SEXUAL SEGREGATION IN MOOSE: EFFECTS OF HABITAT MANIPULATION

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ABSTRACT: We studied effects of mechanical crushing on abundance of forage and quality of feltleaf willow (*Salix alaxensis*) in winter, 3 years following habitat manipulation in interior Alaska, USA. We also examined differences in snow depth and track counts for Alaskan moose (*Alces alces gigas*) between the crushed site and an adjacent area containing old-growth stands of willow. Likewise we tested for differences in foraging by moose between areas, and noted differences in use of the 2 sites by adult males, and females and their young. Mechanical crushing resulted in a 5-fold increase in the number of leaders of current annual growth and a 3-fold increase in dry mass for willows subjected to crushing compared with the uncrushed site. The size of individual leaders of feltleaf willow did not differ between sites, probably because the growth form of leaders resprouting from the crushed area was similar to stump sprouts available to moose on the uncrushed area. Moose took larger bites, however, on the crushed compared with the uncrushed site. No significant differences occurred in the chemical composition of willows, including concentration of tannins, between crushed and uncrushed areas. Similarly, there were no differences in in vitro dry matter digestibility of willows between sites. Moose sexually segregated in winter. Males occurred predominantly on the more open crushed area, whereas females and young used the uncrushed area where the dense vegetation offered substantial concealment cover. We hypothesized that mechanical manipulation of willows benefited primarily male moose 3 years following crushing, and that females and young faced a tradeoff between feeding on the greater abundance of forage on the crushed area and a reduced risk of predation on the uncrushed site. We see merits in considering the sexes of moose as if they were separate species for purposes of management, and recommend that future management of habitat to benefit moose consider differences in requirements of the sexes, especially factors related to risk of predation.

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Sexual segregation, defined as the differential use of space by the sexes during periods other than the mating season, is widespread among sexually dimorphic ruminants (Main et al. 1996, Bleich et al. 1997, Kie and Bowyer 1999, Barboza and Bowyer 2000). This phenomenon is especially well documented for cervids (Bowyer 1984, Beier 1987, Clutton-Brock et al. 1987, McCullough et al. 1989, Main and Coblentz 1990, Bowyer et al. 1996, Main and Coblentz 1996, Kie and Bowyer 1999), including moose (*Alces alces* - Miller and Litvaitis 1992, Miquelle et al. 1992). Causes of

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sexual segregation continue to be debated (Bleich et al. 1997, Gross 1998, Main 1998, Kie and Bowyer 1999, Barboza and Bowyer 2000). Nonetheless, the manner in which the sexes partition space, habitats, and diet clearly is an important component of their life-history tactics (Main et al. 1996, Bleich et al. 1997, McCullough 1999). Sexual segregation also has far-reaching consequences for the population ecology of these large herbivores (McCullough 1979, Bowyer et al. 1997, Bowyer et al. 1999a, McCullough 1999). Indeed, niche partitioning by the sexes of white-tailed deer (*Odocoileus virginianus*) prompted Kie and Bowyer (1999) to suggest that the sexes should be managed as if they were different species.

Where vegetation communities are sufficiently heterogeneous (Miquelle et al. 1992, Bleich et al. 1997, Kie and Bowyer 1999), the sexes of ungulates, including moose, use habitats differently, especially during winter and spring (Miller and Litvaitis 1992, Miquelle et al. 1992). Consequently, manipulation of vegetation to benefit moose (Thompson and Stewart 1998) holds the potential to aid principally one sex, possibly to the detriment of the other.

Although habitat modifications to benefit moose, including mechanical disturbance, fire, and applications of fertilizer and herbicide, were implemented in Alaska, USA, previously (Thompson and Stewart 1998), past studies seldom evaluated outcomes from those management techniques (Oldemeyer and Regelin 1980). More recent studies, however, have overcome such limitations (Collins and Schwartz 1998, Stephenson et al. 1998, Weixelman et al. 1998). Nevertheless, those manipulating habitat to benefit moose typically have not considered that the sexes might respond differently to alterations of their environment. Even researchers who did so (Weixelman et al. 1998) did not quantify such differences.

Willows (*Salix* spp.) are a critical component in the diet of moose throughout Alaska (Peek 1974, Risenhoover 1989, Van Ballenberghe et al. 1989, Miquelle et al. 1992, Molvar et al. 1993, Molvar and Bowyer 1994, Bowyer and Bowyer 1997, Weixelman et al. 1998, Bowyer et al. 1999b). Thus, we undertook a study to quantify effects of mechanical crushing of feltleaf willow (*S. alaxensis*) on forage abundance and quality, and the responses of moose to that manipulation. Specifically, we compared an area where willows were crushed with a nearby reference site that was not manipulated. We tested for differences between areas in biomass and quality of current annual growth of willows, foraging by moose, differences in depth of snow, and an index to density of moose. Finally, we tested whether the sexes of moose used manipulated and reference areas differentially.

STUDY AREA

We conducted research in the Goldstream Valley located about 15 km northwest of Fairbanks in interior Alaska, USA (64° 54' N, 147° 50' W). Ballaine Road bisects the study area, which follows Goldstream Creek both northeast and southwest of the road. The climate is typical of interior Alaska. Summers are short and warm, and winters are long, cold, and often severe; snow can cover the ground for up to 8 months. Winter temperatures range from -10 to -45°C, and snow depth averages 80 cm. Snow usually remains dry and loose throughout winter (Gasaway et al. 1983, Bowyer and Bowyer 1997, Keech et al. 2000).

The study area encompasses a low-elevation (185 m) zone with intermittent permafrost, which is characterized by bogs and riparian vegetation including willows (*Salix* spp.) and scattered alder (*Alnus crispa*). Riparian species gradate into stands of white spruce (*Picea glauca*) intermixed with paper birch (*Betula papyrifera*) at higher elevations or on better-drained soils. Two species of willows (*S. alaxensis* and *S. arbuscoloides*) dominate riparian areas, and many old willows (> 60 years, based on examination of annual growth rings) are tree sized (diameter at 137 cm above the substrate > 10 cm).

Tracks and fecal pellets indicate this area is used frequently by moose. Although we did not estimate the number of moose on our study sites, nearby populations in the Tanana Flats have been increasing and recruiting more young than is typical of most interior Alaska populations (Keech et al. 2000). Some large carnivores also occur in this area even though it is close to Fairbanks.

Between 5-21 March 1996, a Caterpiller™ D8 bulldozer, under contract to the Alaska Department of Fish and Game, crushed, sheared, or broke over old-growth willow on 119 ha adjacent to Goldstream Creek northeast of Ballaine Road, at a cost of US $17,577. This operation was not undertaken until the ground was frozen to a depth of about 30 cm and was covered with snow. The blade on the bulldozer was held approximately 30 cm above the substrate during the manipulation. Vegetation cut or broken by the bulldozer was not accumulated into piles or windrows. There were few places where the blade or tracks of the bulldozer exposed bare soil. The manipulated area was centered on Goldstream Creek, extended > 3 km northeast from Ballaine Road, and ranged 100-800 m in width. A nearly identical area along Goldstream Creek southwest of Ballaine Road was not mechanically crushed, and served as a reference site for our study.

METHODS

Sampling of Willows

We documented responses of feltleaf willows to mechanical crushing and their subsequent use by moose by comparing the crushed and uncrushed areas in late February 1999, 3 years (i.e., growing seasons) following the manipulation. We selected feltleaf willow to sample because it was most abundant along Goldstream Creek, and was an important component in diets of moose and other herbivores during winter (Bryant et al. 1985, Miquelle et al. 1992). Our sampling of willows was confined to riparian areas immediately surrounding (± 30 m) Goldstream Creek, although the manipulated area ranged from 200-400 m in width where we sampled. We extended our sampling about 1,000 m along the creek into the crushed area and an equal distance into the uncrushed area.

We randomly located 10 quadrats, each 5 by 5 m, on both crushed and uncrushed sites. Corners of each quadrat were marked with fluorescent flagging, which we removed at the end of the study. We recorded the number of leaders of current annual growth of feltleaf willow within the reach of moose ($\leq$ 3 m above the packed snow) on each quadrat, and the number of those leaders that had been browsed by moose. We measured (nearest 1 mm) the length of each leader of new growth (i.e., from the bud-scale scar to the terminal bud, or to the point of browsing). We also recorded the diameter of the leader at the bud-scale scar and at the point of browsing with calipers (nearest 0.1 mm). We noted any browsing by snowshoe hare (*Lepus americanus*) on those quadrats. We also clipped a sample of about 15 leaders of current annual growth from feltleaf willow on each quadrat where willows were present. Sample size differs between crushed and uncrushed areas because 3 plots on the uncrushed area contained no feltleaf willow. Clipped leaders were stored frozen in labeled paper bags for later analysis. Some confusion occurred in differentiating twigs of *Salix alaxensis* from *S. arbuscoloides* on 2 quadrats; those quadrats were re-sampled.

Sampling of Moose Tracks and Snow Characteristics

Because snow would be expected to affect the movements of moose (Coady 1974, Telfer and Kelsall 1984), we randomly located 10 transects, each 25 m in length, on both crushed and uncrushed areas. Transects were oriented either N-S or E-W by flipping a coin. We recorded the number of fresh tracks of moose crossing each transect in either direction. Only tracks with sharp edges in the snow that had not accumulated snow in the track and did not show signs of wind erosion or melting were counted. This procedure helped ensure that tracks we sampled were from resident animals and not transient individuals that crossed the area intermittently.

Snow depth also was recorded to the nearest 1 cm at 1-m intervals along each transect (e.g., 25 samples / transect). Those data were used to determine both the mean and coefficient of variation (CV) of snow depth for each transect. Transects were treated as sampling units for subsequent analyses.

Sampling Fecal Pellets of Moose

Fecal pellets of moose were collected while sampling vegetation quadrats for willows and during transect sampling for moose tracks and snow characteristics. In addition, we performed a systematic search of both crushed and uncrushed areas following the initial sampling on quadrats and along transects. We returned to the study area about 1 week following the initial sampling and conducted one additional systematic search of crushed and uncrushed sites for fecal groups. Fecal pellets of moose were collected as groups and stored frozen in labeled plastic bags until analyzed.

Laboratory Analyses

In the laboratory, we measured leader lengths from feltleaf willows clipped in the field to the nearest 1 mm, and their diameters at the bud-scale scar to the nearest 0.1 mm. Leaders then were dried for 4 days at 50°C to a constant level of moisture. Dry mass for each leader was determined to the nearest 0.1 g with an electronic balance. Leaders from each quadrat were pooled into a composite sample, and ground so their fragments would pass through a 1-mm mesh screen.

Measures of forage quality (% dry mass), including acid-detergent fiber, neutral-detergent fiber, acid-insoluble ash, lignin, hemicellulose, cellulose, and nitrogen were determined for willows with standard Van Soest (1982) procedures by R. Kedrowski at the Institute of Arctic Biology of the University of Alaska Fairbanks (UAF). Likewise, in vitro dry matter digestibility (IVDMD) of willows was determined with the method of Tilley and Terry (1963) by R. Kedrowski at UAF using rumen liquor from a fistulated reindeer (*Rangifer tarandus*) accommodated to a diet of willows. Concentration of tannins in current annual growth of feltleaf willow were determined by the methods of Bryant et al. (1985) and Scalbert (1992) at the Department of Chemistry and Biochemistry at UAF by assessing absorbance at 550 nm. Because there is not a defined mass standard for tannins, results are presented in absorbance units per gram.

We calculated the mean volume (mm^3) from measurements (nearest 0.1 mm) of 5 fecal pellets (i.e., length x width x width) from each fecal group with hand-held calipers. We then used results from MacCracken and Van Ballenberghe (1987) to estimate the sex and age class of moose that deposited a particular fecal group. Although ranges in volume of fecal pellets deposited during winter by large adult females and small adult males overlap slightly

(MacCracken and Van Ballenberghe 1987), only 5 fecal groups from moose we sampled fell within that zone of overlap-those samples were withheld from analysis.

Statistical Analyses

We developed regression equations for both study sites (crushed and uncrushed) to predict dry mass of current annual growth of feltleaf willow from diameter of the leader and from leader length; we expected those regressions to be curvilinear (Bowyer and Bowyer 1997). We also fit linear regressions between diameter and leader length for each site. We used the *F*-test to compare slopes of $\log_e$-transformed regression lines used to estimate biomass between crushed and uncrushed sites (Zar 1984). Those equations also were used later, in conjunction with data on diameter at point of browsing, to estimate biomass removed by foraging moose (Telfer 1969, Bowyer and Bowyer 1997, Weixelman et al. 1998).

We compared availability and use of leaders of feltleaf willow, including percentage of leaders browsed, and dry mass (g/m^2) of leaders available to and removed by foraging moose, with multivariate analysis of variance (MANOVA, Rencher 1995). When significant ($P \leq 0.05$) tests occurred with MANOVA, we performed post-hoc comparisons with analysis of variance (ANOVA). Variables necessary to calculate those derived values (e.g., number of leaders available and browsed/m^2) were not subjected to statistical analysis to prevent over-parameterizing the model. Similarly, differences in the diameter of current annual growth measured at both the bud-scale scar and at the point of browsing were examined with MANOVA, followed by individual ANOVAs.

Differences in the quality of forages between areas of crushed and old-growth willows were tested with MANOVA. We used the *t*-test to compare mean concentrations of tannins in leaders of willow from crushed and uncrushed sites (Zar 1984). Similarly, the *t*-test was used to compare differences between areas in snow depth, coefficient of variation (CV) in snow depth, and number of recent moose tracks.

We used the 2-sample *Z*-test for proportions to compare browsing by snowshoe hares between areas (Remington and Schork 1970). Likewise, we employed the *Z*-test to compare the proportion of adult male moose (determined from volume of fecal pellets) occurring on crushed and uncrushed areas. This test is especially appropriate for the latter analysis because it allows for sampling with replacement (Remington and Schork 1970). Thus, this statistical method accommodates potentially sampling more than one fecal group from each moose.

RESULTS

Architecture and Biomass of Feltleaf Willow

We used regression analysis to predict dry mass of current annual growth for feltleaf willow from leader length, and from diameter at the bud-scale scar-both those curvilinear relationships provided predictive models (Table 1). We also obtained a strong linear relationship between leader length and diameter (Table 1).

We employed separate regression equations to estimate biomass of current annual growth of willows available to and removed by foraging moose on crushed and uncrushed areas (Table 1). Nonetheless, $\log_e$-transformed data, which linearized the relationship between willow biomass and diameter at the bud-scale scar, did not exhibit significantly different slopes between areas ($P = 0.7$). Most leaders of current annual growth within the reach of moose on the uncrushed area were stump sprouts from the trunks of old willows, a growth form that was similar in architecture to leaders re-growing in the crushed area.

Table 1. Coefficients of determination and regression equations for leaders of current annual growth of feltleaf willow collected from an area that was crushed mechanically 3 years earlier and a paired site (uncrushed) with an old-growth stand of willow, interior Alaska, USA, February 1999.

	Crushed (n = 147 leaders)		Uncrushed (n = 114 leaders)	
Regression Parameters	R^2	Equation	R^2	Equation
Dry mass (g) predicted from diameter (mm) at the bud-scale scar	0.703	Y=1.9162-1.1794x+0.1814x^2	0.791	Y=3.0750-1.7095x+0.2839x^2
Dry mass (g) predicted from leader length (mm)	0.813	Y=0.6220-0.0456x+0.0015x^2	0.903	Y=2.1997-0.0904+0.0017x^2
Leader length (mm) predicted from diameter (mm) at the bud-scale scar	0.697	Y=-0.2447+7.2996x	0.729	Y=-12.123+11.894x

Effects of Crushing Willows on Forage Availability and Use

Crushing of feltleaf willow resulted in nearly 5 times more leaders of current annual growth available to moose on crushed than uncrushed areas 3 years following the manipulation (Table 2). Likewise, dry mass of leaders was greater than 3-fold higher on the crushed compared with the uncrushed area (Table 2).

Moose browsed a much larger number of willow leaders on crushed versus uncrushed sites, but the proportion of leaders browsed was not significantly different between those areas, although that outcome was marginal (Table 2). Biomass of willow removed by foraging moose, however, was > 17 times higher on the mechanically crushed area than on the uncrushed site with old willows (Table 2).

We also evaluated the proportional use of current annual growth of feltleaf willow by snowshoe hares. Only 0.2 % of 2,233 willow leaders were browsed on the crushed area, whereas 30.5 % of 456 leaders were fed upon by hares in the uncrushed area; a Z-test indicated that difference was highly significant ($P < 0.0001$).

Measures of Forage Quality

Few differences existed among a suite of variables related to the nutritional quality of current annual growth of feltleaf willow on crushed compared with uncrushed areas (Table 3). Values for nitrogen content (N) and in vitro dry matter digestibility (IVDMD) indicated that this winter forage was of low quality (Table 3). In addition to few differences in IVDMD and measures of forage quality obtained from Van Soest analysis, the t-test indicated that tannin concentrations ($\overline{X}$ ± SE), as indexed by absorbance, did not vary significantly ($P > 0.10$) between crushed (0.77 ± 0.033 nm/g) and uncrushed (0.70 ± 0.044 nm/g) areas.

Selection of Stem and Bite Sizes by Moose

No significant difference occurred in the size of stems (e.g., diameter at the bud-scale scar) available for moose to eat between crushed and uncrushed areas (Fig. 1). Moreover, moose did not feed on stems that were different in size from what was available, most likely because leaders of current annual growth on re-sprouting feltleaf willow were large (Fig. 1). Moose, however, took a significantly larger bite (e.g., a larger diameter at the point of browsing) on the crushed compared with the uncrushed area (Fig. 1).

Depth of Snow and Moose Tracks

The *t*-test indicated that the mean (±SE) depth of snow measured along randomly located transects, each 25 m long, did not differ significantly ($P > 0.3$) between the area where willows were crushed mechanically (43 ± 3.2 cm, $n = 10$) and the nearby uncrushed area (42 ± 2.2 cm, $n = 10$). Variation in depth of snow along those transects, however, was significantly ($P < 0.05$) greater on the uncrushed (CV = 19.5%) than on the crushed (CV = 15.6 %) area. Number of fresh tracks of moose crossing those 10 transects (in either direction) did not differ significantly ($P > 0.7$) between crushed (1.6 ± 3.2 tracks) and uncrushed (1.9 ± 3.8 tracks) sites.

Sexual Segregation

Volume of individual fecal pellets of moose collected during other sampling activities, as well as during a systematic search of both study sites, allowed most samples (97 % of 186 fecal groups) to be categorized into broad sex and age classes. Adult male moose occurred most often on the crushed area, whereas adult females and young were most prevalent on the uncrushed site (Fig.2).

DISCUSSION

Effects of Crushing on Forage Abundance

Mechanical crushing of feltleaf willow

Table 2. Characteristics of leaders of current annual growth for feltleaf willow that were available to Alaskan moose on a site that was crushed mechanically 3 years earlier and an adjacent site with old-growth stands of willows (uncrushed), interior Alaska, USA, February 1999.

	Crushed ($n = 10$)		Uncrushed ($n = 10$)		
Variable	$\overline{X}$	SE	$\overline{X}$	SE	*P*-value[1]
No. leaders available / m^2	8.9	3.44	1.8	0.49	___
No. leaders browsed / m^2	5.5	2.27	0.4	0.18	___
Percentage of leaders browsed	61.8	8.35	21.0	10.18	0.06
Dry biomass available (g / m^2)	36.3	10.60	10.7	3.94	0.04
Dry biomass removed (g / m^2)	5.2	2.09	0.3	0.13	0.03

[1] *P*-values are post-hoc comparisons from ANOVA following MANOVA; variables used to calculate dry biomass (e.g., number of leaders) were withheld from analysis to avoid model over-parameterization.

Table 3. Forage quality (% dry mass) of current annual growth of feltleaf willow on an area that was mechanically crushed 3 years earlier and on an adjacent area (uncrushed) with old-growth stands of willow, interior Alaska, USA, February 1999.

	Crushed ($n = 10$)		Uncrushed ($n = 7$)[2]	
Variable[1]	$\bar{X}$	SE	$\bar{X}$	SE
Acid-detergent fiber	46.6	2.09	48.9	4.51
Neutral-detergent fiber	60.8	4.30	63.6	3.84
Acid-insoluble ash	0.4	0.03	0.4	0.03
Lignin	12.0	0.82	11.5	0.74
Hemicellulose	14.1	1.22	14.7	0.66
Cellulose	34.6	2.83	37.4	3.87
Nitrogen	0.77	0.098	0.76	0.077
In vitro dry matter digestibility	31.7	3.32	28.5	4.63

[1] MANOVA indicated that no overall difference in forage quality occurred between crushed and uncrushed areas ($P > 0.50$).

[2] Sample size is smaller for the uncrushed than the crushed area because 3 quadrats on the uncrushed area had no feltleaf willow within the reach of moose (< 3 m in height).

substantially improved the abundance of this important winter forage for moose 3 years following manipulation. Number of leaders of new growth were 5-fold higher and biomass was 3-fold greater on the crushed site compared with the area dominated by old-growth willow (Table 2). Our analysis undoubtedly underestimated the total forage available to moose on the crushed site because we did not consider *Salix arbuscoloides*, which also was present on our quadrats.

Crushing produced rapid changes in biomass of forage available to moose in winter. Twenty years of succession following fire may be required before habitat is optimal for moose (Weixelman et al. 1998), whereas significant increases in biomass of willows occurred within 3 years of crushing (Table 2). How long increases in forage abundance resulting from mechanical manipulation of willows will persist in a subarctic environment requires additional study.

Clearly, mechanical manipulation of willows offers a rapid method to enhance habitat for moose where access for a bulldozer or other heavy equipment is available and logistical and financial constraints can be overcome. One important caveat related to habitat improvement to benefit moose in Alaska, however, is that predators must not regulate the population for which the manipulation is intended. Many moose populations in interior Alaska have been held at low density by intense predation by wolves (*Canis lupus*) and bears (*Ursus*

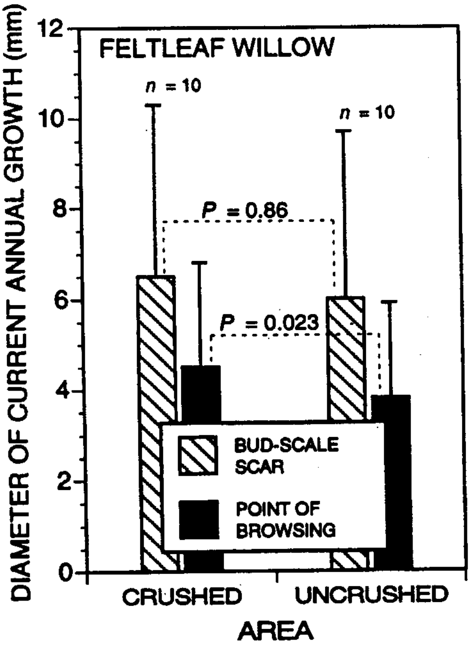

Fig. 1. Mean (±1 SD) diameter of current annual growth of feltleaf willow measured at the bud-scale scar and at the point of browsing by Alaskan moose on an area where willows were mechanically crushed 3 years earlier, and on an adjacent area with an old-growth stand of willows (uncrushed), interior Alaska, USA, February 1999. Dashed lines and associated P-values indicate post-hoc comparisons from ANOVA, following MANOVA.

arctos and *U. americanus*) (Gasaway et al. 1983, 1992; Van Ballenberghe and Ballard 1994; Bowyer et al. 1998). Such populations of moose are not food limited, and individuals often are in excellent physical condition-habitat manipulation holds little promise of increasing these populations (Weixelman et al. 1998). Populations of moose near Fairbanks, Alaska, have been increasing and exhibiting density dependence in physical condition and reproduction in recent years (Keech et al. 2000). Thus, habitat alterations in this area could potentially benefit moose if performed at a sufficiently large scale.

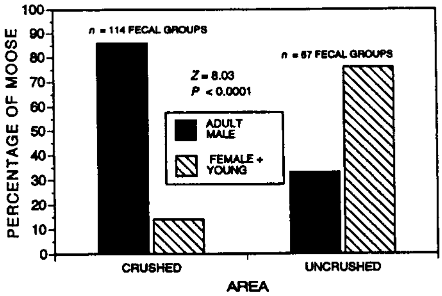

Fig. 2. Percentage of adult males, and adult females and young Alaskan moose occurring on an area where willows were mechanically crushed 3 years earlier, and on an adjacent area with an old-growth stand of willows (uncrushed), interior Alaska, USA, February 1999. Sex and age classes of moose were determined from volume of fecal pellets with the method of MacCracken and Van Ballenberghe (1987). The Z-test and associated P-value are from a comparison of the proportion of adult males occurring on crushed and uncrushed areas.

Effects of Crushing on Forage Quality

Mechanical crushing of feltleaf willow did not alter its chemical composition in winter significantly (Table 3). Similarly, there were few effects of crushing on IVDMD of current annual growth for willows (Table 3). Thus, moose gained no obvious nutritional benefits related to quality of food by foraging on feltleaf willow on the crushed area during winter. Crushing, however, did not increase tannin concentrations in re-sprouting willows, thereby rendering it less palatable, at least during the third year following manipulation.

Differences in Willow Leaders and Size of Bites

We were surprised that the growth form of new leaders on feltleaf willow (Table 1) did not differ between crushed and uncrushed areas (i.e., regression slopes were nearly identical). That outcome likely was the result of leaders of current annual growth on the untreated site, which were within the reach of moose, being composed mostly of elongated stump sprouts. Those stump sprouts resembled the growth form of resprouting willows on the crushed area. That similarity in form is reflected in the absence of a difference in the diameter of leaders (measured at the bud-scale scar) between areas (Fig. 1). Foraging moose, however, took larger bites (i.e., larger diameter at point of browsing) on the crushed compared with the uncrushed area (Fig. 1). Moreover, that difference could not be attributed to the size of bites available to take (Fig. 1). Likewise, depth of snow was similar between areas, as was our index to moose density (e.g., track counts); hence, those variables were unlikely to explain differences in foraging we recorded (Fig. 1).

Moose taking larger bites on the crushed compared with the uncrushed area might reflect less efficient foraging (sensu Molvar and Bowyer 1994) or larger moose (e.g., males) feeding on the crushed site. Perhaps larger bites taken in the crushed area represented less interference or obstruction by boles of large willows than on the uncrushed site, resulting in less selective foraging (e.g., larger bites) by moose. Nevertheless, Miquelle et al. (1992) also reported that larger bites were taken on ranges inhabited by male compared with female moose during winter.

Sexual Segregation

Spatial segregation of the sexes outside rut probably is ubiquitous among polygynous ruminants (Bowyer 1984, Main et al. 1996, Bleich et al. 1997, Barboza and Bowyer 2000). This phenomenon is especially pronounced for the sexes of moose during winter and spring (Miller and Litvaitis 1992, Miquelle et al. 1992, Bowyer et al. 1999b). Allometric and gastrointestinal differences between the sexes (Barboza and Bowyer 2000) and risk of predation (Bleich et al. 1997) are thought to be the principal determinants of why the sexes spatially segregate. Degree of spatial differences in sexual segregation varies among species and habitats (Bowyer et al. 1996), but some ungulates segregate on an exceptionally fine scale (McCullough et al. 1989). Our results document that moose, likewise, can sexually segregate on a fine scale where marked differences in habitat occur (e.g., crushed versus uncrushed stands of willows). Although we do not know the distribution of the sexes of moose prior to the manipulation of willows, home-range size in moose is sufficiently large (Hundertmark 1998) that males and females would have been aware of both crushed and uncrushed sites. We hypothesize that the differential use of crushed and uncrushed sites reflects selection based on the differing needs of the sexes of moose, as suggested by Miquelle et al. (1992).

Some females, which occurred primarily on the uncrushed area, likely ventured into the crushed area to feed, and some males probably did the opposite. Females that followed such a pattern of movement might gain some benefits, because leaders of willow were more abundant on the crushed than uncrushed area (Table 2). Nonetheless, females (notably those with young) foraged less efficiently than adult males (Molvar and Bowyer 1994). Females further reduced their foraging activities as they ventured farther from escape cover, ostensibly a result of predation risk (Edwards 1983, Molvar and Bowyer 1994). Given these limitations on foraging behavior, we are uncertain whether females and young that used the more open crushed area would have gained nutritionally from the more abundant willow that occurred there. In addition, Miquelle et al. (1992) noted nearly complete spatial segregation during winter, whereas we observed more overlap in the distribution of the sexes (Fig. 3). We cannot exclude the hypothesis that the manipulation of willows intensified intersexual competition by altering the distribution of males. If the distribution and foraging activities of males adversely affected the fat reserves of females in winter, a reduction in both reproductive performance of females and survivorship of their young would be expected the following spring (Keech et al. 2000).

Similarly, female moose would not have benefited markedly from a reduction in browsing pressure by males on the uncrushed site as males preferentially exploited the crushed area. The genders of Alaskan moose spatially segregate during winter into separate habitats even where vegetation has not been manipulated (Miquelle et al. 1992). Our results indicated that females and young occurred predominantly on the uncrushed site (Fig. 3). If the manipulation were conducted in an area that was predominantly winter range for females, then there would be a net loss of habitat for females until succession returned the area to a suitable condition for them. Although that alteration might not require 60 years (the estimated age of old-growth willows), how long such a change would entail is unknown.

Few differences in quality of forage occurred between crushed and uncrushed areas (Table 3); such differences hold little promise for explaining the differential use of areas by the sexes of moose in our study (Fig. 2). Similarly, few differences existed in snow depth between areas, and deciduous feltleaf willows offered little overstory cover even on the uncrushed area. Thus, thermal benefits to moose were not likely related to the differential use of areas by the sexes.

Risk of predation has a profound influence on the use of habitat, foraging behavior, and movements of large herbivores (Berger 1991, Bleich et al. 1997, Nicholson et al. 1997, Rachlow and Bowyer 1998, Kie 1999). Those conclusions also hold for moose (Edwards 1983, Molvar and Bowyer 1994, Weixelman et al. 1998, Bowyer et al. 1999b). We hypothesize that use of the more open crushed site predominantly by males and use of the densely vegetated uncrushed area mostly by females and young (Fig. 2) was the result of the uncrushed site providing substantial concealment cover. We believe risk of predation limited use of the crushed area by females and their young, which would be exposed to view in the manipulated area from a coursing hunter such as wolves. Hence, the uncrushed area likely provided a more secure place for females, especially those with young, to forage, but probably represented a tradeoff against the greater amount of forage available on the crushed area (Table 2). Whether such differences in forage abundance and concealment cover on the sites will be maintained over time is uncertain and deserves further study.

Kie and Bowyer (1999) concluded that niche dynamics of male and female white-tailed deer were so different outside the mating season that the sexes should be managed as if they were different species; we forward that same recommendation for moose. Moreover, our study is the first to document that manipulation of habitat to benefit moose, or other species of large herbivores, could have consequences for the manner in which the sexes spatially segregate. Those manipulating habitat to benefit ungulates seldom have reported differences in habitat requirements of the sexes. Density of adult females relative to ecological carrying capacity (*K*) is thought to be a critical factor regulating productivity of large mammals, including moose (McCullough 1979, Van Ballenberghe and Ballard 1994, Bowyer et al. 1999a). Some management practices may not improve habitat for female moose markedly (Fig. 2). Indeed, adult males would have gained most in winter from the effects of manipulating willow on our study area, at least during the third year following that management practice. We recommend that the size of the manipulation and, hence, distance from cover should be a future consideration of manipulation of habitat for moose.

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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.

BEIER, P. 1987. Sex differences in quality of white-tailed deer diets. Journal of Mammalogy 68:323-329.

BERGER, J. 1991. Pregnancy incentives, predation constraints and habitat shifts: experimental and field evidence for wild bighorn sheep. Animal Behaviour 41:61-77.

BLEICH, V. C., R. T. BOWYER, and J. W. WEHAUSEN. 1997. Sexual segregation in mountain sheep: resources or predation? Wildlife Monographs 134.

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. 1999a. Moose on Kalgin Island: are density-dependent processes related to harvest? Alces 35:73-89.

______, 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. 1999b. Birth-site selection in Alaskan moose: maternal strategies for coping with a risky environment. Journal of Mammalogy 80:1070-1083.

BRYANT, J. P., G. D. WIELAND, T. CLAUSEN, and P. KUROPAT. 1985. Interactions of showshoe hare and feltleaf willow in Alaska. Ecology 66:1564-1573.

CLUTTON-BROCK, T. H., G. R. IASON, and F.

E. GUINNESS. 1987. Sexual segregation and density-related changes in habitat use in male and female red deer (Cervus elaphus). Journal of Zoology (London) 211:275-289.

COADY, J. W. 1974. Influence of snow on behavior of moose. Le Naturaliste Canadien 101:417-436.

COLLINS, W. B., and C. C. SCHWARTZ. 1998. Logging in Alaska's boreal forest: creation of grassland or enhancement of moose habitat. Alces 34:355-374.

EDWARDS, J. 1983. Diet shifts in moose due to predator avoidance. Oecologia 60:185-189.

GASAWAY, W. C., R. D. BOERTJE, D. V. GRANGAARD, D. G. KELLEYHOUSE, R. O. STEPHENSON, and D. G. LARSEN. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildlife Monographs 120.

______, 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.

GROSS, J. E. 1998. Sexual segregation in ungulates: a comment. Journal of Mammalogy 79:1404-1409.

HUNDERTMARK, K. J. 1998. Home range, dispersal and migration. Pages 303-335 *in* A. W. Franzmann and C. C. Schwartz, editors. Ecology and management of the North American moose. Smithsonian Institution Press, Washington, D.C., 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 and risk of predation: effects on behavior and social structure in 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.

MACCRACKEN, J. G., and V. VAN BALLENBERGHE. 1987. Age- and sex-related differences in fecal pellet dimensions of moose. Journal of Wildlife Management 51:360-364.

MAIN, M. B. 1998. Sexual segregation in ungulates: a reply. Journal of Mammalogy 80:1410-1415.

______, and B. E. COBLENTZ. 1990. Sexual segregation in ungulates: a critique. Wildlife Society Bulletin 18:204-210.

______, and ______. 1996. Sexual segregation in Rocky Mountain mule deer. Journal of Wildlife Management 60:479-507.

______, F. W. WECKERLY, and V. C. BLEICH. 1996. Sexual segregation in ungulates: new directions for research. Journal of Mammalogy 77:449-461.

MCCULLOUGH, D. R. 1979. The George Reserve deer herd: population ecology of a *K*-selected species. University of Michigan Press, Ann Arbor, Michigan, USA.

______. 1999. Density dependence and life-history strategies of ungulates. Journal of Mammalogy 80:1130-1146.

______, D. H. HIRTH, and S. J. NEWHOUSE. 1989. Resource partitioning between the sexes in white-tailed deer. Journal of Wildlife Management 53:277-283.

MILLER, B. K., and J. A. LITVAITIS. 1992. Habitat segregation by moose in a boreal forest ecotone. Acta Theriologica 37:41-50.

MIQUELLE, D. M., 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.

NICHOLSON, M. C., R. T. BOWYER, and J. G. KIE. 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. Journal of Mammalogy 78:483-504.

OLDEMEYER, J. L., and W. L. REGELIN. 1980. Response of vegetation to tree crushing in Alaska. Alces 16:429-443.

PEEK, J. M. 1974. A review of moose food habits studies in North America. Le Naturaliste Canadien 101:195-215.

RACHLOW, J. L., and R. T. BOWYER. 1998. Habitat selection by Dall's sheep (*Ovis dalli*): maternal trade-offs. Journal of Zoology (London) 75:457-465.

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

RENCHER, A. C. 1995. Methods of multivariate analysis. John Wiley & Sons, New York, New York, USA.

RISENHOOVER, K. L. 1989. Composition and quality of moose winter diets in interior Alaska. Journal of Wildlife Management 53:568-577.

SCALBERT, A. 1992. Quantitative methods for estimation of tannins in plant tissues. Pages 258-280 *in* R. W. Hemmingway and P. E. Laks, editors. Plant Polyphenols. Plenum Press, New York, New York, USA.

STEPHENSON, T. R., V. VAN BALLENBERGHE, and J. M. PEEK. 1998. Response of moose forages to mechanical cutting on the Copper River Delta, Alaska. Alces 34:479-494.

TELFER, E. S. 1969. Twig weight-diameter relationships for browse species. Journal of Wildlife Management 33:917-921.

———, and J. P. KELSALL. 1984. Adaptations of some large North American mammals for survival in snow. Ecology 65:1828-1834.

THOMPSON, I. D., and R. W. STEWART. 1998. Management of moose habitat. Pages 377-401 *in* A. W. Franzmann and C. C. Schwartz, editors. Ecology and management of the North American moose. Smithsonian Institution Press, Washington, D.C., USA.

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 W. B. BALLARD. 1994. Limitation and regulation of moose populations: the role of predation. Canadian Journal of Zoology 72:1345-1354.

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

VAN SOEST, P. J. 1982. Nutritional ecology of the ruminant. O & B Books, Corvallis, Oregon, USA.

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.

ZAR, J. H. 1984. Biostatistical analysis. Second Edition. Prentice-Hall, Englewood Cliffs, New Jersey, USA.