

## EFFECTS OF PREVIOUS BROWSING ON THE SELECTION OF WILLOW STEMS BY ALASKAN MOOSE

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**ABSTRACT:** We tested whether regrowth from stems of willows (*Salix glauca*) browsed by Alaskan moose (*Alces alces gigas*) in the previous winter would effect selection for browse by moose in the following winter. We sampled willow in a power-line corridor near Fairbanks, Alaska, USA, during autumn 1995 and winter 1996. We collected current annual growth for 90 stems from 30 willows to establish relationships among stem length, stem diameter at the bud-scale scar, and dry mass. Strong curve-linear regressions were obtained between stem length and dry mass ( $R^2 = 0.91$ ), and stem diameter and dry mass ( $R^2 = 0.90$ ); stem length was linearly related to diameter ( $r^2 = 0.74$ ). We randomly sampled an additional 30 willows to investigate levels of browsing by moose on leaders of new growth. Overall levels of browsing were high ( $70.4\% \pm 20.2\%$  SD), but feeding on stems that were browsed previously was significantly ( $P < 0.001$ ) higher ( $84.6\% \pm 16.0\%$  SD). We estimated dry mass available to moose on willow stems not browsed in the previous or current winter ( $0.62 \text{ g} \pm 0.18 \text{ g}$  SD), stems browsed in the previous winter but not the current one ( $0.87 \text{ g} \pm 0.48 \text{ g}$  SD), and stems browsed during both winters ( $4.0 \text{ g} \pm 2.7 \text{ g}$  SD); this pattern in biomass available to moose differed significantly ( $P < 0.001$ ). We also estimated that moose removed  $1.6 \text{ g} (\pm 1.0 \text{ g})$  SD of current annual growth from each stem they browsed. This amount was greater than available on stems that were not browsed in winter 1995-1996, and may help explain selection of moose for regrowth from previously browsed stems. Consequently, moose would obtain more food for the same effort by feeding upon stems they had browsed previously. This outcome also may help explain why moose use traditional areas for feeding and other activities.

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Browse is an important component of diets for moose (*Alces alces*) inhabiting boreal forests (Joyal 1976, Ludewig and Bowyer 1985, Van Ballenberghe *et al.* 1989). Indeed, Alaskan moose (*A. a. gigas*) make extensive use of willows (*Salix*) throughout the year (Wolff 1978, Van Ballenberghe *et al.* 1989, Miquelle *et al.* 1992, Van Ballenberghe 1993, Molvar *et al.* 1993). Moreover, the size of stems available to moose for browsing is thought to play a critical role in diet selection by this large herbivore (Vivas *et al.* 1991).

Large herbivores may positively affect their food supply in three fundamental ways. Moose browsing in autumn and winter may release stems from apical dominance and result in regrowth of larger stems with larger

leaves the following spring and summer (Bergstrom and Danell 1987, Molvar *et al.* 1993); additionally, vegetative reproduction by adventitious growth may be enhanced by browsing (Grime 1977). Both experimental (Stafford 1990) and field studies (Molvar *et al.* 1993) demonstrated that biomass per growing point for willows increased with overall levels of browsing on the entire plant.

Moderate levels of browsing may affect the carbon-nitrogen balance of the plant and result in higher-quality regrowth that is poorly defended by secondary compounds (Bryant 1981, Bryant *et al.* 1983, Bryant and Chapin 1986). Leaf litter from such plants has lower levels of secondary compounds and a lower lignin:nitrogen ratio (Molvar *et al.* 1993), and would be expected to decompose rapidly

(Flanagan and Van Cleve 1983), making nutrients available to the plant more quickly than for unbrowsed plants.

Moose may fertilize the plants they feed upon through inputs of feces and urine (McKendrick *et al.* 1980, Molvar *et al.* 1993). Large herbivores tend to defecate where they feed (Etchberger *et al.* 1988), and nitrogen content in feces increases with forage quality (Leslie and Starkey 1985, Hodgman and Bowyer 1986). These factors combine to stimulate rates of nutrient cycling in areas frequented by large herbivores (Ruess and McNaughton 1987, Molvar *et al.* 1993).

Despite increasing evidence that moose play a fundamental role in the structure and function of boreal forests (Pastor *et al.* 1988, Pastor and Naiman 1992, Molvar *et al.* 1993), much remains to be discovered about the foraging ecology of these large herbivores. Gaining insight into why moose forage on a particular plant or select specific stems from that plant is necessary to understand the mechanisms underpinning the overall process.

We tested whether regrowth from stems of willow (*Salix glauca*) browsed by Alaskan moose during the previous winter would effect selection of stems for browsing in the following winter. Moreover, we tested whether biomass of these stems would affect their use by moose, and how this related to the amount of forage per stem obtained by a feeding moose.

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### STUDY AREA

We sampled stems (current annual growth) of willows (*Salix glauca*) at an elevation of 260 m on Chena Ridge near

Fairbanks, Alaska, USA, (64° N, 15° W) during autumn 1995 and winter 1996. Interior Alaska is characterized by low annual precipitation (35 mm) and extreme temperatures. Summer maxima often exceeds 30° C and winter minima below -45° C are not uncommon. Snow averages 73 cm in depth and ranged between 15-60 cm during our study. Snow typically persists for 8 months.

We began sampling in late October after willows had become dormant and had lost most of their leaves. We chose this time so that we initially had large numbers of unbrowsed stems available for establishing relationships among diameter, length, and biomass of current annual growth. Sampling was completed in mid-March to allow the effects of browsing to reflect the use of willows by moose throughout winter.

Our study area was a 15-m wide power-line corridor, which was established in the late 1970s, that extended for about 1 km down a south-facing slope. There was no overstory cover, and a dense growth of willows and a few aspen (*Populus tremuloides*) characterized the understory. The power-line corridor had not been treated with herbicide, and larger trees were last cut from this area in 1989 when early snowfall caused some trees to fall across the power lines. This area was chosen because variation in slope, exposure, and overstory cover was minimal. Likewise, distance from concealment cover, which is known to affect foraging by moose (Molvar and Bowyer 1994), was similar across our study site. Willows ranged in size from bushes (1 m in height) to small trees (2 m in height). The power line was surrounded by boreal forest dominated by white spruce (*Picea glauca*). Such regrowth of willows is typical of power-line corridors in interior Alaska and also occurs along roadcuts throughout the interior. Fresh moose tracks and feces were evident on our study site, and signs of moose browsing were common throughout winter (Fig. 1). We observed

mostly cows and their calves using this area but did not estimate their population size. Populations of moose in interior Alaska typically occur at low ( $< 1$  moose/km<sup>2</sup>) density (Gasaway *et al.* 1992). We did not observe bark-stripping (Miquelle and Van Ballenberghe 1989) or scent-marking of willows (Bowyer *et al.* 1994) on our study area. Evidence of browsing by snowshoe hares (*Lepus americanus*) was rare and confined to lower branches when present.

### METHODS

We collected three stems (current annual growth) from each of 30 willows (*S. glauca*) spaced  $\geq 3$  m apart while walking a transect down the center of the power-line corridor. This spacing was maintained to minimize the likelihood that clumps of individual willows were clones of the same plant (Molvar *et al.* 1993). Current annual growth for unbrowsed willows was clipped at the most recent bud-

scale scar. Upon returning from the field, we measured the length of each stem from the bud-scale scar to the terminal bud, and the diameter of the stem at the bud-scale scar to the nearest 1 mm. Two willow stems were eliminated from further analysis because upon closer examination they showed evidence of insect damage; one stem was lost during transport from the field. The stems were oven-dried at 50° C for 4 days, then weighed individually to the nearest 0.01 g. We used simple linear- and curve-linear regressions (Zar 1984) to established relationships among length, diameter, and dry mass of stems for subsequent analyses.

We sampled an additional 30 willows, excluding those we previously clipped, for browsing by moose. Willows were selected at random distances while pacing down the transect ( $> 3$  m between willows). We then selected about 10 stems from the center of the crown of each plant; if 10 stems were not available from that portion of the plant, adjacent areas from the same plant were sampled. None of these stems was covered by snow. A mean of 13.7 (2.9 SD) stems was examined for each plant. Thus, the individual clumps of willows (likely individual plants) were the sampling units for this analysis. We counted the stems (current annual growth) browsed by moose and noted whether these stems regrew from stems that had been fed upon in the previous winter. We tested for differences in the overall percent of stems browsed, and the percent of stems browsed by moose that had been fed upon in the previous winter with a sign test (Siegel 1956). This nonparametric test for related samples allowed us to control for the overall level of browsing on each willow while examining the preference of moose for regrowth from browsed stems.

To evaluate biomass of forage available on stems with differing histories of moose browsing, we determined the diameter and length of current annual growth that: 1) had

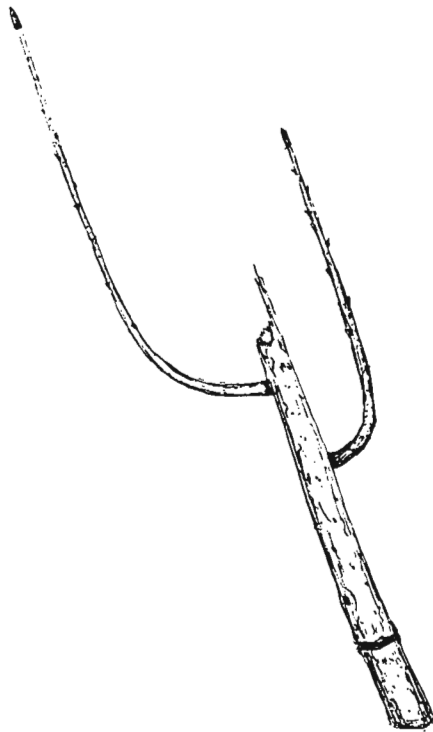


Fig. 1 Characteristic regrowth of a willow stem browsed by a moose. Drawing by E. Molvar.

not been browsed in the last two winters; 2) had been browsed in the previous winter but not the current one; and 3) had been browsed during both winters. Because some proportion of the current annual growth for stems browsed in both winters by moose was removed, we used regression models to estimate dry mass for these stems. We also used this method to estimate dry mass removed by foraging moose for all categories of stems. We tested for differences in the available dry mass among categories of stems with a Kruskal-Wallis test (Siegel 1956).

### RESULTS

Strong curve-linear relations existed between dry mass of willow stems and the length and diameter of those stems; a linear relation occurred between stem length and diameter (Fig. 2). As the size of willow stems increased, the dry mass of current annual growth increased exponentially.

The overall level of browsing by moose on 30 willows was relatively high ( $70.4\% \pm 20.2\%$  SD stems/willow), with moderate variability occurring among plants (C.V. = 29%). Within these same leaders of new growth, however, moose showed a significant (sign test,  $Z = 3.34$ ,  $P < 0.001$ ) preference for leaders that had regrown from previously browsed stems ( $84.6\% \pm 16.0\%$  SD). No branches we examined were browsed beyond current annual growth, but we believe this may have occurred because of the mild winter conditions in 1995-1996.

We investigated whether moose fed on regrowth from stems that were browsed previously by examining the dry mass available on various categories of stems. Overall differences existed in the biomass of stems depending upon their previous history of browsing (Fig. 3). Regrowth from willow stems browsed by moose in 2 consecutive years had more than four times the biomass of current annual growth than did other categories of stems; differences between stems

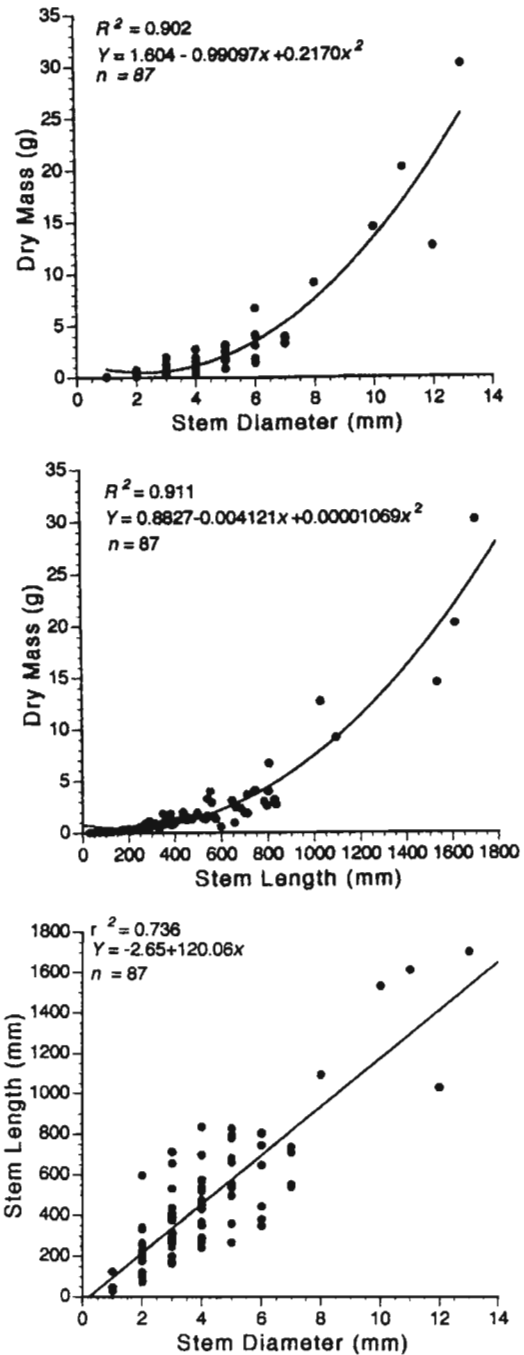


Fig. 2 Relationships for stem length, diameter, and dry mass for current annual growth of *Salix glauca*, Fairbanks, Alaska, U.S.A., winter 1995-1996.

that were not browsed in the previous year or during the current year were small (Fig. 3).

Finally, we estimated the biomass removed by foraging moose for all stems on which browsing occurred. A mean of 1.6 g (1.0 g SD) dry mass was removed from each stem of current annual growth by foraging moose (Table 1).

### DISCUSSION

Moose exhibited a preference for regrowth from willow stems that were browsed in the previous winter. They likely

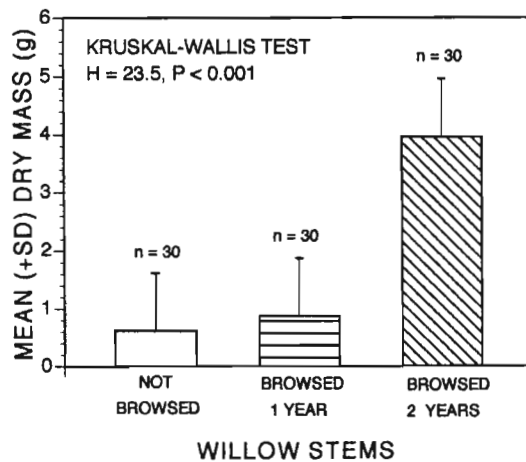


Fig. 3 Dry mass of willow stems (current annual growth) available to moose that were not browsed in winter 1994-1995 or winter 1995-1996 (not browsed), browsed in winter 1994-1995 but not in 1995-1996 (browsed 1 year), or were browsed during both winters (browsed 2 years), Fairbanks, Alaska, U.S.A.

did so because such stems had more forage available than did other ones (Fig. 3). This selectivity occurred even with high levels of browsing on stems (70%) on our study area. Our findings strongly support the views of Vivas *et al.* (1991) and Molvar *et al.* (1993) that moose may maximize forage intake in a shorter period of time by returning to areas where they foraged in previous years. Indeed, regrowth of larger stems following release of apical dominance by moose browsing was expected (Bergstrom and Danell 1987, Molvar *et al.* 1993). Our data document that moose can still obtain leaders of new growth from willows that are high in biomass even from an area that was heavily browsed. This strategy may be less effective, however, where densities of willows are low, and total availability of forage is reduced.

We also demonstrated that regrowth from browsed and unbrowsed stems of willows can vary within the same plant (Fig. 3). This outcome is contrary to results from Molvar *et al.* (1993) and Stafford (1990), who reported that the overall level of browsing on the plant, rather than the individual history of browsing on the stem, was the primary factor determining the size of current annual growth. Our data may differ from these previous studies for several reasons. Molvar *et al.* (1993) studied *S. pulchra*, and Stafford (1990) worked on *S. alaxensis*; perhaps *S. glauca* responds differently than other Alaskan willows to browsing by moose. Even for

Table 1. Characteristics of willow (*Salix glauca*) stems from 30 plants browsed by moose during winter 1995-1996, Fairbanks, Alaska.

Stem characteristics	$\bar{X}$	SD	Range
Diameter (mm)	5.9	1.6	4.0 - 9.0
Estimated length (mm)	69.3	19.2	47.7 - 107.7
Stem remaining (mm)	21.5	14.6	5.4 - 55.5
Estimated length removed (mm)	49.6	12.8	28.8 - 76.2
Estimated dry mass removed (g)	1.6	0.95	0.58 - 3.96

regrowth of stems that were browsed previously, moose exhibited strong selection for stems with greater biomass. We only obtained this result, however, by reconstructing available biomass using regression models. Had we only measured remaining unbrowsed stems, we would have concluded there was little effect of browsing history on size of individual stems. Additionally, clipping experiments may not mimic the feeding of herbivores closely enough to yield meaningful results (Baldwin 1990). Browsing by moose in successive years may help keep willows from growing out of reach. No plants on our study site, however, were large or robust enough that moose could not have bent over branches to feed upon them. Our results indicate that understanding both the pattern and the intensity of herbivory on individual plants may be necessary to determine the characteristics of regrowth. This area deserves further research.

Our estimates of willow removed by foraging moose are consistent with those of Miquelle *et al.* (1992) and are somewhat higher than reported by Risenhoover (1989). These authors, however, reported biomass per bite removed by moose; our data represent total biomass removed per stem and could have resulted from more than one successive bite on the same stem.

We caution against extrapolating our data too far. Variation in density of moose relative to available stems of willow would likely cause radically different outcomes. High levels of browsing sustained through time would probably have deleterious effects on both the quantity and quality of current annual growth of willows (Molvar *et al.* 1993). Strong negative feedbacks between population size of ungulates and their forage are well documented (McCullough 1979). Indeed, changes in the population size of moose would likely affect selectivity for stems of varying size and perhaps the biomass removed; there is probably some level of brows-

ing that yields optimal regrowth of stems.

Testing whether previously browsed stems were of higher quality than unbrowsed ones was beyond the scope of this study. Molvar *et al.* (1993) failed to document this relationship for moose foraging on *S. pulchra*, but indicated more research was necessary.

Moose in interior Alaska have been held at low levels by predation (Gasaway *et al.* 1992, Van Ballenberghe and Ballard 1994). Under these circumstances, the opportunity for a positive feedback between moose and their food supply exists (Molvar *et al.* 1993). We demonstrated that browsing by moose resulted in leaders of regrowth that were larger than unbrowsed stems. Thus, moose would obtain more food for the same effort by feeding on stems they had browsed in previous years. This may help explain the traditional use of areas by moose for feeding and other activities (Miquelle *et al.* 1992). The reasons underpinning why moose use particular areas may have far-reaching consequences for understanding nutrient cycling and productivity of boreal forests (Pastor 1988, Molvar *et al.* 1993, Bowyer *et al.*, in press).

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