland Society* 18:104-111.
- VAN BALLEMBERGHE, V. 1992. Behavioral adaptations of moose to treeline habitats in subarctic Alaska. *Alces Supplement* 1:193-206.
- , D. G. MIQUELLE, and J. G. MACCRACKEN. 1989. Heavy utilization of woody plants by moose during summer in Denali National Park, Alaska. *Alces* 25:31-35.
- VAN SOEST, P. J., J. B. ROBERTSON, and B. A. LEWIS. 1991. Methods for dietary fiber, neutral detergent fiber and non-starch polysaccharides in relation to animal nutrition. *Journal of Dairy Science* 74:3583-3597.
- VIVAS, H. J., B.-E. SÆTHER, and R. ANDERSON. 1991. Optimal twig-size selection of a generalist herbivore, the moose *Alces alces*: implications for plant-herbivore interactions. *Journal of Animal Ecology* 60:395-408.
- WEIXELMAN, D. A., R. T. BOWYER, and V. VAN BALLEMBERGHE. 1998. Diet selection by Alaskan moose during winter: effects of fire and forest succession. *Alces* 34:213-238.
- WHITE, K. S., J. W. TESTA, and J. BERGER. 2001. Behavior and ecologic effects of differential predation pressure on moose in Alaska. *Journal of Mammalogy* 82:422-429.
- WHITE, R. G. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. *Oikos* 40:377-384.