RESPONSE OF MOOSE FORAGES TO MECHANICAL CUTTING ON THE COPPER RIVER DELTA, ALASKA

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ABSTRACT: A change in the natural disturbance regime on the Copper River Delta, Alaska, has reduced the level of early seral vegetation communities suitable for moose (*Alces alces*) wintering habitat. Consequently, we evaluated the use of a rotary-axe to increase willow (*Salix* spp.) mass and reduce competing species in stands that provide winter forage. We developed equations to predict mass of current-annual-growth, older growth, and leaves for 7 shrub species. We compared forage mass among treatment and control areas in 11 sites composed of 4 vegetation types important to moose. Alder (*Alnus sinuata*) mass generally declined following cutting, whereas Sitka willow (*Salix sitchensis*) current-annual-growth twig and leaf mass were greater ($P < 0.01$) in cut than uncut stands.

Willow (*Salix* spp.) and other early successional browse species compose the majority of the diet of moose (Peek 1974, Stephenson 1995, MacCracken *et al.* 1997). On the Copper River Delta (CRD), glacial retreat and shifting of active river channels provide important moose habitat as willows invade these areas (Stephenson 1995). Flood patterns have changed on the CRD in recent years such that the proportion of early successional habitats on the winter range is declining (Stephenson 1995).

Vegetation stands with declining willow mass on the CRD may potentially be modified to increase forage value for moose. Although exposed mineral soils are required for willow seed germination and establishment (Chapin *et al.* 1994; Collins 1996), willow resprouts following removal of above-ground mass (Oldemeyer and Regelin 1980). Alder (*Alnus* spp.) exerts an allelopathic effect on the germination of new willow seedlings and in addition, a closed-canopy inhibits the development of shade intolerant willow seedlings (Chapin *et al.* 1994). Harrington (1984) observed that red alder (*Alnus rubra*) stump survival and sprouting was minimal in older stands following cutting. Thus, a reduction in densities of alder may occur following manipulation.

Enhancement efforts on the Kenai Peninsula, Alaska, employed mechanical treatments that reset vegetation succession by eliminating nonbrowse species such as spruce while favoring browse species such as aspen (*Populus tremuloides*), birch (*Betula papyrifera*), and willow (Oldemeyer and Regelin 1980).

Silvicultural treatments may benefit moose as well. Coniferous sites usually require scarification to produce moose browse because mature timber typically contain minimal shrubs. However, harvest of mature aspen may provide considerable browse through sprouting (Collins 1996).

The literature on habitat manipulation illustrates the need for well designed experiments. Our objective was to evaluate

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responses of moose forage following mechanical habitat manipulation on the CRD for large scale application. We hypothesized that cutting of mature stands reduces alder mass and increases willow mass.

STUDY AREA

The 2,835 km² CRD is located along the north coast of the Gulf of Alaska east of Prince William Sound. The topography of the delta is characterized by marsh and glacial outwash plain dissected by tidal sloughs and glacial rivers. Prior to the 1964 earthquake which elevated the CRD 1-2 m, much of the marsh was maintained as early successional vegetation because of continual flooding. The CRD is bordered by the Gulf of Alaska to the south, and mountain ranges (1,000-3,000 m) deeply dissected by glaciers to the west, north, and east. The Copper River divides the CRD into western and eastern subunits (MacCracken 1992). This study was conducted on the western CRD. Elevations on the delta range from sea level to 200 m. Mean annual precipitation is 231 cm with mean annual snowfall of 310 cm. Mean monthly temperatures range from -6°C in January to 12°C in July. Moose are not endemic to the CRD, having been excluded by the local topography, but were introduced during 1949-1958.

METHODS
Experimental Design

Experimental manipulation occurred on 11 representative sites on the West CRD moose winter range. During early April 1990, one member of each of a pair of plots in tall/closed alder-willow (TCAW) and tall/open alder-willow (TOAW) was mowed with a rotary axe (hydro-axe) to <0.25 m above ground level. A rotary axe uses a 2 m blade that spins at high speed to cut woody vegetation up to 15 cm diameter. During April and May 1991, the rotary-axe treatment was applied randomly to one member of each of 4 pairs of plots in TCAW, 2 pairs of plots in TOAW, 2 pairs of plots in woodland spruce (*Picea sitchensis*, WOSP), and 1 pair of plots in low willow/sweetgale (*Myrica gale*, WISW). Experimental cuts varied from 10 to 100 ha. Furthermore, adjacent plots were separated by buffer strips (>10 m) to avoid "edge effects" (Wiens *et al.* 1986).

Mass Estimation

Forage mass was determined annually at the end of the growing season (August/September) in control and treatment sites. Mass was estimated according to MacCracken and Van Ballenberghe (1993) by: (1) developing regression equations to predict forage mass on an individual stem from its basal diameter; (2) measuring the basal diameter of stems in plots in control and treatment sites; (3) applying the regression equations to the stems measured in a plot; and (4) summing estimates for each stem in a plot by species. The high variability typical of shrub communities (Lyon 1968) required sampling only homogeneous stands in the community types most used by moose. Alaback (1986) found site to be an insignificant factor in mass regressions in this region. However, site-specific regression equations in treatment areas (cut vegetation) were developed annually during this study because of substantial annual changes in morphology of sprouted stems following cutting. MacCracken and Van Ballenberghe's (1993) regression equations were applied to the control areas (uncut vegetation) following validation with samples collected during this study.

For each community type, in treatment areas, a minimum of 10 stems were cut 5 cm above ground level to develop regressions to predict mass of twig current annual growth, leaves, and older twig parts as defined by maximum diameter-at-point-of-browsing (DPB) at a site. In addition, a

minimum of 5 stems were harvested in each community type in all control and treatment areas to validate regression equations. A stratified random sampling design was used to select stems, insuring a range of basal diameters was sampled for each species at a site. Prior to harvest, basal stem diameters were measured to the nearest 0.1 mm using calipers. Following harvest, edible portions of stems (leaf, CAG twig, and older growth twig components) were oven-dried at 60°C for 48 hours and weighed to the nearest 0.1 g.

Zero-intercept regression equations were developed to predict leaf, current-annual-growth (CAG), and available [sum of CAG and old-growth (OG) up to maximum diameter-at-point-of-browsing] mass for each species separately in first and second year treatment areas. The percent deviation between actual mass values and predicted mass values of the validation samples for each species was used to determine the accuracy of regression equations (MacCracken and Van Ballenberghe 1993). Models were selected primarily based on the smallest percent deviation but also on maximum r^2 and minimum standard error of the estimate. MacCracken and Van Ballenberghe's (1993) regression equations used for shrubs in control areas were validated similarly.

Permanent sampling plots were established in control and treatment areas. Plots were randomly located and composed of a minimum of 20 4 m² subplots spaced at 5 m intervals along 4 parallel transects 5 m apart (MacCracken 1992). In control area plots, all basal stem diameters in each subplot were measured for prediction of shrub mass. However, in treatment area plots, due to the large number of rooted stems following cutting, a random sample of basal diameters was measured and the density of all rooted stems in a plot was determined. The number of stems measured in a treatment plot was

determined using the equation:

$$\bar{x} \pm t_{1-0.5\alpha} \frac{s}{\sqrt{n}}$$

In control areas, where the basal diameters of all stems were measured, leaf, CAG, and available mass regression equations were applied to each stem and the sum of the predicted values represented the mass per plot. In treatment areas, where only a portion of the basal diameters (BD) were measured, regressions were applied to the random sample and a mean was calculated for each plot. The mean mass/stem/plot was then multiplied by the density of stems in each plot to obtain the mass per plot.

We measured browse burial by snow at permanent sampling sites every 3-4 weeks during winter. At each site, 10 twigs in each of 5 height classes (<1.0, 1.0-1.5, 1.5-2.0, 2.0-2.5, and 2.5-3.0 m) were identified with color-coded flagging prior to winter (Schwab and Pitt 1987). The number of stems of each species with flagged twigs was proportional to their availability at each site. The number of exposed flags from each height zone was recorded during each visit. Missing flags were accounted for in subsequent calculations. Percent browse burial was calculated for each site and visit as (the number of exposed flags / the total number of flags) X 100. Maximum browse burial during each winter was determined for each site as an indication of minimum browse availability. Because of the highly variable nature of snow depth on the CRD within 3-4 week intervals (Stephenson 1995), we were unable to reliably extrapolate browse burial on a daily basis.

Browse Use

Estimates of relative browsing of shrub species were compared between control and treatment areas by conducting use surveys in early summer using the permanent

plots established for sampling browse mass. In each 4-m^2 plot, the number of stems exhibiting browsing, since the last growing season, was recorded. Furthermore, DPB was measured to the nearest 0.1 mm for each browsed twig and classified as moose or snowshoe hare (*Lepus americanus*) and age of twig. Following validation using at least 10 samples collected during this study, regression equations developed by MacCracken and Van Ballenberghe (1993) were used to predict mass removed distal to the DPB.

Statistical Analysis

Mass data were analyzed using a randomized block split-plot design. Whole plot effect was vegetation treatment (cut or uncut), slit-plot effect was season (12; 4 seasons x 3 years), and the treatment by season interaction was tested. Blocks were location (11) and included 4 vegetation community types. Because dependent variables (mass estimates) within each analyses were interrelated and to provide protection against Type I errors, multivariate analysis of variance (MANOVA) was used. In addition, statistical significance of MANOVA's was based on family-wise error rates where $\alpha = 0.1$/number of comparisons (generally species and plant parts) to further control Type I errors. Following a significant MANOVA, univariate analysis of variance (ANOVA) was used to test for main effects and interactions for each dependent variable. Significant ANOVA's were followed by Fisher's protected least-significant difference tests.

RESULTS

Mass regression equations (Tables 1-3) generally were more accurate for younger stems with less complex branching and little browsing. Predictive equations for juvenile growth-form stems (1-2 years) tended to be log-log and exhibited much steeper slopes

than the equations for older stems. Alder (*A. sinuata*) and sweetgale mass eaten were better predicted using Sitka and Barclay willow (*Salix barclayi*) equations, respectively (Table 4).

Only alder and Sitka willow exhibited an overall treatment effect on mass variables (MANOVA, $P < 0.04$, Tables 5-9). Sitka willow and alder CAG twig and leaf mass and use were greater in cut than uncut stands (ANOVA, $P < 0.01$). Although there were insufficient error degrees of freedom to run MANOVA's, sweetgale exhibited treatment and year effects (ANOVA, $P < 0.01$). Only Barclay willow exhibited a significant block effect (MANOVA, $P < 0.04$), but substantial differences between treatments and blocks that were not statistically significant occurred for other species.

The variability in shrub measurements reduced the power of statistical tests even when differences were by orders of magnitude. Mass response of undergreen willow (*Salix commutata*) to treatments was similar (although statistically not significant) to that of other willows. The lower occurrence of this species is reflected in twig mass estimates that did not exceed 50 kg/ha. Black cottonwood (*Populus trichocarpa*) and feltleaf willow (*Salix alaxensis*) each occurred in only 3 blocks with twig mass estimates less than 22 and 80 kg/ha, respectively.

Except for 4 cut sites where alder use was 4.9 - 12.9%, use of alder ranged between 0 and 3% (Table 5). Use of willow varied between 0 and 25%, with the exception of 90% use of undergreen willow on a site heavily used by moose during most winters. Use of sweetgale and sitka willow was higher for cut regrowth than uncut twigs (Tables 6 and 9). Use of black cottonwood was <1% in all but 2 sites where it was 7 and 32%.

Maximum browse burial by snow var-

ied considerably among years and sites (Table 10). Browse burial within the primary winter range (see Stephenson 1995) tended to be least in TCAW and TOAW communities and greatest in the WOSP type. Secondary winter range browse burial was 100% in many height classes during some years indicating less browse availability. The maximum height of browse is indicated by the presence of missing values

for height zones in Table 10.

DISCUSSION

The data support our hypothesis that cutting of mature stands of alder not only reduced alder mass but generally killed the stump. Minimal stump sprouting of alder was observed and sprouts usually survived <1 year. Harrington (1984) observed similar patterns in red alder and suggested that

Table 1. Mass-diameter regressions[1] for moose browse species in uncut experimental control sites on the Copper River Delta, Alaska, during 1990-1993. Equations estimate mass of leaf, current-annual-growth (CAG) twig, and available mass (CAG and old growth within range of moose diameter-at-point-of-browsing). Model validation expressed as percent deviation of model prediction and actual mass of validation samples.

SPECIES	MASS COMPONENT	MODEL	r^2	% DEVIATION
BROWSE MASS				
Alnus sinuata	CAG twig	$=-3.97(BD^{1.77})$	0.76	83.6
	available mass	$=2.33(BD)$	0.49	8.7
	leaf	$=4.53(BD)$	0.63	51.2
Myrica gale	CAG twig	$=1.2(BD)$	0.16	63.1
	available mass	$=-3.33(BD^{2.15})$	0.61	-45.8
	leaf	$=3.65(BD)$	0.36	85.4
Populus trichocarpa	CAG twig	$=0.98(BD)$	0.75	
	available mass	$=2.37(BD)$	0.58	
	leaf	$=4.82(BD)$	0.69	
Salix alaxensis	CAG twig	$=0.51(BD)$	0.64	15.5
	available mass	$=1.0(BD)$	0.54	5.5
	leaf	$=2.52(BD)$	0.55	67.2
S. barclayi	CAG twig	$=0.36(BD)$	0.62	-10.3
	available mass	$=1.51(BD)$	0.44	-5.4
	leaf	$=1.43(BD)$	0.52	62.9
S. commutata	CAG twig	$=0.16(BD)$	0.37	-9.7
	available mass	$=0.55(BD)$	0.48	-3.9
	leaf	$=0.94(BD)$	0.50	68.9
S. sitchensis	CAG twig	$=-5.29(BD^{2.35})$	0.56	8.6
	available mass	$=11.07(lnBD)$	0.20	-16.6
	leaf	$=10.69(lnBD)$	0.28	-10.8

[1]Equations from MacCracken and Van Ballenberghe (1993) but validated using samples from this study.

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sprouting success was related to moisture accumulation on the stump and lack of resistance to stump decay. Former closed-canopy alder stands with an organic soil layer were rapidly dominated by bluejoint (*Calamagrostis* spp.) following exposure to full sunlight as Collins (1996) also observed. Thus, stands that are primarily alder with few willow stems should not be selected for rotary-axe treatment. Alder dominated stands can be converted to willow by exposing mineral soil to permit seedling establishment (Collins 1996). Therefore, efforts at habitat enhancement are more effective if they are directed at delaying the maturation of plant communities that contain abundant browse. Mechanical enhancement efforts should be initiated in maturing plant communities with decadent but still abundant willow prior to disappearance of willow in the stand. Manipulation of stands that have lost willow will have to involve disturbance exposing mineral soil to permit willow seedling establishment.

Willow forage mass differed by orders of magnitude among plant community types, however, often these differences were not statistically significant due to the variability in shrub distribution and density. Sitka willow did exhibit substantial resprouting following cutting of mature, decadent individuals. The vigorous response of Sitka willow to treatment resulted in CAG mass the first year after cutting that surpassed the CAG mass in uncut controls. Furthermore, by the second year after cutting many stands also exhibited leaf and total twig mass that equalled control levels.

Table 2. Mass-diameter regressions for moose browse species in first year cut experimental treatment sites on the Copper River Delta, Alaska, during 1990-1993. Equations estimate mass of leaf, current-annual-growth (CAG) twig, and available mass (CAG and old growth within range of moose diameter-at-point-of-browsing). Model validation expressed as percent deviation between model prediction and actual mass of validation samples.

SPECIES	MASS COMPONENT	MODEL	r^2	% DEVIATION
BROWSE MASS				
Alnus sinuata	CAG twig	$=-3.89(BD^{2.77})$	0.93	-2.2
	leaf	$=-2.97(BD^{2.29})$	0.85	-12.6
Myrica gale	CAG twig	$=0.12(BD)$	0.89	-4.2
	leaf	$=0.3(BD)$	0.96	21.9
Populus trichocarpa[1]	CAG twig	$=-4.22(BD^{2.85})$		
	leaf	$=-3.12(BD^{2.24})$		
Salix alaxensis	CAG twig	$=-4.22(BD^{2.85})$	0.96	
	leaf	$=-3.12(BD^{2.24})$	0.92	
S. barclayi	CAG twig	$=3.5(BD^{2.72})$	0.94	-18.5
	leaf	$=-2.5(BD^{2.04})$	0.88	0.9
S. commutata	CAG twig	$=-3.12(BD^{2.48})$	0.92	2.2
	leaf	$=-2.46(BD^{2.06})$	0.90	15.2
S. sitchensis	CAG twig	$=-3.16(BD^{2.52})$	0.94	-2.5
	leaf	$=-2.39(BD^{2.02})$	0.93	-0.2

[1]Used *Salix alaxensis* equation

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Table 3. Mass-diameter regressions for moose browse species in second and third year cut experimental treatment sites on the Copper River Delta, Alaska, during 1990-1993. Equations estimate mass of leaf, current-annual-growth (CAG) twig, and available mass (CAG and old growth within range of moose diameter-at-point-of-browsing). Model validation expressed as percent deviation between model prediction and actual mass of validation samples.

SPECIES	MASS COMPONENT	MODEL	r^2	2 YR DEV.	3 YR DEV.
BROWSE MASS					
Alnus sinuata	CAG twig	$=-2.86(BD^{2.0})$	0.77	-18.7	
	available mass	$=-2.45(BD^{1.8})$	0.71	-13.8	
	leaf	$=-2.7(BD^{2.21})$	0.83	4.5	
Myrica gale	CAG twig	$=0.22(BD)$	0.93	-5.1	
	available mass	$=0.22(BD)$	0.93	-26.1	
	leaf	$=-2.68(BD^{2.04})$	0.77	14.5	
Populus trichocarpa	CAG twig	$=0.49(BD)$	0.80	-33.1	
	available mass	$=0.64(BD)$	0.94	-1.9	
	leaf	$=-1.64(BD^{1.78})$	0.91		
Salix alaxensis	CAG twig	$=-3.26(BD^{2.27})$	0.71	-6.7	
	available mass	$=0.99(BD)$	0.92	10.6	
	leaf	$=0.78(BD)$	0.87	-13.5	
S. barclayi	CAG twig	$=0.63(BD)$	0.86	-31.2	-35.2
	available mass	$=0.98(BD)$	0.73	-1.3	-36.0
	leaf	$=-2.72(BD^{2.17})$	0.85	12.5	21.1
S. commutata	CAG twig	$=0.47(BD)$	0.88	20.2	
	available mass	$=0.56(BD)$	0.91	19.2	
	leaf	$=-2.75(BD^{2.06})$	0.83	-7.9	
S. sitchensis	CAG twig	$=-2.66(BD^{2.08})$	0.72	25.0	33.6
	available mass	$=-0.93(BD^{1.46})$	0.72	19.4	-18.8
	leaf	$=-2.86(BD^{2.14})$	0.87	8.1	14.8

Post-treatment willow mass was positively related to pretreatment willow stem density. Willow plants suppressed by closed canopies often were sufficient to provide for abundant post-treatment mass. Manipulation that stimulates resprouting of existing browse stems results in more rapid benefits to moose when compared to efforts that use scarification and require seed germination (Regelin *et al.* 1987).

Current-annual-growth twig mass of Barclay willow in control stands varied between 1 and 382 kg/ha in TCAW and WISW stands, respectively. Similarly, Sitka willow CAG varied between 3 and 112 kg/ha in TOAW and TCAW control stands, respectively. During the second year of regrowth following mechanical treatment, mass of CAG twigs surpassed 1,343 and 418 kg/ha in stands of Barclay and Sitka willow, re-

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Table 4. Mass-diameter regressions[1] for moose browse species on the Copper River Delta, Alaska, during 1990-1993. Equations estimate mass eaten by moose/twig during winter. Model validation expressed as percent deviation between model prediction and actual mass of validation samples.

SPECIES	MODEL	r^2	%DEVIATION
MASS EATEN			
Alnus sinuata	$= 0.03 + 0.06(DPB^{2.5})$		-2.9
Myrica gale	$= 0.05 + 0.03(DPB^{2.7})$		-3.5
Populus trichocarpa	$= 0.04(DPB^{2.6})$		
Salix alaxensis	$= 0.08 + 0.01(DPB^{3.4})$	0.95	
S. barclayi	$= 0.05 + 0.03(DPB^{2.7})$	0.81	-18.1
S. commutata	$= 0.05 + 0.03(DPB^{2.7})$		
S. sitchensis	$= 0.03 + 0.06(DPB^{2.5})$	0.80	10.6

[1]Equations from MacCracken and Van Ballenberghe (1993) but validated using samples from this study.

spectively. Spalinger *et al.* (1988) noted that mule deer (*Odocoileus hemionus*) forage densities <5kg/ha limited intake rate. Considering the high absolute browse intake rates required by moose, the low forage mass observed in some mature (uncut) browse communities on the CRD is likely suboptimal. Suboptimal browse mass limits the ability of moose to consume sufficient forage to meet energetic requirements. Minimum browse abundance is often overlooked in habitat assessments.

In treated stands, mass-diameter regression equations were developed and validated for plant communities defined by their age. In addition to species, age was considered a primary variable in developing regressions due to the gross differences in morphology, browsing intensity, and productivity as a result of cutting. The rapidly growing juvenile growth-form of resprouting shrubs necessitated the development of separate predictive equations for mature and immature plants. In validating MacCracken and Van Ballenberghe's (1993) equations for mature stems (Table 1), most deviations fell within their 20% recommendation. However, the less complicated growth form of 1 and 2 year-old stems resulted in more precise estimation of mass (Tables 2 and 3).

Winter browse availability is determined partially by snowfall. Snow depths exhibit wide variation among and during winters on the CRD (Stephenson 1995) and affect moose energetics by burying browse (Schwab and Pitt 1987) and increasing energy expenditure during travel (Parker *et al.* 1984). Thus, determination of browse mass during snow-free periods may not estimate the available winter mass. In particular, Sitka willow of full height (5 m) becomes more important during periods of deep snow as moose migrate to glacial outwash plain habitats (TCAW and TOAW) where Sitka willow is more abundant (Stephenson 1995). In contrast, Barclay willow is more abundant in low WISW and uplifted marsh WOSP habitats that are more readily buried by deep snow. In some cases, willow regrowth in cuts, although shorter in stature, may be more accessible than taller plants with denser canopies that intercept snow and are buried. Areas of the secondary winter range sampled, exhibited greater maximum browse burial than primary winter range regardless of year and winter severity.

Table 5. *Alnus sinuata* mass (kg/ha) by plant part and percent use by moose in 11 experimental blocks on the Copper River Delta, Alaska, during 1990-1993[1].

YEAR	BLOCK[2]	TREATMENT	CAG TWIG	LEAF	TOTAL TWIG	USE
1	EACAW	CUT	14.0	14.8	8.3	10.8
		UNCUT	173.2	1814.3	933.1	0.4
	EAOAW	CUT	18.6	21.5	13.3	5.3
		UNCUT	0.6	53.6	27.6	0.3
	EHWOSP	UNCUT	0.02	2.5	1.3	0
	ESCAW	CUT	20.6	92.7	49.1	4.9
		UNCUT	205.7	2076.3	1068.0	0.03
	NSCAW	CUT	11.4	12.7	7.46	0
		UNCUT	272.5	2935.3	1509.8	0.01
	NSOAW	CUT	10.0	176.2	142.9	0
		UNCUT	11.0	321.9	165.5	0.2
	SSCAW	CUT	9.9	199.1	103.1	1.3
		UNCUT	169.5	1809.7	930.8	0.01
	SSOAW	CUT	9.6	102.5	54.8	0.1
		UNCUT	8.0	398.2	204.8	0.9
	WACAW	CUT	22.2	32.4	17.1	12.9
		UNCUT	208.1	2049.1	1054.0	0
2	EACAW	CUT	6.0	10.7	6.2	0
		UNCUT	152.2	1554.2	799.4	0
	EAOAW	CUT	6.6	9.9	7.9	0
		UNCUT	1.3	106.0	54.5	0.1
	ESCAW	CUT	24.3	164.0	86.5	0.3
		UNCUT	203.8	2061.9	1060.5	0
	NSCAW	CUT	7.9	24.8	14.5	0
		UNCUT	255.6	2645.6	1360.7	0
	NSOAW	CUT	22.5	254.5	133.2	0.5
		UNCUT	16.0	401.4	206.4	3.0
	SSCAW	CUT	28.4	73.6	37.5	0
		UNCUT	164.8	1708.6	878.8	0
	SSOAW	CUT	22.1	72.9	43.1	0.9
		UNCUT	12.2	546.4	281.1	1.5
	WACAW	CUT	0.9	1.5	1.0	0
		UNCUT	220.1	2121.9	1091.4	0.02
	WAWISW	CUT	0.9	1.3	1.0	0
3	EACAW	CUT	1.6	2.8	1.6	0
		UNCUT	154.0	1981.3	815.3	0
	EAOAW	CUT	9.8	15.0	11.6	0
		UNCUT	1.8	145.1	74.6	0

[1]MANOVA treatment effect significant $P < 0.014$ ("family-wise")

[2]EACAW = East Alaganik Closed Alder-Willow, EAOAW = East Alaganik Open Alder-Willow, EHWOSP = East Haystack Woodland Spruce, ESCAW = East Sherman Closed Alder-Willow, NSCAW = North Sherman Closed Alder-Willow, NSOAW = North Sherman Open Alder-Willow, SSCAW = South Sherman Closed Alder-Willow, SSOAW = South Sherman Open Alder-Willow, WACAW = West Alaganik Closed Alder-Willow, WAWISW = West Alaganik Willow-Sweetgale, WHWOSP = West Haystack Woodland Spruce

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Table 6. *Myrica gale* mass (kg/ha) by plant part and percent use by moose in 11 experimental blocks on the Copper River Delta, Alaska, during 1990-1993[1].

YEAR	BLOCK	TREATMENT	CAG TWIG[2,3]	LEAF[2,3]	TOTAL TWIG[2,3]	USE[2,3]
1	EHWOSP	CUT	6.9	17.3	6.8	0
		UNCUT	287.0	872.8	71.3	18.8
	WAWISW	CUT	25.8	40.9	25.8	1.2
		UNCUT	719.3	2187.8	256.0	4.3
	WHWOSP	CUT	350.7	1035.8	143.7	13.6
		UNCUT	271.9	827.0	90.8	5.4
2	EHWOSP	CUT	22.8	31.5	19.8	0
		UNCUT	284.7	866.0	80.6	18.0
	WAWISW	CUT	30.8	49.9	30.8	2.9
		UNCUT	719.3	2187.8	256.0	2.6
	WHWOSP	CUT	431.4	1060.4	226.7	10.7
		UNCUT	290.9	884.9	102.5	5.8

[1]Insufficient error degrees of freedom for MANOVA

[2]Within column, ANOVA treatment effect significant $P < 0.01$

[3]Within column, ANOVA block effect significant $P < 0.01$

Browse use estimates vary greatly with plot location, vegetation structure, and moose movements resulting from annual snow conditions. The relatively low levels of willow use observed during this study lend support to the conclusion of MacCracken *et al.* (1997) that CRD moose are below ecological carrying capacity under the winter conditions we observed. However, use measured in late spring must be related to estimates of browse burial by snow to represent winter browse availability. In some cases low use may be related less to lack of use by moose than to browse burial by snow if snow persists. Even during the mild winters observed during this study (Stephenson 1995), periods with the maximum browse burial observed would have limited access to considerable browse.

Moose habitat enhancement must be evaluated for its value as forage rather than just additional vegetation. Thus, mass must be weighted by frequency of consumption as determined by diet composition (Hobbs and Spowart 1984). Observations of winter foraging of habituated moose on the CRD (Stephenson 1995) combined with MacCracken's (1992) data on fecal analysis suggests the following winter diet composition (under relatively mild snow depths and no available aquatic forages) on the CRD: alder (3%), sweetgale (7%), cottonwood (1%), feltleaf willow (1%), Barclay willow (56%), undergreen willow (1%), and Sitka willow (31%). As winter severity increases, the proportion of Barclay willow and sweetgale likely declines and Sitka willow, cottonwood, and alder increases because of their relative availability in glacial outwash plain communities. Furthermore, although forage mass is a critical component in maintaining a positive energy balance, Hobbs (1989) determined that increases in winter forage quality had a more

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Table 7. *Salix barclayi* mass (kg/ha) by plant part and percent use by moose in 11 experimental blocks on the Copper River Delta, Alaska, during 1990-1993.

YEAR	BLOCK[1]	TREATMENT	CAG TWIG	LEAF	TOTAL TWIG	USE
1	EACAW	CUT	143.7	101.9	120.6	3.9
		UNCUT	8.1	32.3	34.1	10.6
	EAOAW	CUT	617.3	490.4	567.1	4.3
		UNCUT	230.6	916.1	967.3	3.5
	EHWOSP	CUT	220.7	236.6	253.0	1.5
		UNCUT	100.5	399.0	421.4	3.0
	ESCAW	CUT	3.3	3.4	3.3	0
		UNCUT	13.0	51.6	54.5	8.8
	NSCAW	UNCUT	1.4	5.4	5.7	0
	NSOAW	CUT	3.0	4.4	3.8	7.9
		UNCUT	2.2	8.7	9.2	0
	SSCAW	CUT	1.7	1.8	1.8	22.2
		UNCUT	3.2	12.8	13.5	0
	SSOAW	CUT	17.7	21.5	21.7	5.1
		UNCUT	6.6	26.3	27.8	7.9
	WAWISW	CUT	600.7	625.2	600.7	19.8
		UNCUT	382.1	1517.6	1602.5	4.6
	WHWOSP	CUT	80.2	106.6	104.9	2.3
		UNCUT	145.1	576.5	608.8	1.4
2	EACAW	CUT	75.0	109.9	116.7	15.8
		UNCUT	7.7	30.4	32.1	2.8
	EAOAW	CUT	545.9	531.5	849.1	7.5
		UNCUT	215.1	854.2	902.0	3.0
	EHWOSP	CUT	451.2	514.5	738.0	3.5
		UNCUT	91.3	362.7	382.9	3.3
	ESCAW	CUT	8.6	5.1	13.3	10.5
		UNCUT	10.0	39.6	41.8	13.9
	NSCAW	UNCUT	1.4	5.5	5.9	0
	NSOAW	CUT	17.7	12.3	27.5	1.8
		UNCUT	5.7	22.7	24.0	7.9
	SSCAW	CUT	6.5	6.8	10.1	10.9
		UNCUT	3.3	13.0	13.7	5.1
	SSOAW	CUT	50.5	35.6	78.5	1.2
		UNCUT	7.0	27.7	29.2	0
	WAWISW	CUT	1343.6	1240.6	2090.0	6.0
		UNCUT	382.1	1517.6	1602.5	6.2
	WHWOSP	CUT	179.6	154.0	298.4	3.8
		UNCUT	134.0	532.2	561.9	1.7
3	EACAW	CUT	80.5	160.8	125.0	6.6
		UNCUT	4.8	19.2	20.3	1.0
	EAOAW	CUT	583.1	739.1	907.1	2.9
		UNCUT	216.7	860.8	909.0	2.6

[1]MANOVA block effect *P*=0.038

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Table 8. *Salix commutata* mass (kg/ha) by plant part and percent use by moose in 11 experimental blocks on the Copper River Delta, Alaska, during 1990-1993.

YEAR	BLOCK	TREATMENT	CAG TWIG	LEAF	TOTAL TWIG	USE
1	EAOAW	CUT	30.8	28.9	30.1	0
		UNCUT	7.0	41.4	24.2	16.1
	EHWOSP	CUT	10.2	10.8	10.2	2.0
		UNCUT	3.7	21.8	12.8	9.4
	WAWISW	UNCUT	1.2	6.8	4.0	90.0
	WHWOSP	CUT	13.2	21.1	15.9	8.8
		UNCUT	1.6	9.5	5.6	64.3
2	EAOAW	CUT	50.4	49.5	60.1	3.0
		UNCUT	11.2	65.8	38.5	8.6
	EHWOSP	CUT	13.6	13.0	16.2	9.3
		UNCUT	4.0	23.2	13.6	7.4
	SSOAW	CUT	0.4	0.3	0.4	0
		UNCUT	0.2	0.9	0.5	0
	WAWISW	CUT	2.2	1.1	2.6	0
		UNCUT	1.2	6.8	4.0	90.0
	WHWOSP	CUT	46.4	42.9	61.0	7.5
		UNCUT	16.6	97.4	57.0	3.9
3	EAOAW	CUT	47.8	57.0	56.9	4.4
		UNCUT	14.5	85.0	49.7	8.5

positive impact on mule deer survival. Although moose will consume alder and cottonwood in limited quantities, the chemical defenses of these plants limit their intake when the moose's detoxification system is exceeded (Bryant *et al.* 1991). Thus, the high available mass of alder should not be perceived as a large supply of useable forage.

Thompson and Stewart (1997) noted that information is lacking on the effects of large-scale habitat management programs for moose populations. Mechanized treatments such as rotary-axe and crushing are often perceived as expensive relative to prescribed fire and logging, yet the magnitude of the response when applied routinely over multiple years may justify the effort. The benefits to moose of prescribed fire or adequate scarification following logging operations often are limited because of logistical restrictions. However, highly productive regrowth, even in small patches, may provide significant amounts of forage relative to maturing stands with low densities of browse species.

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Table 9. *Salix sitchensis* mass (kg/ha) by plant part and percent use by moose in 11 experimental blocks on the Copper River Delta, Alaska, during 1990-1993[1].

YEAR	BLOCK	TREATMENT	CAG TWIG[2]	LEAF[2]	TOTAL TWIG	USE[2]
1	EACAW	CUT	65.3	56.7	55.6	19.1
		UNCUT	87.3	135.1	139.9	10.9
	EAOAW	CUT	408.0	337.8	298.3	10.5
		UNCUT	70.0	719.5	745.1	3.7
	EHWOSP	CUT	35.8	32.8	33.8	0
		UNCUT	6.4	41.2	42.6	0
	ESCAW	CUT	27.8	32.2	27.8	25.2
		UNCUT	26.1	14.4	14.9	0.3
	NSCAW	CUT	5.1	5.6	5.1	7.8
		UNCUT	32.2	9.5	9.8	0
	NSOAW	CUT	96.3	141.9	125.0	13.8
		UNCUT	3.1	84.5	87.5	2.7
	SSCAW	CUT	6.3	6.2	5.5	0.7
		UNCUT	6.2	5.2	5.4	1.5
	SSOAW	CUT	141.8	167.5	157.4	6.9
		UNCUT	50.8	493.5	544.0	1.3
	WACAW	CUT	281.1	255.2	251.0	8.8
		UNCUT	63.3	31.2	32.3	0.6
	WHWOSP	CUT	7.0	9.7	9.7	8.2
		UNCUT	3.6	59.5	61.6	1.1
2	EACAW	CUT	78.0	73.3	1409.3	8.2
		UNCUT	57.6	123.2	127.5	2.9
	EAOAW	CUT	418.4	390.4	629.8	10.9
		UNCUT	61.9	612.0	633.7	4.4
	EHWOSP	CUT	48.2	44.7	77.4	7.1
		UNCUT	5.1	24.7	25.6	4.3
	ESCAW	CUT	36.4	32.9	75.3	3.7
		UNCUT	112.8	27.4	28.3	0
	NSCAW	CUT	9.5	8.7	16.6	0
	NSOAW	CUT	262.5	261.6	553.4	3.3
		UNCUT	16.2	182.2	188.6	3.4
	SSCAW	CUT	12.4	11.5	19.5	0.1
	SSOAW	CUT	195.4	177.9	381.4	1.6
		UNCUT	48.6	486.3	503.6	2.4
	WACAW	CUT	346.3	322.2	536.4	1.6
		UNCUT	46.6	24.8	25.7	1.6
	WHWOSP	CUT	9.9	9.1	17.0	12.9
		UNCUT	3.3	55.6	57.6	0.7
3	EACAW	CUT	103.8	99.4	120.2	2.8
		UNCUT	87.0	160.6	166.3	0.4
	EAOAW	CUT	568.7	537.4	748.6	4.1
		UNCUT	70.8	702.9	727.9	1.2

[1]MANOVA treatment effect *P*=0.04

[2]Within column, ANOVA treatment effect significant *P* < 0.01

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Table 10. Maximum browse burial by snow for 5 height classes of moose forage in experimental blocks on the Copper River Delta, Alaska, during 1990-1993.

YEAR	BLOCK	TREATMENT	MAXIMUM BROWSE BURIAL (%) BY HEIGHT CLASS				
			<1 m	1-1.5 m	1.5-2 m	2-2.5 m	2.5-3 m
1990/1991	EACAW	CUT	10	43	0		
		UNCUT	10	0	0	0	0
	EAOAW	CUT	20	40	50	0	0
		UNCUT	60	20	30	38	40
1991/1992	EACAW	CUT	40	0			
		UNCUT	0	0	0	0	0
	EAOAW	CUT	0	0	0	0	0
		UNCUT	0	0	0	0	0
	EHWOSP	CUT	30				
		UNCUT	30	30	0		
	ESCAW*	CUT	100				
		UNCUT	100	60	30	20	20
	NSCAW*	CUT	100				
		UNCUT	100	100	100	100	100
	NSOAW*	CUT	100				
		UNCUT	100	30	30	20	33
	SSCAW*	CUT	90				
		UNCUT	80	50	40	40	30
	SSOAW*	CUT	60				
		UNCUT	70	30	30	0	0
	WACAW	CUT	40				
		UNCUT	20	0	0	0	0
	WHWOSP	CUT	30				
		UNCUT	40	40			
1992/1993	EACAW	CUT	20	43	50		
		UNCUT	0	0	0	0	0
	EAOAW	CUT	20	0	0		
		UNCUT	40	30	17	0	0
	EHWOSP	CUT	0	0			
	EHWOSP	UNCUT	20	40	0		
	ESCAW*	CUT	100	50			
		UNCUT	40	10	10	10	10
	NSCAW*	CUT	60	50			
		UNCUT	100	100	100	100	100
	NSOAW*	CUT	80				
		UNCUT	50	20	20	0	0
	SSCAW*	CUT	50	43			
		UNCUT	10	0	0	0	0
	SSOAW*	CUT	10	0			
		UNCUT	10	0	12	0	0
	WACAW	CUT	0	0	0		
		UNCUT	0	0	0	0	0
	WAWISW	CUT	0	0			
		UNCUT	0	0	0		
	WHWOSP	CUT	40	50	0		
		UNCUT	90	72			

Note: Blocks designated with an "*" are secondary winter range; remaining blocks are primary winter range.

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REFERENCES

ALABACK, P. B. 1986. Biomass regression equations for understory plants in coastal Alaska: effects of species and sampling design on estimates. Northwest Sci. 60:90-103.

BRYANT, J. P., F. D. PROVENZA, J. PASTOR, P. B. REICHARDT, T. P. CLAUSEN, and J. T. DU TOIT. 1991. Interactions between woody plants and browsing mammals mediated by secondary metabolites. Annu. Rev. Ecol. Syst. 22:431-436.

CHAPIN, F. S.. III, L. R. WALKER, C. L. FASTIE, and L. C. SHARMAN. 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. Ecol. Monogr. 64:149-175.

COLLINS, W. B. 1996. Wildlife habitat enhancement in the spruce-hardwood forest of the Matanuska and Susitna Valleys. Alaska Dept. of Fish & Game. Federal Aid in Wildlife Restoration Final Report, Proj. W-23-5, W-24-1, W-24-2, W-24-3, Study 1.44, Juneau. 52 pp.

HARRINGTON, C. A. 1984. Factors influencing initial sprouting of red alder. Can. J. For. Res. 14:357-361.

HOBBS, N. T. 1989. Linking energy balance to survival in mule deer: development and test of a simulation model. Wildl. Monogr. 101. 39 pp.

———— and R. A. SPOWART. 1984. Effects of prescribed fire on nutrition of mountain sheep and mule deer during winter and spring. J. Wildl. Manage. 48:551-560.

LYON, L. J. 1968. An evaluation of density sampling methods in a shrub community. J. Range Manage. 21:16-20.

MACCRACKEN, J. G. 1992. Ecology of moose on the Copper River Delta, Alaska. Ph.D. Diss., Univ. Idaho, Moscow. 320 pp.

———— and V. VAN BALLENBERGHE. 1993. Mass-diameter regressions for moose browse on the Copper River Delta, Alaska. J. Range Manage. 46:302-308.

————, ————, and J. M. PEEK. 1997. Habitat relationships of moose on the Copper River Delta in coastal south-central Alaska. Wildl. Monogr. 136. 52 pp.

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

PARKER, K. L., C. T. ROBBINS, and T. A. HANLEY. 1984. Energy expenditures for locomotion by mule deer and elk. J. Wildl. Manage. 48:474-488.

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

REGELIN, W. L., C. C. SCHWARTZ, and A. W. FRANZMANN. 1987. Effects of forest succession on nutritional dynamics of moose forage. Swedish Wildl. Res. Suppl. 1:247-263.

SCHWAB, F. E. and M. D. PITT. 1987. Comparison of a direct and indirect method for estimating available winter browse. Wildl. Soc. Bull. 15:544-548.

SPALINGER, D. E., T. A. HANLEY, and C. T. ROBBINS. 1988. Analysis of the functional response in foraging in the Sitka black-tailed deer. Ecology 69:1166-1175.

STEPHENSON, T. R. 1995. Nutritional ecology of moose and vegetation suc-

Alces

cession on the Copper River Delta, Alaska. Ph.D. Diss., Univ. Idaho, Moscow. 172 pp.

THOMPSON, I. D. and R. W. STEWART. 1997. Management of moose habitat. Pages 377-401 *in* A. W. Franzmann and C. C. Schwartz (eds.) Ecology and management of the North American moose. Smithsonian Inst. Press, Washington, DC.

WIENS, J. A., J. T. ROTENBERRY, and B. VAN HORNE. 1986. A lesson in the limitations of field experiments: shrubsteppe birds and habitat alteration. Ecology 67:365-376.