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Factors influencing the use of willow and birch by moose in winter

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Abstract We evaluated browsing patterns of moose during 37 individual feeding trials conducted over a 3-day period in winter in which hand-assembled, species-specific trials containing various densities of either willow (*Salix scouleriana*) or birch (*Betula papyrifera*) saplings were presented to human-habituated moose (*Alces alces andersoni*). At the trial (patch) level, the pre-trial weight of both willow and birch was the most important factor in explaining the amount of biomass eaten, the length of all shoot materials removed from saplings, and the amount of edible biomass left uneaten by moose. For willow, the number of days moose were fed saplings partially explained the average bite diameters and the amount of edible biomass left uneaten following trials. The position of the sapling within the feeding station helped to explain the shoot length removed by moose, while sapling density influenced the amount of edible willow biomass left uneaten. At the individual sapling level, the pre-trial weight of birch and willow was important in helping to explain the amount of biomass eaten and the amount of edible biomass left behind. In addition, sapling density influenced the amount of willow biomass eaten, and both sapling density and trial day helped to explain the amount of edible willow biomass left behind.

Keywords *Alces* · *Betula* · Feeding · Trial · Forage · *Salix*

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Introduction

In winter, moose feed extensively on twigs of early-seral deciduous woody plants such as willow (*Salix* spp.) and birch (*Betula* spp.; Renecker and Schwartz 1998). These two genera are a major winter staple of moose throughout much of their range and are considered both preferred and principal food items, depending on availability (Renecker and Schwartz 1998). Moose generally browse in the upper and outer portions of these and other shrub and tree species and will often break plant stems down to access upper twigs where possible (Telfer and Cairns 1978; Bryant and Kuropat 1980; Bergström and Danell 1987). Moose are known to select smaller, less fibrous shoots when available, but will also select basal shoots from previously browsed and otherwise damaged trees (Bergström and Hjeljord 1987; Risenhoover 1987). Moose will crop twigs to large bite diameters in order to increase intake rates on individual trees with fewer shoots or when tree density per patch is limited (Vivås and Sæther 1987; Shipley et al. 1999). Edenius (1991) described decreases in bite mass removal by moose (as indexed by bite diameters) when feeding on Scots pine (*Pinus sylvestris*) but also reported constant bite diameters for aspen (*Populus tremuloides*) as browse was depleted.

To establish how browsers use plants during winter, rangeland ecologists conduct browse-use surveys in spring (e.g., Hamilton et al. 1980; Cumming 1987; Keilland and Osborne 1998). Such surveys can help ecologists assess browse biomass removal from winter ranges and, specifically, which shoots from plants and which plants from patches are used by browsers (Vivås et al. 1991; Milchunas and Noy-Meir 2002). Although informative from a range-use perspective, such surveys convey little information about how much and what kinds of twigs are eaten from various plants and even less about animal foraging ecology, per se. Foraging dynamics, the mechanics of browsing, and the use of plant biomass to determine biomass consumption by species are best

understood through direct observations of foraging animals (Renecker and Hudson 1986; Gillingham et al. 1997) or through the use of feeding trials (Schwartz et al. 1988; Lundberg et al. 1990; Shipley and Spalinger 1995).

Feeding trials with captive moose have been used to distinguish principal (most eaten) from preferred food items (Renecker and Schwartz 1998) and winter browse preferences (Lundberg et al. 1990). Feeding trials have also been used to examine cropping and intake rates of moose eating fresh alfalfa (Gross et al. 1993) and single shoots of red maple (*Acer rubrum* L.) in winter (Shipley and Spalinger 1992), the latter in relation to—among other things—size and distribution of patches (Shipley and Spalinger 1995). Such trials also help establish changes in feeding patterns relative to the time of day and the number of days animals are exposed to a particular forage item (Parsons et al. 1994; Bernays et al. 1997). Changes in forage consumption throughout the day or from one day to the next, however, do not appear to have been previously studied with moose (Nordengren and Ball 2005). Although plant density per patch (Shipley et al. 1999; Vivås and Sæther 1987) and the spatial distributions of plants (Shipley and Spalinger 1995) are separately known to influence foraging decisions by moose, how the combination of these factors influences moose browsing is unclear and remains to be evaluated.

Here, we describe experiments that compared the amount of shoot biomass and shoot length removed, edible biomass left uneaten as well as bite diameters taken by moose in relation to plant biomass, plant density, and the position of plants within trials. Delineating how the density of plants within trials and the pre-trial weight (hereafter referred to as pre-weight) of individual saplings influenced browse consumption was of particular interest. We compared how moose browsed on the shoots of willow and birch in separate experiments, both in terms of all saplings in a trial (patch) and of browsing within individual saplings.

Specifically, we predicted that moose would consume relatively more shoot biomass and shoot length and crop shoots to larger diameters while leaving less edible shoot material behind—when browsing on smaller plants in low-density trials (i.e., less available biomass). Further, we predicted that moose would decrease their intake (as indexed through decreased biomass intake, shoot length consumption, and smaller bites) with time (number of hours and days into the trials) as gut-filling increased and changes in the animal's physiological state changed throughout the experiment (Newman et al. 1995).

Materials and methods

Sapling collections and pre-browse measurements

We collected whole, previously unbrowsed saplings—110 individual saplings of willow (*Salix scouleriana* Barratt ex

Hook.) and 105 of birch (*Betula papyrifera* Marsh.)—within an ~10-ha area of the endowment lands of the University of Northern British Columbia (UNBC), Prince George, Canada, on 20 February 2009. Saplings were selected based on prior knowledge of what moose in the region eat in winter and were selected at a size (~1.5–2.5 m tall), which provided both young and adult moose access to all shoots within plant crowns.

Once collected, all saplings were weighed (to the nearest gram) and tagged using a unique aluminum tag. We removed a thin linear strip of bark from along the bottom of each sapling near its base and oriented saplings in a prostrate position with the bark-stripped portion facing upwards (Fig. 1) on a table containing a measurement grid divided into 5-cm increments. A 2-m-long ruler with 5-cm increments was held along the length of the sapling suspended at ~50 cm above the table. Saplings were then photographed with high-resolution photography. Once weighed and photographed, we separated saplings by species then bundled and wrapped saplings into two separate tarps and stored them outside in the cold (0 to -17 °C). On 25 February 2009, we transported all saplings to the Northern Lights Wildlife Shelter in Smithers, BC, Canada, in the back of a pick-up truck so that saplings were kept at ambient outdoor winter temperatures en route (-24 to -30 °C).

Feeding trials

We conducted cafeteria-style feeding trials over a 3-day period from February 25–27, 2009 (-9 to -28 °C) with three unfasted, free-ranging human-habituated moose (one adult female and two 9-month-old calves), which had been raised at the Northern Lights Wildlife Shelter in Smithers, BC, Canada (54° 50' 59.24" N; 127° 06' 01.65" W), in what would be described by Shipley (2010) as semi-natural conditions. To conduct whole-sapling trials in a fashion that closely resembled feeding in nature, we designed a feeding station device out of two 15.2 cm × 15.2 cm × 4.9 m long pine beams and two ratchet straps. These beams were used to clamp saplings at their base so that they stood erect and could not be dislodged by

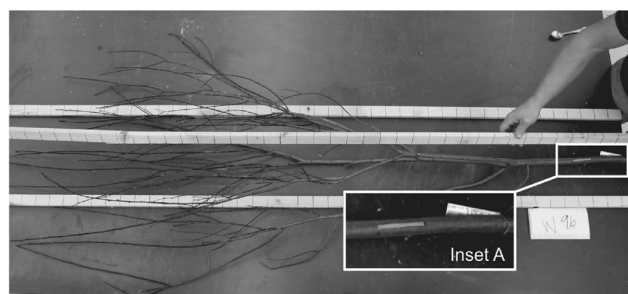


Fig. 1 Photograph of the procedure we used to tag, bark strip, and record shoot presence and length on unbrowsed saplings. Note: inset A shows the aluminum tag and bark-stripped area applied to each sapling that were used to identify and orient plants for post-experiment photographs and analysis

moose during feeding. Saplings were inserted and pinched between these beams and held in position with ratchet straps for bouts of feeding (Fig. 2). Trials consisted purely of willows (day 1 afternoon and day 2 morning) followed by birch (day 2 afternoon and day 3 morning) with bundles and individual plants within bundles selected haphazardly so that both willows and birch saplings were presented at all hours of the day.

To test the influence of sapling density on biomass removal and shoot selection, we varied the spacing and number of saplings per trial (four saplings—122 cm apart; five saplings—91.4 cm spacing; eight saplings—61 cm spacing; presented to moose successively for both species trials in that order, namely fewest to most plants; Fig. 3) using single-species trials of willows ($n=19$ trials) then birch ($n=18$ trials). In this way, we were able to examine and test differences in moose feeding patterns on those saplings nested within trials (a small patch or thicket) of varying densities. Willow and birch were tested in separate sets of trials. Fresh saplings not exposed to moose in previous trials were selected haphazardly for each trial. Saplings were kept wrapped in tarps both before and after trials and were stored in an enclosure at outdoor ambient temperatures.

Normally, saplings were exposed to moose for 15-min feeding bouts (hereafter referred to as trials) regardless of the number of saplings presented or the number of moose participating throughout the trial. Trials varied somewhat in length, however, so we corrected for trial duration in our analysis (see below). Moose were given 5- to 10-min breaks between trials, which was the amount of time that was required to replace trialed with untried saplings. All saplings were immediately rewrapped in tarps once trials were complete.

The same three moose fed during each trial each day, but for different amounts of time. We did not identify and record individual bites taken by individual moose nor were we able to assign the amount of browsing to individual moose. The number of moose feeding and the number of minutes per trial were



Fig. 2 Photograph of the feeding station used during the feeding trials which was constructed of heavy wooden beams that were used to pinch and anchor the saplings to the ground to simulate natural feeding conditions. 25 February 2009

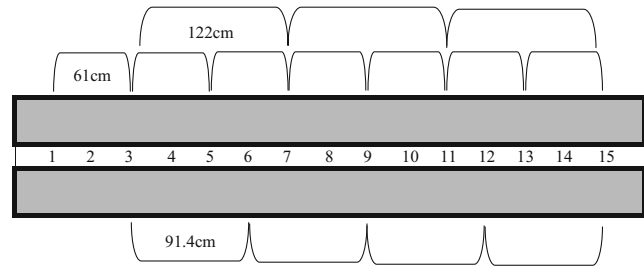


Fig. 3 Depiction of the feeding station foundation that was constructed out of two 4.9m long wooden beams (grey bars). Positions were 30.5 cm apart. In high density trials, those 8 saplings spaced at 61 cm apart were in positions 1, 3, 5, 7, 9, 11, 13, 15 while low-density trials that contained 4 saplings spaced at 122 cm apart were anchored in positions 3, 7, 11 and 15 during the trials. Positions 3, 6, 9, 12, and 15 were used for trials where saplings were spaced at 91.4 cm

recorded for each trial so that average browse consumption per minute per average moose could be calculated. The moose in these trials were unrelated individuals that had been brought to the shelter as orphaned calves from various regions of northern British Columbia. Moose raised at the shelter are unpenned and free-ranging, and all have access to surrounding areas into which they all range following their first year of care, some of which return in following winters (as had the cow that participated in the trial). All animals were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care (ACUC No. A2009.0216.011; see Guide to the Care and Use of Experimental Animals, vol. 1 (2nd ed., 1993) and vol. 2 (1984).

Post-browse measurements

Following the completion of all trials, saplings were transported wrapped in tarps back to UNBC for the posttrial assessments. Saplings were reweighed, with the difference between the pre- and post-browse mass (i.e., wet weight) constituting biomass removal from browsing. Saplings were then reoriented on our photographic backdrop according to the bark-stripped marking we had made on each trunk before the pre-browse photographs were taken and rephotographed. Because saplings were continuously kept wrapped in tarps (except for trials) and measurements and weight losses due to dehydration were negligible in birch during an earlier experiment conducted under similar conditions (Rea et al. 2010), we did not measure or correct for weight loss due to dehydration.

Along with reweighing and rephotographing each sapling after the feeding trials, we started from the bottom and progressed to the top of each sapling and recorded the stem diameter (bite mark) and height above the ground (cm) for each bite taken from each stem by moose. Carson et al. (2007) concluded that several browse species eaten by moose in our area were cropped in winter to a 4-mm diameter on average. Using this average, we classified all materials remaining on saplings

after trials as edible (≤ 4 mm; even though moose did take larger bites) or inedible (> 4 mm) and clipped away all “edible” shoot materials ≤ 4 mm in diameter before saplings began to dehydrate in the warm (21 °C) dry air of the laboratory. We then weighed the amount of material clipped from each sapling to the nearest gram and termed this edible biomass left uneaten.

Photographic analysis

Pre-browse and post-browse photographs were imported into ArcGIS (version 9.3.1, ESRI 2010, Redlands, CA) and assessed side by side so that we were able to determine which shoots were removed by moose during trials. Following calibrations using photographs of saplings on the measurement grid, we used ArcView's measurement tool to determine the length of each shoot(s) removed by moose from each branch on each photograph. This GIS technique has been tested with Scouler's willow against hand measuring (GIS measurement = $0.991(\text{hand-measured technique}) + 2.1455$; $F_{1,48} = 3853.9$, $P < 0.0001$; $r^2 = 0.988$; J. Svendsen, unpublished data) and allowed us to determine if shoot materials removed from saplings above each bite mark were comprised of a single or branched shoot that we could then use to determine the length of all shoot materials removed.

Statistical analyses

We adjusted all trial data for the number of moose and duration of feeding in each trial. For example, if one moose fed for a 15 min. trial, but was joined by another moose for the last 7.5 min. of the trial, we calculated 1.5 moose feeding for the 15-min trial period (i.e., 0.1 moose/min). Because we did not track browsing by individual moose, we were unable to include moose identity, and thus, the effect individual browsing patterns had on our results as a factor in the analysis. Our approach, rather, assumes that the rate of consumption by an ‘average’ moose within each trial is fairly consistent even though we recognize that it is not likely that three moose eating at once equals one moose eating at three different times. To compare browsing patterns and the efficiency of feeding by moose in trials and on individual saplings within trials both, we examined the amount of biomass removed (biomass eaten) and the amount of edible biomass left behind (edible biomass left uneaten) per moose per minute of trial.

To understand the effects of browsing by moose on all saplings during a trial, twig biomass removed, average diameter of bites taken on shoots, total length of shoots removed, and amount of edible material left over and uneaten by moose were examined at the trial (containing four, five, or eight saplings) level. To potentially account for any effects of saplings that were on the ends of the feeding station (see Fig. 2), all measurements were calculated separately for outer saplings

(saplings on the ends of the station) and for inner saplings (all other saplings presented during the trial).

We ran separate analyses for birch and willow and for each of our dependent variables (e.g., percentage of biomass eaten, shoot length removed, average bite diameter, edible biomass left uneaten; STATA: reg) with sapling density, time of day the trial was conducted, which day within the experiment (day 1, 2, or 3) the trial was conducted, original sapling biomass (pre-weight), and where within the trial browsing occurred (on plants fastened to middle [inner] or outer positions of the feeding station) as independent variables. We used shoot length removed in addition to bite diameter because length-diameter relationships of shoots can vary within species (Rea and Gillingham 2008). Sapling position was a categorical variable, while all other independent variables were continuous. Metrics were summed (biomass eaten, shoot length removed, biomass left uneaten) or averaged (average bite diameter) as appropriate across all saplings in each trial. The pre-weight of saplings was summed for all saplings within a trial relative to inner and outer positions (and therefore depends on the weight of the individual sapling and the number of saplings within the trial) so that, on average, biomass for trials of eight saplings would be double that for trials of 4. For all models, continuous independent variables were examined for collinearity (STAT A: collin; Ender 2010); variables with a variance inflation factor < 10 were considered to be independent.

In order to understand the effects of browsing at the level of the individual sapling (the replicate), the same trials and saplings were reanalyzed with individual sapling nested (as random effects) within a trial (the experimental unit) using a mixed-effects linear regression (STATA: xtmixed). Again, the density of saplings within the trial, trial time, trial day, as well as position of the sapling in the trial were independent variables with density of saplings, trial time, and trial day being continuous variables while position was a categorical variable. For all models, continuous independent variables were again examined for collinearity (STATA: collin; Ender 2010); variables with a variance inflation factor < 10 were considered to be independent. Residuals from all models were examined for model fit and homogeneity of residual variances. All intercepts were included in all models while all analyses were conducted in STATA 12 (StataCorp, College Station, TX). We set an α of 0.05 for our level of significance.

Results

Trials

The amount of willow biomass removed by moose increased with increasing available pre-weight trial biomass as did shoot length removed from trials (Table 1). More shoot length was

Table 1 The relative importance of independent variables used in multiple regressions in explaining total biomass and shoot lengths removed and average bite diameters taken from trials as well as the amount of edible biomass left uneaten within the trial by moose following trials with willow ($N=19$) and birch ($N=18$). Note: For the

categorical variable of position, the coefficient is inner relative to outer (see *text*). Although intercepts were included in all regressions, their coefficients are not reported here. P values ≤ 0.05 are considered significant and marked in italics

Dependent variable	Independent variable	Sapling species					
		Willow			Birch		
		Coefficient	S.E.	P	Coefficient	S.E.	P
Biomass eaten	Density	-0.474	0.383	0.216	-0.357	0.319	0.262
	Start time	-0.000	0.005	0.984	-0.002	0.003	0.501
	Trial day	-0.107	1.965	0.956	0.222	0.303	0.464
	Pre-weight	0.007	0.001	<0.001	0.004	0.001	<0.001
	Sapling position	1.779	1.028	0.084	0.055	0.761	0.943
Shoot length removed	Density	-2.3882	3.983	0.549	1.147	6.717	0.864
	Start time	-0.031	0.048	0.520	-0.064	0.050	0.199
	Trial day	-10.828	20.536	0.598	-6.915	8.157	8.157
	Pre-weight	0.057	0.008	<0.001	0.045	0.016	0.005
	Sapling position	27.463	10.793	0.011	12.784	22.771	0.575
Average bite diameter	Density	0.010	0.077	0.896	0.030	0.037	0.421
	Start time	-0.001	0.001	0.122	0.001	0.001	0.560
	Trial day	-1.076	0.367	0.003	-0.033	0.041	0.425
	Pre-weight	-0.001	.0002	0.205	0.001	0.001	0.510
	Sapling position	0.154	0.196	0.432	-0.097	0.093	0.297
Edible biomass left uneaten	Density	-0.765	0.363	0.035	-0.156	0.127	0.219
	Start time	0.006	0.004	0.094	0.001	0.001	0.702
	Trial day	5.812	1.666	<0.001	0.019	0.086	0.822
	Pre-weight	0.005	0.001	<0.001	0.001	0.000	<0.001
	Sapling position	-0.143	0.844	0.866	0.559	0.306	0.067

removed from willows positioned in the middle (inner) than on the ends (outer) of the feeding station (Table 1). Average bite diameters taken by moose decreased as trial days progressed (Table 1). The amount of edible biomass left on willows after the trials increased with increasing trial biomass and the number of days into the trial and decreased with increasing sapling density within the trial (Table 1).

The amount of birch biomass eaten, shoot length removed, and edible biomass left uneaten increased with an increase in available pre-weight trial biomass (Table 1). Average bite diameters taken by moose were not influenced by any of those factors that we measured during the trials. No other relationships were significant for birch or willow (Table 1).

Saplings within trials

As the pre-weight of both willow and birch saplings increased, so did the amount of biomass eaten and the amount of edible biomass left uneaten per sapling. The amount of biomass eaten decreased with increasing sapling density for willow, but not with increasing density of birch saplings. The amount of

edible biomass left behind on willows also increased as trial days progressed, but decreased with increasing density of saplings. No other relationships were significant for the two species (Table 2).

Discussion

Biomass consumption

Biomass removal for birch and willow increased with increasing sapling pre-weight under every circumstance (both at the trial and sapling levels) we evaluated. Although the specific relationship of total sapling weight to biomass removal does not appear to have been previously evaluated in this way, the amount of available forage or its estimated biomass is known to explain absolute consumption by moose at the patch and several other spatial scales (Åström et al. 1990; Lundberg et al. 1990; Gross et al. 1993; Månsson et al. 2007). The total number of browsed saplings per plot has been found to

Table 2 The relative importance of independent variables in explaining total biomass removed and edible biomass left uneaten on individual saplings by moose following trials withwillow ($N=19$) and birch ($N=18$). Individual saplings were considered to be nested within individual trials (see text). P values ≤ 0.05 are considered significant and marked in italics

Dependent variable	Independent variable	Sapling species					
		Willow			Birch		
		Coefficient	S.E.	<i>P</i>	Coefficient	S.E.	<i>P</i>
Biomass eaten	Density	-0.404	0.150	<i>0.007</i>	-0.199	0.109	0.067
	Start time	-0.001	0.002	0.584	-0.001	0.001	0.231
	Trial day	-0.995	0.770	0.197	0.065	0.073	0.372
	Pre-weight	0.009	0.001	<i><0.001</i>	0.004	0.001	<i><0.001</i>
	Sapling position	0.308	0.250	0.218	-0.309	0.180	0.086
Edible biomass left uneaten	Density	-0.335	0.140	<i>0.017</i>	-0.060	0.043	0.165
	Start time	0.003	0.002	0.076	0.001	0.000	0.473
	Trial day	2.197	0.718	<i>0.002</i>	0.033	0.026	0.194
	Pre-weight	0.008	0.001	<i><0.001</i>	0.001	0.001	<i><0.001</i>
	Sapling position	-0.010	0.247	0.965	0.100	0.063	0.112

increase with increasing sapling density in Scots pine (Heikkilä and Mikkonen 1992; Heikkilä 1993). Within a foraging bout, however, Vivås and Sæther (1987) and Shipley and Spalinger (1995) reported—as our data from our smaller, hand-assembled trials indicate for individual willows (but not for birch) in denser trials—that moose used fewer twigs (biomass) per sapling with an increase in sapling density. These findings suggest that moose eat more when more is available per sapling, but also become more selective of what they eat as willow density per trial increases. Why this particular relationship appears to have held true in our study for willows, but not for birch, may be related to plant preference with moose simply cropping fewer birch shoots to smaller diameters—removing the digestive processing constraints reached by moose when browsing willow to larger (and more fiber-rich) diameters (Shipley and Spalinger 1992).

Shoot length removal

Measuring both shoot length removal and biomass removal may at first appear redundant given the reported direct relationship of biomass to length (Provenza and Urness 1981; MacCracken and VanBallenberge 1993). Shoot biomass-to-length, biomass-to-diameter, and length-to-diameter relationships, however, can vary between and within species (see Rea and Gillingham 2008) and likely influence how moose browse plants. Furthermore, the metric shoot-length removal (a sum of all current and past year's growth removed by moose and summed across all saplings within a trial), has not been previously examined. Using this metric, we found that patterns of shoot length removal did not mirror patterns of biomass consumption and varied by species.

Birch saplings used in our trials were slightly larger overall than willows (birch, height—205.0 37.1 cm; pre-weight—523.5±122.5 g; base diameter—20.87±2.82 mm/willow, height—180.79±30.06 cm; pre-weight—469 154.64 g; base diameter—18.41±2.63 mm), with the additional weight and height of birches being partially attributable not only to larger diameter main stems (trunks) but also to their more long, thin-branched morphometry. These “branchier birches” as reported by Shipley et al. (1999) are used differently by moose, which regularly break off more than one twig when browsing birch, but not when browsing on other hardwoods like willow. The cumulative length of two thinner birch shoots cropped in a single bite would, when added together, be longer than a single thicker willow shoot of the same weight—a difference detectable using shoot length removal, but not biomass consumption.

Although the shoot length removed by moose from both willow and birch trials increased with increasing sapling pre-weight, the amount of removal varied by position of the plant within the trial for willow, but not for birch. Specifically, more shoot length was removed from willows within the trial (middle positions of the feeding station) than those positioned on either end. Why willows, but not birches, that were placed in the middle positions of the feeding station appeared to lose more shoot length (but not biomass) to browsing than station ends is surprising, but may be related to which animals fed where in trials. Dominant cattle preferentially take middle positions in feeding stalls and spend more time eating than those with lower social rank (Friend and Polan 1974). Although we did not take systematic measures of individual animal's feeding positions at the station, photographs taken occasionally throughout the feeding trials indicate that the adult cow (who was dominant over the calves) often occupied

the middle positions of the feeding station to the exclusion of the calves (see Fig. 2). If the larger cow spent more time selecting thinner and more numerous shoots, shoot length, but not biomass, may show an increased removal from saplings in the middle, but not outer positions. Again, why such patterns were not evident in birch is unknown but may be related to a lower-intensity browsing that generally seemed to characterize the use of birch by moose in our trials. If we had been able to record individual moose foraging (i.e., by a video camera system or by matching observers to individual moose during each trial), we could have accounted for the foraging contributions by each individual during a trial. Instead, we can only consider the variable contributions of all animals as the browsing effort in a trial.

Bite diameter

During winter, moose select bites from twigs that maximize energy and nutrient gains, but limit fiber intake (Vivås et al. 1991). Because shoot quality decreases with an increase in shoot diameter (Hjeljord et al. 1982; Vivås and Sæther 1987), browsers such as moose carefully select bites to ensure physiologically appropriate intake rates are in balance with the amount of time required to process forage (Robbins 1983). Such choices are influenced by factors such as cropping rates and twig characteristics, which can vary by species (Vivås et al. 1991). Contrary to our expectations, we found that bite diameters taken on willows, but not birch, became smaller as days into the trials progressed, but remained unaffected by other independent variables we tested. Illius et al. (2002) reported that roe deer (*Capreolus capreolus*) showed similar declines in bite mass removal as patch exploitation progressed by demonstrating that animals depleted larger shoots first. Vivås and Sæther (1987) and Shipley and Spalinger (1995) noted that bite sizes taken by moose increased and quality declined as stem/forage availability decreased, yet Shipley et al. (1998) indicated that contrary to their expectations, the average diameters of twigs selected by moose were not influenced by browse density. Edenius (1991) also pointed out—as our results seem to indicate—that parameters other than bite size, such as the number of bites per sapling (or possibly shoot length removed), may be better predictors of browse use by moose in winter. Because nutritional quality can vary between shoots (bites) of similar sizes (Rea and Gillingham 2001), determining the nutritional quality of bites taken, although procedurally difficult to accomplish, could help to reveal patterns we are currently unable to detect.

Minimal variability in bite diameters and associated shoot quality taken by moose within and among trials within a species may be partly accounted for by the fact that moose were not fasted prior to or during our 3-day experimental period. Moose at the shelter have continuous access to forest lands and native browses (including the species of willow and birch

in our trials) in and around the shelter and are also supplementally fed with vegetative materials (extra produce from local grocery stores) twice daily by shelter staff, which in our case was done each day before and after trials. As a result, moose were able to feed selectively among available shoots, cropping them to diameters that likely reflected a selection for shoot quality rather than a need for gut-filling.

Edible biomass uneaten

We used a 4-mm bite diameter threshold to estimate edible biomass left uneaten. Moose do browse plant shoots beyond 4 mm. A 4-mm cutoff diameter, however, is a locally documented average (Carson et al. 2007) and has been used as a cutoff diameter by others simulating moose browsing and in assessing browse quality (Danell et al. 1985; Danell et al. 1991; Shipley et al. 1999). Further, increasing or decreasing this 4-mm threshold would have had the same relative effect across trials.

Larger plants not only had more biomass for moose to consume but also contained more twig materials (≤ 4 mm) for moose to leave uneaten, which our results show happened at both the sapling and trial levels for both willow and birch. As a consequence of smaller average bite diameters, moose left more biomass uneaten on birch compared to willow and for both species biomass uneaten increased with pre-weight. For willow, but not for birch, biomass left uneaten increased with trial day. The satiety hypothesis (Bailey and Provenza 2008) suggests that animals may build up an aversion to foods with time in the short term, which may help explain differences in willow use by moose in the first 2 days of our trials. Explaining why this did not happen for birch is difficult, but may simply be due to moose eating less total birch (7.8 kg) at smaller, fixed diameters than willow (10.2 kg) over a similar time frame; it is also likely related to differences in twig types cropped, secondary chemistry, and other species-specific factors.

Why there were fluctuations in willow biomass left uneaten, but not biomass removal with trial day, may be due to differences in the types of twigs moose selected as they took sequential bites from plants within trials. Fluctuations may have also in part been due to how we classified “edible” biomass left over using the 4-mm threshold we adopted as previously discussed. If moose took fewer, larger diameter bites from bigger saplings, but also left an increased number of smaller (≤ 4 mm) diameter shoots on those saplings as trials progressed, biomass removal and edible biomass left over (as we classified, cut, and weighed it) could remain static and increase, respectively. A strategy of selecting fewer, larger bites by moose may also help to explain how more edible biomass remained on willows from trials of lower sapling density (see Vivås and Sæther 1987) and, if such a strategy were used, may reconcile how more (>4 mm in diameter) and

less or equal to (≤ 4 mm) willow biomass could have been consumed simultaneously by one or multiple moose at both the trial and sapling levels.

Willow is important to moose (Palo 1984; Regelin et al. 1987; Renecker and Schwartz 1998). Willow is also easier to process and of higher quality than birch (Nordengren and Ball 2005), all of which may help to explain some of the differences we saw in how moose used willows and birch, albeit trial sequence (willow then birch) cannot be disregarded. Previous experience as well as species and biomass availability of various browses naturally occurring in the forest surrounding the shelter—to which moose have continuous access—may have also predisposed moose to browse willow and birch differentially. Because birch on average had smaller twigs from which smaller bites were taken (2.69 mm bite diameter on average for birch [$N=4189$ bites] versus 4.48 mm for willows [$N=2609$ bites]) and because smaller shoots are better defended against herbivores (at least within species; Stolter 2008), simple differences in shoot size to chemistry ratios between the two species may have additionally influenced differences observed in our trials.

In conclusion, the pre-weight of saplings consistently influenced patterns of browse removal by moose at both the trial and sapling levels. This finding suggests that moose eat more from more massive plants (e.g., more vigorous plants growing under good light and soil conditions). Sapling position within the trial, the density of saplings within trials, and the day in which feeding occurred within the trial also influenced some aspects of how moose fed on willows, but not birch. Moose browsed shoots to larger diameters and removed more biomass from willows than from birches. However, willow and birch were not offered together or in alternate trials, so we make no inferences about the relative preference of moose for these two species.

We acknowledge that it is difficult to generalize patterns of winter browsing by moose using data collected over a short time frame with a limited number of moose and saplings, especially when moose impacts are averaged and not individualized. As pointed out by Moen et al. (1997), however, measurements of intake on free-ranging animals are extremely difficult to obtain, and feeding experiments that take minutes or hours in artificial landscapes must be used to infer longer-term foraging decisions in moose and other large ungulates. Furthermore, Bergman et al. (2001) suggested that short-term studies are necessary to reconcile persistent debates over the respective roles that short- and long-term intake play in controlling energy consumption. Still, longer pen and field trials using different plant species as well as various species mixes (depending on objectives), while accounting for the variable pressure applied by individual animals (e.g., in a random effects model), would be required to determine more conclusively if factors such as

pre-weight of plants, plant density, differences in plant architecture, and feeding duration influence longer-term browsing patterns in moose.

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