EFFECTS OF BROWSING HISTORY BY ALASKAN MOOSE ON REGROWTH AND QUALITY OF FELTLEAF WILLOW

R. Terry Bowyer[1] **and Juliette A. Neville**

Institute of Arctic Biology, and Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, AK 99775-7000, USA

ABSTRACT: We studied effects of browsing history by Alaskan moose (*Alces alces gigas*) on regrowth and quality of feltleaf willow (*Salix alaxensis*) during late winter 2002 in interior Alaska, USA. We recorded extensive browsing on willows, with 55.6% of leaders on 43 plants browsed by moose and 3.9% browsed by snowshoe hares (*Lepus americanus*). Foraging moose removed, on average, 15.1 mm of current annual growth from willow twigs, which averaged 24.1 mm in length (62.3% removed). Twigs re-growing from 2-year-old stems that were browsed previously had larger diameters at their bud scale scar than those re-growing from stems that were not browsed in the previous year. Browsing history by moose, however, had no effect on nitrogen content, in vitro dry matter digestibility, or tannin content of willow twigs. Willows did not respond to browsing on individual twigs with an inducible defense system that involved tannins. Diameter at point of browsing (bite size) was larger on twigs that had been browsed previously than for twigs re-growing from second-year growth that had not been browsed. Moose did not exhibit an optimal bite size, but took larger-diameter bites from larger compared with smaller leaders of current annual growth. Forage selection by moose for previously browsed twigs likely relates to greater forage biomass on those twigs rather than to forage quality. We caution, however, that foraging behavior by moose cannot be understood fully without considering additional factors, including predation risk in relation to forage availability.

ALCES VOL. 39: 193-202 (2003)

Key words: Alaskan moose, *Alces alces gigas*, browsing history, digestibility, feltleaf willow, foraging behavior, nitrogen, *Salix alaxensis*, tannins

Moose (*Alces alces*) are among the largest browsing mammals, with adult males of *A. a. gigas* (the largest subspecies) attaining > 770 kg and adult females reaching > 570 kg (Schwartz et al. 1987). Moose possess a narrower incisor arcade relative to body mass than do other ruminants, especially grazers—an allometric relationship that ostensibly is an adaptation for selective browsing (Spaeth et al. 2001). Indeed, browse is a critical component in the diet of moose throughout their distribution in North America, especially during winter (Peek 1974, Ludewig and Bowyer 1985). Moreover, in Alaska, USA, willows (*Salix* spp.) are the mainstay in the diet of moose (Molvar et al. 1993, Bowyer and Bowyer 1997, MacCracken et al. 1997, Weixelman et al. 1998, Bowyer et al. 2001, and many others), and those shrubs are consumed year-round in some areas (Van Ballenberghe et al. 1989; Molvar et al. 1993; Bowyer and Bowyer 1997; Bowyer et al. 1998, 1999a). A more-complete knowledge of interactions between moose and this crucial food supply is essential for understanding their distribution (Telfer 1978), population dynamics (Bowyer et al. 1999b), reproductive

---

[1] Present address: Department of Biological Sciences, Idaho State University, Pocatello, ID 83209, USA

performance (Schwartz and Hundertmark 1993), life-history characteristics (Keech et al. 2000), and effects on ecosystem structure and function (Pastor and Naiman 1992, Molvar et al. 1993, Bowyer et al. 1997, Berger et al. 2001).

Large herbivores tend to congregate in areas where they have foraged previously (Fryxell 1991) and use of traditional areas is common among some ungulates (Hjeljord 2001). For instance, moose sometimes use the same migratory routes (Andersen 1991) as well as locations for mating (Van Ballenberghe and Miquelle 1993) and giving birth (Bowyer et al. 1999a). Likewise, cervids (Duncan et al. 1998, Moore et al. 2000), including moose (Molvar et al. 1993, Bowyer and Bowyer 1997, Bergquist et al. 2001), preferentially forage on leaders of new growth that have re-grown from twigs that were browsed previously. Such re-growth on previously browsed twigs is characterized by larger twigs and leaves than on unbrowsed leaders (Bergstrom and Danell 1987, Molvar et al. 1993, Bowyer and Bowyer 1997). Whether previous browsing of plants and their subsequent reuse by foraging herbivores influences use of traditional areas by these large mammals is unknown. We contend, however, that understanding why large herbivores re-browse particular plants, or parts thereof, is an essential step in understanding the overall process of diet selection and habitat use.

The browsing history on trees and shrubs is well known to affect subsequent foraging by moose (Molvar et al. 1993, Bowyer and Bowyer 1997, Bergquist et al. 2001). Consequently, we tested whether re-browsing by Alaskan moose on leaders of new growth on feltleaf willow (*S. alaxensis*) was a result of increased size of twigs, quality of new growth, or both variables. We also tested whether moose would vary bite size in relation to the size of twigs available to browse.

STUDY AREA

We conducted research concerning moose browsing on feltleaf willows in interior Alaska, USA, about 15 km northwest of Fairbanks (64° 54’ N, 147° 50’ W). The study site was near Ballaine Road and followed Goldstream Creek northeast of the road. The area is a low-elevation bog (185 m a.s.l.) underlain with intermittent permafrost, and includes a riparian zone dominated by willows and scattered alders (*Alnus crispa*), which gradates into mixed stands of paper birch (*Betula papyrifera*) and white spruce (*Picea glauca*) on better-drained soils. Willows in this area were mechanically crushed with a bulldozer in March 1996 to improve habitat for moose; substantial re-sprouting of those shrubs has occurred since that treatment (Bowyer et al. 2001). The crushed area, which encompasses 119 ha, extends 3 km northeast along Goldstream Creek, and is 100-800 m in width (Bowyer et al. 2001).

The climate of interior Alaska is characterized by short, warm summers and long, cold, and often severe winters—temperatures range from -10 to -45° C in winter and snow depth averages 80 cm (Gasaway et al. 1983), but has been about one-half that depth in recent years (Keech et al. 2000, Bowyer et al. 2001). Moose density in nearby areas has increased recently (Keech et al. 2000). Although the area is near Fairbanks, large mammalian carnivores, including wolves (*Canis lupus*), are present (Bowyer et al. 2001). The crushing of willows resulted in substantial stump sprouting, which created favorable foraging conditions for moose (Bowyer et al. 2001). Moose using the crushed area were mostly (~80%) adult males; females and young occurred infrequently on the open crushed area (Bowyer et al. 2001).

METHODS

We sampled feltleaf willows during late winter (March 2002), while those plants were dormant, on 43 quadrats, each 5 x 5 m, which were located randomly along 500 m of Gold Stream Creek and extended ≤30 m on either side of the creek. Samples were concentrated in this riparian zone to enhance the probability of locating feltleaf willows. Only 1 willow, the individual plant (clump) closest to the Cartesian coordinates used to select the random plot, was sampled from each quadrat. If no feltleaf willows were present on a particular quadrat, another random quadrat was chosen for sampling. All quadrats were >10 m apart. Selecting only 1 plant per quadrat minimized the likelihood of obtaining multiple samples from clones of the same plant (Molvar et al. 1993). We estimated length of leaders of current annual growth for feltleaf willow from their diameter at the bud scale scar using regression equations developed for this crushed area by Bowyer et al. (2001). All leaders of current annual growth were counted on each willow, and the number of twigs foraged upon by moose and snowshoe hares (*Lepus americanus*), which were distinguished easily from one another (Bowyer and Bowyer 1997), were recorded. We assumed all current annual growth was available as forage, but recognize that moose may not forage on some small twigs (Bowyer and Bowyer 1997). The crown of the willow was examined for leaders with particular patterns of browsing history by moose. Those patterns of browsing included: (1) unbrowsed 2-year-old growth with unbrowsed current annual growth; (2) unbrowsed 2-year-old growth with browsed current annual growth; (3) browsed 2-year-old growth with unbrowsed current annual growth; and (4) both 2-year-old and current annual growth from that twig browsed by moose. Diameter at the bud scale scar for 1-year-old twigs (i.e., current annual growth), and diameter at point of browsing for current annual growth (where appropriate) were recorded with dial calipers to the nearest 0.1 mm. More than one pattern of browsing on twigs was recorded for some individual willows, whereas other willows lacked various combinations of browsing history—not all patterns of browsing occurred on each plant. We sampled 90 twigs of current annual growth on 43 willows in evaluating effects of browsing history on diameter of twigs and re-browsing by moose.

We clipped current annual growth of willows that had re-grown from 2 patterns of previous browsing by moose from 35 quadrats: second-year growth that was browsed and unbrowsed. Those twigs were placed in labeled paper bags in the field, and later dried at 50°C in a forced-air oven for 4 days. Samples were then ground in a Wiley mill and passed through a 1-mm screen. In vitro dry matter digestibility (IVDMD) was determined with the method of Tilley and Terry (1963) modified to use ANKOM Technology filter bags (Fairport, NY). Rumen inoculum for the digestion trial was obtained from a fistulated captive reindeer (*Rangifer tarandus*) held at the R. G. White Large Animal Research Station at the University of Alaska Fairbanks, which had been accustomed to a diet of willows. We determined nitrogen content of willows using an elemental analyzer (Leco # CNS 2000). Tannins were extracted in 50% ethanol and assayed with the Folin-Dennis method (Martin and Martin 1982, Spaeth et al. 2002). A standard developed from *Salix pulchra* was analyzed with samples for *S. alaxensis*.

We tested for differences in use of leaders of current annual growth with a 2-sample *z* test for proportions (Remington and Schork 1970). We used analysis of variance (ANOVA) to test for differences in diameters of willow twigs in relation to browsing history by moose (Neter et al.

1985). In that analysis, diameter of current annual growth was the dependent variable, with location on the twig (at the bud scale scar or bite) where diameter was measured, previous browsing history (browsed or unbrowsed), and their interaction as main effects. We tested for and met assumptions of homogeneous variances prior to analysis, and performed a posteriori tests with Tukey's HSD. We arbitrarily reduced α to 0.02 for that analysis to compensate for a potential lack of statistical independence from sampling >1 combination of browsing histories from the same plant.

We tested for effects of forage quality of willow twigs in relation to browsing history by moose using weighted multivariate analysis of variance (Johnson and Wichern 1982). Nitrogen concentration (N), IVDMD, and tannin concentration were dependent variables, and whether current annual growth re-grew from browsed or unbrowsed second-year growth was the main effect. Mass of current annual growth for a particular browsing history on a willow sometimes was insufficient to allow nutritional analyses. In those circumstances, we combined plants to obtain adequate sample mass. Consequently, we weighted those combined samples by the number of plants included in the analysis. Percentage data were square-root, arc-sine transformed prior to conducting analysis to meet assumptions of MANOVA; we also tested for and met the assumption of multivariate homogeneity of variances. We set $\alpha = 0.05$ for MANOVA. We also examined partial correlations among dependent variables from the error sum-of-squares cross-product matrix in that analysis of forage quality conducted with MANOVA.

RESULTS

Mean (± SD) number of leaders of current annual growth occurring on 43 feltleaf willow was 115.3 ± 98.2 (range = 12-389 leaders). All 43 willows we selected exhibited some use by moose, but hares fed on 39.5% of those plants—typically on twigs near the base of the plant. Of leaders available as forage on willows, a mean (± SD) of 55.6 ± 21.2% (range = 19.4-91.0%) were browsed by moose, whereas 3.9 ± 9.3% (range = 0-39.6%) of leaders were fed upon by hares; that difference was highly significant ($z = 231.1, P < 0.0001$). Comparatively low levels of browsing by hares probably had limited effects on regrowth of twigs by willows.

Based on regression analysis predicting leader length from twig diameter, a mean (± SD) of 24.1 mm (± 1.2 mm) of current annual growth was available on each twig for foraging by moose. Foraging moose removed, on average, 15.1 mm (± 1.0 mm) of current annual growth, or 62.3% of each twig. Overall removal of current annual growth on 43 feltleaf willows by foraging moose (based on leader length) was estimated at 34.6% (55.6% of potential leaders browsed x 0.623 proportionally removed from each leader).

Previous foraging on feltleaf willow by moose had an effect on subsequent regrowth of twigs, and on the bite size (diameter of twigs) taken by moose (Fig. 1; $F = 29.83, P < 0.0001$). Tukey's HSD indicated twig diameters at the bud scale scar were larger for leaders of current annual growth re-growing from second-year growth that had been browsed by moose than from second-year growth that was not browsed ($P < 0.001$). Likewise, moose took larger bites from twigs re-growing from previously browsed second-year growth than from that same age of twigs that had not been browsed ($P < 0.001$).

Measure of forage quality for feltleaf willow, including N content, IVDMD, and tannins, did not differ based on previous browsing history by moose (Table 1). Partial correlation coefficients, from that analy-

Table 1. Effects of previous browsing by moose on measures of forage quality, including percent dry mass of nitrogen (N), in vitro dry matter digestibility (IVDMD), and tannins, for current annual growth of feltleaf willow, interior Alaska, USA, winter 2002. Individual willows ($n = 35$) were combined from random quadrats into 19 samples to provide sufficient material for nutritional analyses; consequently, statistical analysis (multivariate analysis of variance; MANOVA) is weighted by the number of plants in each sample.

	Browsing History			
	Unbrowsed ($n = 10$)		Browsed ($n = 9$)	
[1]Measures of forage quality (%)	$\bar{X}$	SE	$\bar{X}$	SE
N	1.18	0.053	1.17	0.056
IVDMD	37.9	1.14	37.2	0.78
Tannins	11.4	0.79	12.7	0.69

[1] Weighted MANOVA indicated no effect of browsing history on measures of forage quality (Wilks' Lambda, $F_{1,17} = 0.79$, $P = 0.39$).

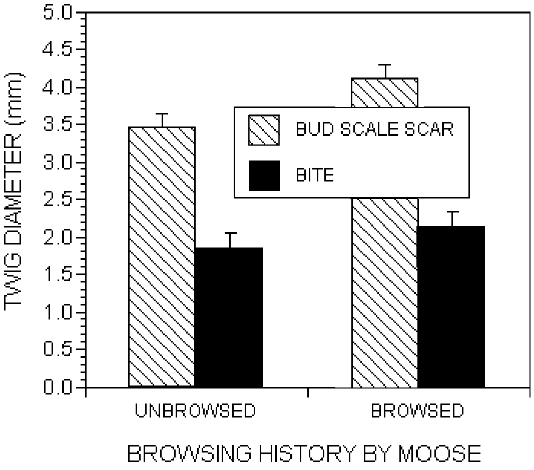

Fig. 1. Mean (+ SE) diameter of current annual growth measured at the bud scale scar and at the bite on 90 twigs from 43 feltleaf willows in relation to browsing history by Alaskan moose in late winter 2002, interior Alaska, USA.

sis of forage quality with MANOVA (Table 1), indicated a weak positive relationship between N and IVDMD ($r = 0.30$, $P = 0.21$), and a weak negative correlation between N and tannins ($r = -0.17$, $P = 0.51$). There was a significant positive relation between IVDMD and tannins ($r = 0.52$, $P = 0.03$) for current annual growth of feltleaf willow.

DISCUSSION

Our findings concerning re-growth of twigs on feltleaf willow following browsing by moose confirm other results documenting that willows respond in the subsequent year with increased current annual growth (Molvar et al. 1993, Bowyer and Bowyer 1997). Increased re-growth of twigs from browsing by moose may relate to 3 factors: release of lateral twigs from apical dominance; greater plant resources to invest in fewer growing points; and fertilization of plants from inputs of urine and feces from browsing herbivores (Molvar et al. 1993, Bowyer and Bowyer 1997 for reviews). The latter two factors, however, cannot explain variation in size of individual leaders from differences in browsing history, which should be similar for all current annual growth on the same plant. Whatever the cause, moose foraging selectively would benefit from an increase in available size of bites on willows.

Large mammalian herbivores, including moose, forage preferentially on leaders of new growth that have re-grown from twigs that were browsed previously (Molvar et al. 1993, Bowyer and Bowyer 1997, Moore et al. 2000, Bergquist et al. 2001). Moose obtained more forage per bite, and perhaps decreased handling time of forage, from browsing re-growth on willows that had been foraged upon formerly. Moose varied the size of their bite with respect to the size of the available leader; a pattern also noted by Shipley et al. (1999). Consequently, moose do not take an optimum-sized bite, but may still be attempting to optimize diet quality.

Whether patterns of browsing history and subsequent re-growth of twigs help explain use of traditional areas, including travel paths, by moose is unknown. Clearly, forage plays an important role in selection of areas by moose during critical periods of the year (Bowyer et al. 1997, Bowyer et al. 1999a), and has far-reaching implications for nutritional condition, reproduction, and survival of moose (Schwartz and Hundertmark 1993, Keech et al. 2000). Variation in abundance of forage may help explain the distribution of sexes outside the mating season (Bowyer et al. 2001). Spatial separation of sexes in ruminants (sensu Bowyer 1984, Bowyer et al. 1996, Kie and Bowyer 1999, Bowyer et al. 2002) likely has a dietary component related to forage abundance, with males using areas with more but not necessarily higher-quality food than localities inhabited principally by females (Barboza and Bowyer 2000, 2001). Indeed, males predominated in the crushed areas where we studied browsing by moose, which had more available forage than an adjacent area where females and young were more common (Bowyer et al. 2001). Whether browsing history is related to resource partitioning by the sexes of moose (Miquelle et al. 1992, Bowyer et al. 2001), however, requires additional study.

We rejected the hypothesis that browsing history of willows was related to the quality of subsequent re-growth of twigs (Table 1). That conclusion is in keeping with results from Molvar et al. (1993), who also reported little variation in quality of twigs re-sprouting from browsed or unbrowsed leaders of *Salix pulchra*, or for re-growth of twigs on plants experiencing differing levels of browsing intensity. Likewise, mechanical crushing of *S. alaxensis* had limited effects on quality of current annual growth in our study area (Bowyer et al. 2001). We caution, however, that our data and those of others on browsing history and forage quality of willows come mostly from autumn and winter—we are uncertain whether browsing might enhance quality of current annual growth in spring and summer. Browsing of twigs during winter results in re-growth of large leaves the following spring (Molvar et al. 1993), and moose often leaf-strip that productive growth (Miquelle 1983). In addition, we could only measure quality on leaders of current annual growth that moose had not browsed. If moose selectively foraged on higher-quality twigs from those re-growing from a previously browsed twig (thereby removing our opportunity to sample those twigs), our analysis would underestimate quality (Bowyer et al. 1999a). We suspect such a bias is slight because of the overall low quality of willows during winter (Bowyer et al. 2001; Table 1). Nonetheless, slight differences in forage quality can be magnified over time as herbivores accumulate resources via foraging (White 1983).

Understanding differences in quality of forage for moose and other large herbivores is complicated by variation in growing conditions for plants (Chapin 1983, Molvar et al. 1993, Lenart et al. 2002), which may result in fine-scale divergence in quality of individual willows (Spaeth et al. 2002). Such spatial variation in quality of trees and shrubs throughout the year in relation to browsing history by large herbivores is a topic in need of additional research.

Salix alaxensis is an important component in the winter diet of moose in interior Alaska (Van Ballenberghe et al. 1989, Miquelle et al. 1992, Bowyer et al. 2001). Yet, overall quality of those willows on our study site was low (Table 1; Bowyer et al. 2001). That outcome is not likely biased by our relatively small sample sizes, because of the near-identical values in measure of forage quality between current annual growth re-growing from browsed and unbrowsed twigs (Table 1). Moreover, levels of tannins, which are thought to be an important deterrent to browsing mammals (Bryant and Kuropat 1980, Robbins et al. 1987), were comparatively high (Table 1) in *Salix alaxensis* on our study area, yet moose browsed those willows extensively. Surprisingly, IVDMD was positively correlated with tannin concentrations in willows, an outcome antithetical to the hypothesis that those secondary compounds interfere with digestion of structural carbohydrates. How widespread that positive relationship is between tannins and IVDMD among willows or other species of browse is uncertain, but warrants further investigation. Moreover, moose possess tannin-binding proteins in their saliva, which would further ameliorate affects of tannins on digestion (Hagerman and Robbins 1993). We caution that measures of forage quality have been difficult to link with diet selection in free-ranging moose (Weixelman et al. 1998), and that a more complete understanding of that process will require data on other aspects of the ecology and behavior of moose.

Population density relative to environmental carrying capacity (*K*) and risk of predation unquestionably affect foraging behavior by large herbivores, including moose (Molvar and Bowyer 1994, Weixelman et al. 1998, Bowyer et al. 1999b). Tradeoffs between avoiding predation and acquiring essential resources have been well-documented for large herbivores (Molvar and Bowyer 1994, Rachlow and Bowyer 1998, Bowyer et al. 1999a, Kie 1999, Barten et al. 2001, and numerous references therein). We propose that a full understanding of foraging behavior, including hypotheses explaining bite size, browsing history, and diet selection by moose will require a synthesis of these two important fields. We hope our data on forage abundance and quality in relation to browsing history by moose will help lay the groundwork for such research.

ACKNOWLEDGEMENTS

This research was funded, in part, by the Institute of Arctic Biology, and Department of Biology and Wildlife at the University of Alaska Fairbanks (UAF). We are indebted to C. Adler, C. Brockman, A. E. Collins, L. J. Huges, S. J. Isham, Y. Kawaguchi, K. Kellie, N. I. Kohlenberg, R. A. Long, T. M. Massie, T. A. McLaughlin, H. Moncrief, B. Soiseth, and D. Stewart from UAF for their assistance in the field and laboratory. We thank R. Kedrowski for conducting nutritional analysis on our willow samples at the Forage Quality Analysis Laboratory at UAF. We acknowledge J. G. Kie, D. F. Spaeth, P. S. Barboza, and K. M. Stewart for their advice and assistance in the preparation of this manuscript.

REFERENCES

Andersen, R. 1991. Habitat deterioration and the migratory behavior of moose (*Alces alces*) in Norway. Journal of Applied Ecology 28:102-108.

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.

Barten, N. L., R. T. Bowyer, and K. J. Jenkins. 2001. Habitat use by female caribou: tradeoffs associated with parturition. Journal of Wildlife Management 65:77-92.

Berger, J., P. B. Stacey, L. Belis, and M. P. Johnson. 2001. A mammalian predator-prey imbalance: grizzly bear and wolf extinction affect avian Neotropical migrants. Ecological Applications 11:229-240.

Bergquist, G., R. Bergstrom, and L. Edenius. 2001. Patterns of stem damage by moose (*Alces alces*) in young *Pinus sylvestris* stands in Sweden. Scandinavian Journal of Forest Research 16:363-370.

Bergstrom, R., and K. Danell. 1987. Effects of simulated winter browsing by moose on morphology and biomass of two birch species. Journal of Ecology 75:533-544.

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. 1984. Sexual segregation in southern mule deer. Journal of Mammalogy 65:410-417.

_______, J. G. Kie, and V. Van Ballenberghe. 1996. Sexual segregation in black-tailed deer: effects of scale. Journal of Wildlife Management 60:10-17.

_______, 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 Alaskan moose: effects of habitat manipulation. Alces 37:109-122.

_______, K. M. Stewart, S. A. Wolfe, G. M. Blundell, K. L. Lehmkuhl, P. J. Joy, T. J. McDonough, and J. G. Kie. 2002. Assessing sexual segregation in deer. Journal of Wildlife Management 66:536-544.

_______, V. Van Ballenberghe, 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. Bissonette, 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.

Chapin, F. S., III. 1983. Direct and indirect effects of temperature on arctic plants. Polar Biology 2:47-52.

Duncan, A. J., S. E. Hartley, and G. R. Iason. 1998. The effect of previous browsing damage on the morphology and chemical composition of Sitka spruce (*Picea sitchensis*) saplings and on their subsequent susceptibility to browsing by red deer (*Cervus elaphus*). Forest Ecology and Management 103:57-67.

Fryxell, J. M. 1991. Forage quality and aggregation by large herbivores. American Naturalist 138:478-498.

Gasaway, W. C., R. O. Stephenson, J. L. Davis, P. E. K. Shepherd, and O. E. Burris. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildlife Monographs 84.

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. 2001. Dispersal and migration in northern forest deer—are there unifying concepts? Alces 37:353-370.

Johnson, R. A., and D. W. Wichern. 1982. Applied multivariate statistical analysis. Prentice Hall, Englewood Cliffs, New Jersey, USA.

Keech, M. A., R. T. Bowyer, J. M. Ver Hoef, R. D. Boertje, B. W. Dale, and T. R. Stephenson. 2000. Life-history consequences of maternal condition in Alaskan moose. Journal of Wildlife Management 64:450-462.

Kie, J. G. 1999. Optimal foraging in a risky environment: life-history strategies for ungulates. Journal of Mammalogy 80:1114-1129.

______, and R. T. Bowyer. 1999. Sexual segregation in white-tailed deer: density dependent changes in use of space, habitat selection, and dietary niche. Journal of Mammalogy 80:1004-1020.

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.

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.

MacCracken, J. G., V. Van Ballenberghe, and J. M. Peek. 1997. Habitat relationships of moose on the Copper River Delta in coastal and south-central Alaska. Wildlife Monographs 136.

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.

Miquelle, D. G. 1983. Browse regrowth and consumption following summer defoliation by moose. Journal of Wildlife Management 47:17-24.

______, J. M. Peek, and V. Van Ballenberghe. 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 Ballenberghe. 1993. Moose herbivory, browse quality, and nutrient cycling in an Alaskan treeline community. Oecologia 94:472-479.

Moore, N. P., J. D. Hart, P. F. Kelly, and S. D. Langton. 2000. Browsing by fallow deer (*Dama dama*) in young broadleaved plantations: seasonality, and the effects of previous browsing and bud eruption. Forestry 73:437-445.

Neter, J., W. Wasserman, and M. H. Kutner. 1985. Applied linear statistical models: regression, analysis of variance, and experimental designs. Second edition. Irwin, Homewood, Illinois, USA.

Pastor, J., and R. J. Naiman. 1992. Selective foraging and ecosystem processes in the boreal forests. American Naturalist 134:690-705.

Peek, J. M. 1974. A review of moose food habit studies in North America. Naturaliste Canadien 101:131-141.

Rachlow, J. L., and R. T. Bowyer. 1998. Habitat selection by Dall's sheep (*Ovis* *dalli*): maternal trade-offs. Journal of Zoology (London) 345:457-465.

Remington, R. D., and M. A. Schork. 1970. Statistics with applications to the biological and health sciences. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

Robbins, C. T., 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.

Schwartz, C. C., and K. J. Hundertmark. 1993. Reproductive characteristics of Alaskan moose. Journal of Wildlife Management 57:454-468.

______, W. L. Regelin, and A. W. Franzmann. 1987. Seasonal weight dynamics of moose. Swedish Wildlife Research Supplement 1:301-310.

Shipley, L. A., A. W. Illius, K. Danell, N. T. Hobbs, and D. E. Spalinger. 1999. Predicting bite size selection of mammalian herbivores: a test of a general model of diet optimization. Oikos 84:55-68.

Spaeth, D. F., R. T. Bowyer, T. R. Stephenson, P. S. Barboza, and V. Van Ballenberghe. 2002. Nutritional quality of willows for moose: effects of twig age and diameter. Alces 38:143-154.

______, 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? Alces 37:217-226.

Telfer, E. S. 1978. Cervid distribution, browse and snow cover in Alberta. Journal of Wildlife Management 42:352-361.

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 Ballenberghe, V., and D. G. Miquelle. 1993. Mating in moose: timing, behavior and male access patterns. Canadian Journal of Zoology 71:1687-1690.

______, ______, and J. G. MacCracken. 1989. Heavy utilization of woody plants by moose during summer in Denali National Park, Alaska. Alces 25:31-35.

Weixelman, D. A., R. T. Bowyer, and V. Van Ballenberghe. 1998. Diet selection by Alaskan moose during winter: effects of fire and forest succession. Alces 34:213-238.

White, R. G. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. Oikos 40:377-384.