# DIET SELECTION BY ALASKAN MOOSE DURING WINTER: EFFECTS OF FIRE AND FOREST SUCCESSION

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ABSTRACT: We studied forage available to and used by Alaskan moose (*Alces alces gigas*) during winter 1988-1989 on the Kenai Peninsula, Alaska, USA, to test the hypothesis that changes in the quality and abundance of browse during winter affected selection of diet. Random plots were located in 3 age classes of vegetation (7-10, 20-30, and 70-80 years since the last fire), which varied in abundance and quality of browse. Dominant species of browse we studied on those seral stands included scouler willow (*Salix scouleriana*), Kenai birch (*Betula papyrifera kenaica*), aspen (*Populus tremuloides*), and black cottonwood (*Populus trichocarpa*). We made twig counts of current annual growth in early (December), mid- (February), and late (April) winter to determine amounts of woody browse available to and used by moose. Overall, moose browsed scouler willow, Kenai birch, and aspen in proportion to their availability, and avoided black cottonwood. Plant secondary compounds offer a likely explanation for moose avoiding cottonwood and not consuming white spruce (*Picea glauca*). Percent use of a browse species, however, was not significantly related to its availability or to those measures of nutrient content we analyzed. Black cottonwood was not browsed to a greater degree in stands with low resource availability, contrary to a prediction of optimal foraging theory. Patterns of diet selection did not vary between periods of winter even though abundance of forage did so. Distance from escape cover affected diet selection by moose; selectivity of diet declined with increasing distance from cover, indicating risk of predation played a role in the foraging dynamics of moose. The use of fire holds the potential to improve habitat for moose, but the population dynamics of this large herbivore also need to be considered for such management to be effective. Likewise, the sound management of moose requires that suitable habitat be available in other seasons as well as winter.

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Many questions about diet selection by moose (*Alces alces*) during winter, and diet selection by large northern herbivores, in general, remain unresolved despite a vast literature on this subject (LeResche and Davis 1973, Freeland and Janzen 1974, Westoby 1974, Cushwa and Coady 1976, Pyke *et al.* 1977, Belovsky 1978, Wolff 1978, Nudds 1980, Jenkins 1982, Oldemeyer 1983, Schwartz *et al.* 1984, Ludewig and Bowyer 1985, Miquelle and Van Ballenberghe 1989, Risenhoover 1989, Van Ballenberghe *et al.* 1989). Optimal foraging theory predicts that diet selection of an herbivore should vary with the quality and availability of forage (Westoby 1974; Pyke *et al.* 1977; Belovsky 1978, 1984). Forage characteristics vary greatly between habitats occupied by moose during winter (Spencer and Hakala 1964, Miquelle *et al.* 1992), and as winter progresses, forage becomes depleted or less available because of prior use and deepening snows.

Studies on diet selection by white-tailed deer (*Odocoileus virginianus;* Wetzel *et al.* 1975, Theberge 1978, LaGory *et al.* 1985) and moose (Renecker and Hudson 1986, Vivas and Saether 1987, Risenhoover 1989) during winter have tested the hypothesis that patterns of foraging change with resource abundance. Vivas and Saether (1987) reported that moose fed selectively in forage patches of high density in mid-winter. Renecker and Hudson (1986), however, reported that moose became more of a generalist in their feeding as forage availability declined from summer to winter. Thus, why moose select a particular diet remains unresolved.

Optimal foraging theory predicts that herbivores should specialize (show preferences) when resource levels are high and generalize (feed in proportion to availability) when they are low (Westoby 1974, Pyke *et al.* 1977, Belovsky 1978, Nudds 1980, Stephens and Krebs 1986). At high levels of resource abundance, herbivores should be diet specialists and select a diet that optimizes a mixture of nutrients within a fixed bulk of food (Westoby 1974, Belovsky 1978). Nonetheless, some of these models have been modified to predict that low-valued but abundant food should be eaten more than high-valued but rare foods (Emlen 1966, Estabrook and Dunham 1976, Stenseth and Hansson 1979).

Nudds (1980) argued that energy acquisition should become the critical factor for survival during winter and optimization of the diet for other nutrients should be relaxed (energy-optimizing, equal-food-value model). At low resource levels, herbivores should not bypass low-valued foods to specialize on rare but high-quality foods and, therefore, should generalize. Alternatively, herbivores may be obligated to feed selectively to optimize energy intake (Belovsky 1981).

Pyke *et al.* (1977) argued that simple models, which assume that natural selection maximizes caloric intake, were inadequate as a paradigm for large herbivores that consume a wide array of foods. For example, there may be adaptive value in sampling from the entire range of available foods, irrespective of caloric value, to "prime" the rumen microflora so that newly ingested compounds could be broken down as availabilities of food changed. Such feeding also might detoxify secondary compounds (Freeland and Janzen 1974, Westoby 1978). Indeed, Freeland and Janzen (1974) explained generalization of diet in large herbivores as a means of limiting intake of any one toxic compound from a plant. Likewise, Bryant and Kuropat (1980) argued that diet selection of herbivores during winter was largely influenced by secondary chemistry of woody browse rather than proximal nutrient or energy contents. Westoby (1978) and Jenkins (1982), however, argued that a generalist diet could result from the need to obtain a proper mix of nutrients (nutrient-optimizing, unequal-food-value model).

Bunnell and Gillingham (1985) suggested that optimal foraging theory was inadequate to describe feeding behavior of ruminants. These authors argued that variation in chemistry among and within plant species and subsequent effects on the animal were too variable to predict diet by criteria of optimization. Bunnell and Gillingham (1985) proposed an alternative approach, termed satisficing, to describe diet selection by large herbivores during winter. An animal adopting such a feeding pattern acts not to optimize its allocation of time or choice of habitat or diet, but to stay alive. Such an animal may survive and reproduce without optimizing any single variable (Bunnell and Gillingham 1985).

Numerous studies have reported that production of woody forage is greater in early successional habitats than in later ones (Spencer and Chatelain 1953, Spencer and Hakala 1964, LeResche *et al.* 1974, Bailey 1978; Bangs and Bailey 1980). Spencer and Hakala (1964), MacCracken and Viereck (1990), and Loranger *et al.* (1991) noted that fire improved moose habitat through increased productivity and availability of deciduous woody plants; generally, stands appeared to furnish abundant forage for 15-20 years following fire. Other studies have shown that early successional habitats provided higher-quality forage than those in late-successional stages (Cowan *et al.* 1950, Dewitt and Derby 1955, Dietz 1970, Oldemeyer 1974, Oldemeyer *et al.* 1977). Cowan *et al.* (1950) reported total carbohydrates and proteins in the vegetation of a 6, and a 20-30 year-old forest were superior to those of a 70 year-old forest, and that the most nutritious forage occurred in younger forests.

Risk of predation also affects diet selection by moose (Edwards 1983). Molvar and Bowyer (1994) reported that moose fed more selectively when closer to concealment cover, and that sex and age classes of moose that were more vulnerable to predation (i.e., females with young) fed less efficiently. Alaskan moose, especially young, may experience high rates of mortality as a result of predation (Ballard *et al.* 1981, Gasaway *et al.* 1992, Bowyer *et al.* 1998).

We tested hypotheses concerning diet selection by Alaskan moose by determining whether forage was consumed in relation to its availability, and whether measures of forage quality predicted use or selection of diet. We predicted that diet selection would differ among successional stages because of differences in availability of forage, and that selection would change through winter as moose depleted available forage. We also predicted that increasing snow depth would decrease selectivity via effects on availability of browse. We tested if moose employed a nutrient-mixing strategy by determining if they used more of a less-preferred forage in stands with an abundance of more-preferred foods. We also tested for a difference between distance from cover and diet selection to examine the role of risk of predation in forage selection. Finally, we discuss our findings in relationship to the winter ecology and management of moose.

## STUDY AREA

This study was conducted on the Chugach National Forest on the Kenai Peninsula in southcentral Alaska, USA (Fig. 1). The study area encompassed approximately 300 km$^2$ in the northcentral Kenai Mountains. The area was bounded on the west by the Kenai National Wildlife Refuge and on the north by Turnagain Arm of Cook Inlet. Anchorage, the largest city in Alaska, lies 70 km to the northwest.

The study area was characterized by rugged mountains interlaced with narrow valleys running north and south. Elevations varied from sea level to about 2,000 m. Moose typically occurred at elevations of 100-800 m during summer, and 100-400 m in winter, depending on snow depth. Wintering moose occurred on upland benches in seral stands of hardwood created by fire, but also used areas along river bars and valley bottoms in shrub-fields of willow (*Salix* spp.). Wolves (*Canis lupus*) inhabited the study area and were the primary predators of moose during winter (Peterson *et al.* 1984) although black bears (*Ursus americanus*) may kill moose in other seasons (Schwartz and Franzman 1991). Trees and shrubs in this zone were dominated by white spruce (*Picea glauca*), Kenai birch (*Betula papyrifera kenaica*), quaking aspen (*Populus tremuloides*), black cottonwood (*P. trichocarpa*), scouler willow (*Salix scouleriana*), and barclay willow (*S. barclayi*). Steeper slopes on mountains generally were covered by thick stands

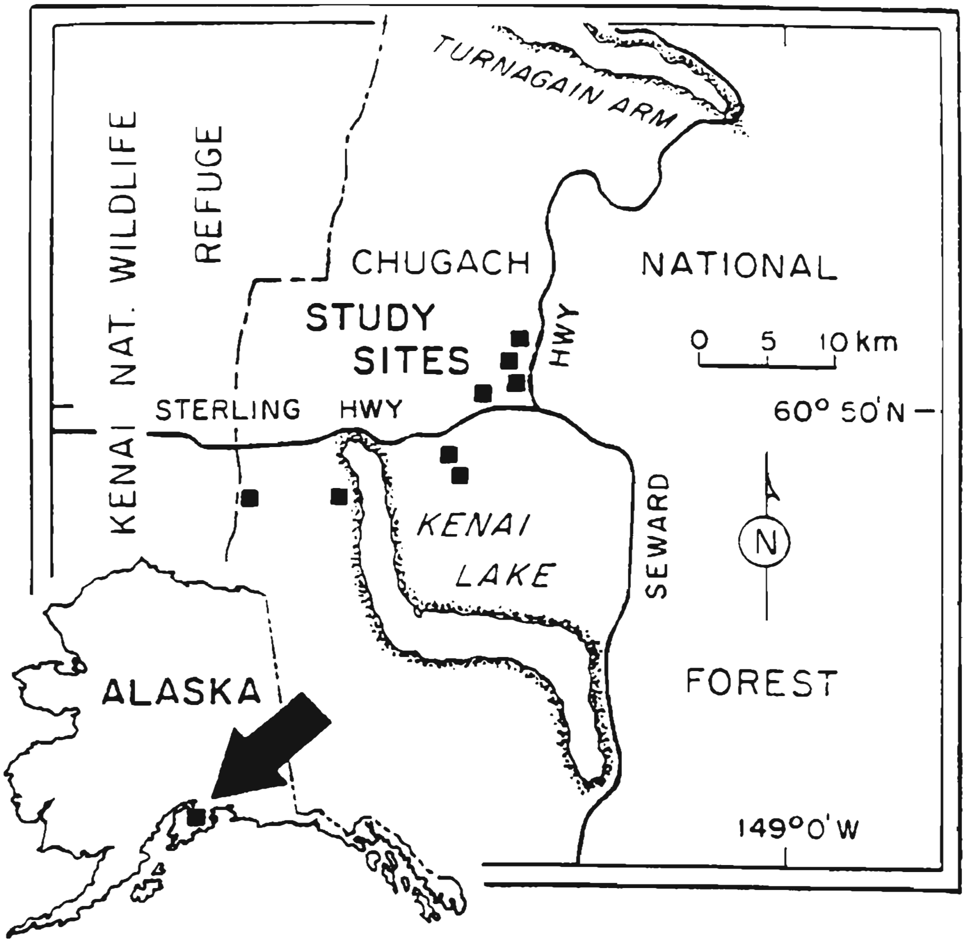

Fig. 1. Location of the study area on the Kenai Peninsula, Alaska, USA. Black squares indicate locations of stands we sampled ($n = 8$).

of alder (*Alnus crispa*) from 500-900 m in elevation. Above 900 m, grassy alpine meadows with outcroppings of barren rock dominated the landscape. Plant nomenclature followed Viereck and Little (1972).

Annual precipitation averaged 62 cm in valley bottoms with much of this occurring as snow in winter and rain in spring or autumn. The first snow fell in mid-October and usually persisted in valleys until early May. Snow depths varied widely among winters depending on amount of snowfall and temperatures. Average snow depth in March ranged from 45 cm in valley bottoms to 90 cm at an elevation of 300 m. The proximity to the Pacific Ocean influenced the climate. Summer temperatures averaged 12°C; maxima occasionally reached 25°C. Winter temperatures averaged -3°C, with extreme lows falling to -18°C.

Study sites (Fig. 1) were in seral stands of hardwoods created by wildfires or prescribed burns within the traditional winter range of moose. Elevation of stands ranged from 200 to 360 m. Soil was a sandy loam that was classified as Cryorthods. Diet selection by moose was studied in 3 age classes of stands: 7-10 years postfire; 20-30 years postfire; and 70-80 years postfire.

Vegetation in the 7-10 year-old stands

had numerous seedlings and saplings of scouler willow, Kenai birch, quaking aspen, and black cottonwood. Herbaceous vegetation was primarily bluejoint grass (*Calamagrostis canadensis*), dewberry (*Rubus arcticus*), and wintergreen (*Pyrola* spp.). Overstory vegetation in 20-30 year-old stands consisted of seedlings, saplings, and young trees of scouler willow, Kenai birch, quaking aspen, and black cottonwood. Herbaceous vegetation was similar to that in 7-10 year-old stands, but also included *Vaccinium*. Vegetation in the 70-80 year-old stands was composed mostly of an open stand of white spruce and hardwood trees without a closed overstory. Scattered seedlings and saplings of scouler willow, Kenai birch, quaking aspen, and black cottonwood were typical in the understory. Herbaceous vegetation was dominated by bluejoint grass, wintergreen species, and the mosses *Hylocomium splendens* and *Pleurozium schreberi*. Forage species that dominated stands and were surveyed for availability and use by moose were scouler willow, Kenai birch, aspen, and black cottonwood. These species represented most of the forage used by moose in winter on seral sites in the Kenai Mountains (Oldemeyer 1983).

## METHODS

### Availability and Use of Forage

Forage production and use by moose were estimated from twig counts of current annual growth (CAG) on randomly located quadrats within each stand. Three replicate stands were sampled within the 7-10 year age class, 2 within the 20-30 year age class, and 3 were sampled in the 70-80 year age class. Stands were sampled in early winter (December), mid-winter (February), and late winter (April). Size of replicate stands averaged 75 ha for the 7-10 year age class, 600 ha for the 20-30 year age class, and 400 ha for the 70-80 year age class.

Ten quadrats were located randomly within each replicate for all age classes of stands, and new random plots were sampled during each period of winter (e.g., early, mid-, and late). This number of quadrats provided a standard error within ±25% of the sample mean for counts of browsed and unbrowsed twigs on all replicates. Quadrat size varied from 5 by 5 m to 15 by 15 m; smaller plots were used in denser stands. For each stem of each forage species in a quadrat, the species, height class, and number of twigs of CAG browsed and unbrowsed were recorded (Shafer 1963). Height classes were seedling ($<1.3$ m height), sapling ($>1.3$ m height and $\leq 2.5$ cm dbh), and tree ($>1.3$ m height and $>2.5$ cm dbh). Only twigs in the height range available to moose were counted (i.e., from ground or snow level to 2.5 m). CAG was defined as that portion of the twig from the terminal bud to the nearest bud-scale scar. A stem was defined as appearing unbranched at 30 cm above the ground. We did not observe substantial bark stripping (Miquelle and Van Ballenberghe 1989) or scent marking (Bowyer *et al.* 1994) of trees. Browsing by moose and snowshoe hares (*Lepus americanus*) was recorded separately; the latter was rare during our study ($<1\%$ of all browsing).

Biomass consumed by moose was calculated using diameter-mass regressions developed from twigs for each species (Table 1). Although exceptionally long twigs of CAG resulted in curvilinear regressions between diameter and dry weight of browse (Bowyer and Bowyer 1997), our twigs were comparatively short, and linear regressions provided the best fit for all species of forage. An average bite mass (g) for each species during each period of winter was calculated from diameter at points of browsing for a minimum of 50 freshly browsed twigs from each study site. Biomass consumed (kg/ha) for a species was the product of mean bite size and density of browsed

Table 1. Regression equations for predicting dry mass (g) of current annual growth from twig diameter (mm) for species of woody plants eaten by moose during winter, Kenai Mountains, Alaska, USA, 1988-1989.

| Plant Species | *n* | Regression Equation (y = weight, x = diameter) | $r^2$ | *P*-value |
|---|---|---|---|---|
| *Salix scouleriana* | 300 | y = -0.09 + 0.36x | 0.908 | 0.006 |
| *Betula papyrifera* | 250 | y = -0.07 + 0.27x | 0.893 | 0.021 |
| *Populus tremuloides* | 300 | y = -0.01 + 0.32x | 0.943 | 0.002 |
| *Populus trichocarpa* | 300 | y = -2.19 + 1.00x | 0.804 | 0.050 |

twigs.

Mean mass (g) of twigs for CAG was calculated for each species using diameters of 50 twigs as previously described for consumption of biomass. Twig counts for each species were combined with mean mass of twigs to estimate forage availability (kg/ha) by species, age of stand, and period of winter.

### Distance from Cover, Moose Density, and Snow Depth

To assess the effects of distance from cover on forage use in the 7-10 year-old stands, random quadrats were placed at distances of 0-20, and 40-60 m from the edge of the mature forest. Height of forage in the 7-10-year stands ranged from 1.0 to 1.5 m and provided little concealment cover for moose; other age classes of stands were too densely vegetated to perform similar analyses.

Three random measurements of snow depth were recorded in each stand during each period of winter. These measurements allowed for comparisons between depth of snow and availability and use of forage by moose. An index to relative density of moose in each stand was provided by track counts. A line transect of 150 m was located randomly and used to count tracks in each replicate stand. All tracks crossing the transect were counted. Moose tracks were sampled in early and mid-winter in each replicate stand for each age class. No counts were made in late winter because snow was absent on some areas of the transects.

### Forage Quality

Samples of twigs (CAG) in the range of sizes consumed by moose were collected for each species to determine nutritional quality. Moose forage selectively on twigs of larger size even on the same plant (Bowyer and Bowyer 1997), and our analysis excludes twigs that were too small to have been selected as forage. The entire CAG of each twig was analyzed for nutrient content because moose populations on the Kenai Peninsula are not held at low density by predation as are some populations in interior Alaska (Gasaway *et al.* 1992). Consequently, more CAG of twigs was consumed on the peninsula than in areas with lower densities of moose. Samples were collected in mid-winter 1989 in all replicate stands in the 3 seral stages. Each sample of forage was a composite of 1 twig collected from 15-20 individual plants per species. Twigs were collected only from saplings because this growth form was available on all quadrats and sampling only saplings avoided a bias in comparing different growth forms across stands. Samples of twigs were oven dried at 60° C for 24 h. Detergent analysis (Goering and Van Soest 1970) was used to determine structural composition of plant cells (% dry weight of neutral-detergent fiber—NDF; acid-detergent fiber—ADF; cellulose; hemicellulose; and lignin—L). Crude protein (nitrogen [N] x 6.25) was determined by semi-microkjeldahl techniques (AOAC 1965). Calcium (Ca) content was determined by atomic absorption spectrophotometry, potassium (K) by atomic flame-emission spectrophotometry, and phosphorus (P) by the ammonium molybdate procedure of Gommorri (1942).

*In vitro* dry matter digestibility (IVDMD; Tilley and Terry 1963) was determined in duplicate (2 separate analyses of combined samples from multiple plants) for each forage species and plot in each age class of stand during mid-winter. Fresh rumen inoculum for the *in vitro* digestion trials was obtained from a road-killed moose in winter. IVDMD and nutrient analyses were performed under contract by the University of Alaska Agricultural Research Station, Palmer, Alaska. Predicted dry matter digestibility was calculated using the equation of Van Soest (1965).

### Diet Composition

Data on diet composition were obtained by microhistological analysis of fecal samples. During early, mid-, and late winter, fresh groups of fecal pellets were collected at each study site. In each period of winter, a fecal sample was collected from each stand. Each sample was a composite collection of 2 fecal pellets from each of 6 groups. Fresh fecal pellets were recognizable by their odor and mucous sheen. Analyses were performed under contract by Washington State University, Pullman, Washington. Fifty microscopic fields were examined per slide (2 slides per replicate stand) to determine relative density of identifiable plant fragments occurring in feces of moose. Results were summarized by plant genera. Data from microhistological analysis were corrected for digestibility as recommended by Fitzgerald and Waddington (1979). Moose have smaller home ranges in winter than at other times of year (Hundertmark 1998) and use traditional, localized areas during that season (Miquelle *et al.* 1992). Although moose undoubtedly obtained some foods from other areas than the plots we sampled, we believe the diets estimated from fecal analysis provide an index to foods obtained in stands of different age.

### Statistical Analyses

Differences in availability, use, height classes of browse, and nutrient content of plant species by age of stand and period of winter were compared using univariate analysis of variance (ANOVA). Statistically significant differences ($P < 0.05$) disclosed by analysis of variance were partitioned by Scheffe's multiple comparisons. Assumptions of univariate normality and homegeneity of variances were met in these analyses (Neter *et al.* 1985). Relationships between browse availability and snow depth were explored using snow depth as a covariate in an analysis of covariance (ANCOVA).

Differences in relative use and availability (i.e., selection) of forage species by age of stand and period of winter were compared using multivariate analysis of variance (MANOVA), following the methods of Bowyer *et al.* (1995) and Nicholson *et al.* (1997), with stand age and period as main effects (Morrison 1976). A species was significantly avoided if relative use was less than relative availability and selected if use exceeded availability at $P \leq 0.05$ (Bonferroni $t$-test). Relative use and availability also were compared using rank ANOVA (Conover and Iman 1981), based on mass of forage available and consumed (kg/ha). Relationships between moose abundance and foraging patterns on species of browse were explored using track counts as a covariate in MANCOVA. Because of heterogeneous variances, data for relative use and availability were arcsine transformed prior to analysis (Zar 1984). Bonferroni's $t$-test was used for multiple comparisons. Preference or selection indices have been widely used to determine the likelihood that an animal will select a particular food (Heady and Van Dyne 1965, Wetzel *et al.* 1975, and many others). Often such indices are calculated as if forage availability and use were measured without error. For instance, a rare forage that was seldom eaten could have an extremely high preference index (i.e., use/availability). This approach is limited because it uses a simple ratio that does not consider sampling error. Although we presented such ratios to show the direction of selection (i.e., preference vs. avoidance), our analyses were based on MANOVAs, which compared relative use and availability in a manner that retained the variances associated with those variables. Importance was portrayed as use times availability rescaled to 100% (Bowyer and Bleich 1984).

Relationships between diameters and weights of browsed twigs were determined by linear regression (Zar 1984). Stepwise multiple regression was used to test for relationships between nutrients and relative use of browse species. Data were pooled by replicate stands for each species ($n$ = 32) for this analysis. Nutrients that were highly intercorrelated (absolute value of $r \geq 0.60$) were omitted from the stepwise analysis to avoid problems associated with multicollinearity (Neter *et al.* 1985). All analyses were performed using an SPSS/PC+ statistical package.

## RESULTS

### Availability of Browse

Based on ANOVA, age classes of stands differed in availability (twigs/m$^2$) of forage ($F = 26.7$; 2,7 df; $P < 0.001$; Fig. 2). The 20-30 year-old stands provided the most forage for moose in all periods of winter. Availability of forage was greater in the 20-30 year stands than in the 7-10 year stands ($P = 0.05$), and availability in 7-10 year-old stands was greater than in the 70-80 year-old stands when periods of winter were pooled ($P < 0.0001$).

With species of forage pooled, availability of browse (twigs/m$^2$) differed among periods of winter for all stands ($F = 4.2$; 2,7 df; $P = 0.02$; Fig. 2). Availability of browse declined from early to mid-winter (Scheffe's multiple comparisons; $P < 0.001$) and increased from mid-to late winter ($P = 0.015$). Similarly, the density of unbrowsed twigs (kg/ha) for each age class and period of winter was analyzed by ANOVA to determine whether availability of browse varied with use by moose during winter. Density of unbrowsed twigs declined ($P < 0.001$) from early to mid-winter and increased ($P = 0.01$) from mid- to late winter. Relative proportions of unbrowsed twigs available for each species within age classes, however, did not change during winter ($P > 0.15$). Depth of snow (Fig. 3) had a significant effect on abundance of forage (twigs/

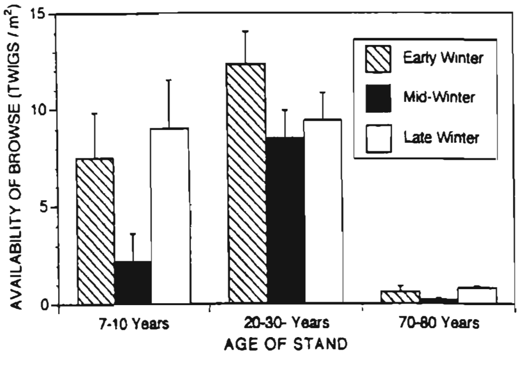

Fig. 2. Availability of twigs of current annual growth ($\bar{X}$+ SE) of browse species for Alaskan moose by age of stand and period of winter, Kenai Mountains, Alaska, USA, 1989-1990. Note that 20-30 year-old stands provided the most forage for moose.

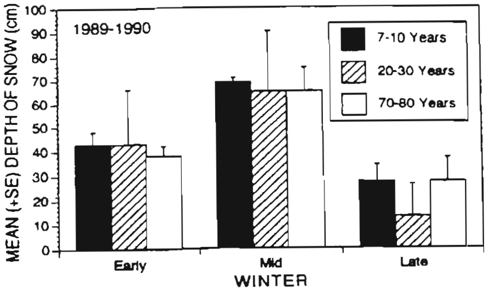

Fig. 3. Depth of snow on sampling plots ($n = 8$) by period of winter and age of stand, Kenai Mountains, Alaska, USA, 1989-1990. Note the marked reduction in snow depth in late winter.

m²) when considered as a covariate in the analysis ($P = 0.004$). Melting snows during late winter resulted in an increase in browse availability from mid- to late winter (Fig. 3).

Significant differences determined by MANOVA occurred in the availability of individual browse species within stands for all periods of winter ($F = 8.5$; 3,7 df; $P < 0.001$). In the 20-30 year-old stands, Kenai birch was the most abundant species of browse followed by scouler willow, aspen, and black cottonwood (Table 2). No difference ($P > 0.05$) occurred in availability of Kenai birch, scouler willow, aspen, and black cottonwood in the 7-10 year-old stands. In the 70-80 year-old stands, scouler willow was the most abundant species, followed by Kenai birch, black cottonwood, and aspen. MANOVA indicated that relative proportions of twigs available for each species within age classes did not change during winter ($F = 0.9$; 3,7 df; $P > 0.4$). Most twigs available to moose were from seedlings in all age classes of stands, but saplings also were plentiful, especially in stands of 20-30 years-of-age (Fig. 4).

Table 2. Availability of current annual growth (twigs/m²) to moose for 4 species of browse by age of stand and period of winter, Kenai Mountains, Alaska, USA, 1989-1990. Stands ($n = 8$) are sampling units for summary statistics.

| | Age of Stand | | | | | |
|---|---|---|---|---|---|---|
| | 7-10 years | | 20-30 years | | 70-80 years | |
| Period and Species | $\bar{X}$ | SE | $\bar{X}$ | SE | $\bar{X}$ | SE |
| Early Winter | | | | | | |
| *Salix scouleriana* | 1.7 | 0.43 | 4.7 | 2.64 | 0.5 | 0.14 |
| *Betula papyrifera* | 4.1 | 1.49 | 7.1 | 2.53 | 0.1 | 0.07 |
| *Populus tremuloides* | 3.1 | 1.61 | 0.3 | 0.07 | <0.1 | 0.02 |
| *Populus trichocarpa* | 0.8 | 0.46 | 0.3 | 0.26 | <0.1 | 0.02 |
| Mid-Winter | | | | | | |
| *Salix scouleriana* | 0.4 | 0.10 | 4.4 | 1.96 | <0.1 | 0.02 |
| *Betula papyrifera* | 0.5 | 0.13 | <0.1 | <0.01 | <0.1 | <0.01 |
| *Populus tremuloides* | 0.5 | 0.23 | 0.1 | 0.07 | <0.1 | <0.01 |
| *Populus trichocarpa* | 0.8 | 0.37 | 3.9 | 0.82 | 0.3 | 0.16 |
| Late Winter | | | | | | |
| *Salix scouleriana* | 4.2 | 1.51 | 5.2 | 0.69 | <0.1 | 0.01 |
| *Betula papyrifera* | 0.9 | 0.28 | 0.2 | 0.09 | <0.1 | 0.01 |
| *Populus tremuloides* | 1.1 | 0.38 | 0.3 | 0.31 | <0.1 | 0.01 |
| *Populus trichocarpa* | 2.8 | 0.83 | 3.5 | 1.81 | 0.4 | 0.12 |

Table 3. Acid-detergent fiber (ADF), neutral-detergent fiber (NDF) cellulose, and hemicellulose for woody plants browsed by moose by age of stand, Kenai Mountains, Alaska, USA, during mid-winter, 1990. Stands ($n = 8$) are sampling units for summary statistics.

| | Dry Matter (%) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Age of Stand | ADF | | NDF | | Cellulose | | Hemicellulose | |
| and Species | $\bar{X}$ | SE | $\bar{X}$ | SE | $\bar{X}$ | SE | $\bar{X}$ | SE |
| 7-10 Years Old | | | | | | | | |
| *Salix scouleriana* | 39.3 | 1.6 | 50.3 | 1.6 | 26.9 | 3.1 | 30.1 | 1.2 |
| *Betula papyrifera* | 44.5 | 3.2 | 58.7 | 3.0 | 23.6 | 1.9 | 30.8 | 1.0 |
| *Populus tremuloides* | 37.4 | 1.1 | 47.8 | 1.4 | 23.0 | 2.2 | 33.4 | 1.4 |
| *Populus trichocarpa* | 38.6 | 2.3 | 43.9 | 2.3 | 16.6 | 2.8 | 24.2 | 2.0 |
| 20-30 Years Old | | | | | | | | |
| *Salix scouleriana* | 42.8 | 1.6 | 51.8 | 3.4 | 19.0 | 1.4 | 20.9 | 1.0 |
| *Betula papyrifera* | 44.2 | 2.2 | 55.52 | 2.2 | 18.3 | 3.7 | 23.8 | 3.6 |
| *Populus tremuloides* | 35.2 | 2.7 | 45.3 | 3.1 | 16.3 | 0.8 | 27.9 | 1.6 |
| *Populus trichocarpa* | 34.9 | 1.9 | 43.3 | 3.1 | 14.2 | 0.7 | 18.8 | 0.9 |
| 70-80 Years Old | | | | | | | | |
| *Salix scouleriana* | 45.3 | 1.2 | 57.3 | 1.8 | 22.2 | 0.2 | 24.2 | 0.9 |
| *Betula papyrifera* | 45.5 | 2.3 | 54.9 | 0.9 | 20.9 | 3.2 | 26.2 | 2.0 |
| *Populus tremuloides* | 36.6 | 1.5 | 50.5 | 0.6 | 22.0 | 0.2 | 28.9 | 1.1 |
| *Populus trichocarpa* | 32.9 | 2.7 | 39.9 | 2.8 | 15.0 | 1.0 | 21.5 | 0.5 |

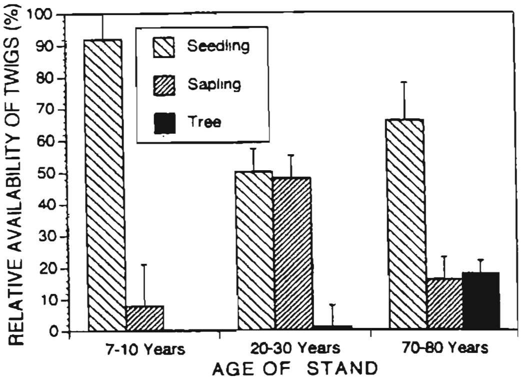

Fig. 4. Relative availability ($\bar{X}$ + SE) of twigs of current annual growth for species of browse eaten by Alaskan moose by age of stand and growth form of plant, Kenai Mountains, Alaska, USA, winter 1989-1990. Note that seedlings were relatively more available to moose in all age classes of stands.

## Quality of Browse

Multivariate ANOVA indicated age classes of stands differed in overall nutritional measures for species of browse (forage quality and minerals) in mid-winter ($F = 15.4$; 2,10 df; $P < 0.001$; Figs. 5, 6, Table 3). Forage in 7-10 year-old stands was significantly higher in cellulose, hemicellulose, and lignin than other age classes of stands ($P < 0.05$). Individual species of browse differed in overall measures of nutrients when all stands were pooled for this analysis ($F = 9.59$; 3,10 df; $P = 0.006$). Multiple comparisons indicated that black cottonwood ranked highest ($P < 0.05$) in digestibility, whereas aspen, Kenai birch, and scouler willow did not differ statistically from one another (Fig. 5).

Analysis of variance indicated differences in the protein content of browse species with Kenai birch exhibiting the greatest levels of crude protein ($F = 10.1$; 7 df; $P < 0.05$; Fig. 5). No significant difference occurred among species in ADF, NDF, cellulose, or hemicellulose content of forage ($F = 0.2$; 3,7 df; $P = 0.9$; Table 3). Black cottonwood, however, was significantly lower in lignin content than other species ($F = 12.9$; 3,7 df; $P < 0.05$; Fig. 5). Kenai birch was lower in calcium content than scouler willow, aspen, or black cottonwood ($F = 14.2$, 3,7 df; $P < 0.05$; Fig. 6). Other differences in mineral content of forage were not significant ($P > 0.1$).

The relationship between measured IVDMD and predicted dry-matter digestibility for forage species indicated that measured IVDMD of forages were depressed below that predicted from components of proximate analyses. IVDMD for black cottonwood and aspen showed the smallest departures from predicted dry-matter digestibilities, whereas scouler willow and Kenai birch showed the largest departures from the calculated values (Fig. 7). Departures of predicted digestibilities from measured IVDMD for each species ($\bar{X}$ + SD) were: scouler willow (23.1 ± 10.2%); paper birch (23.7 ± 10.2%); aspen (16.6 ± 10.8%); and black cottonwood (16.4 ± 5.3%).

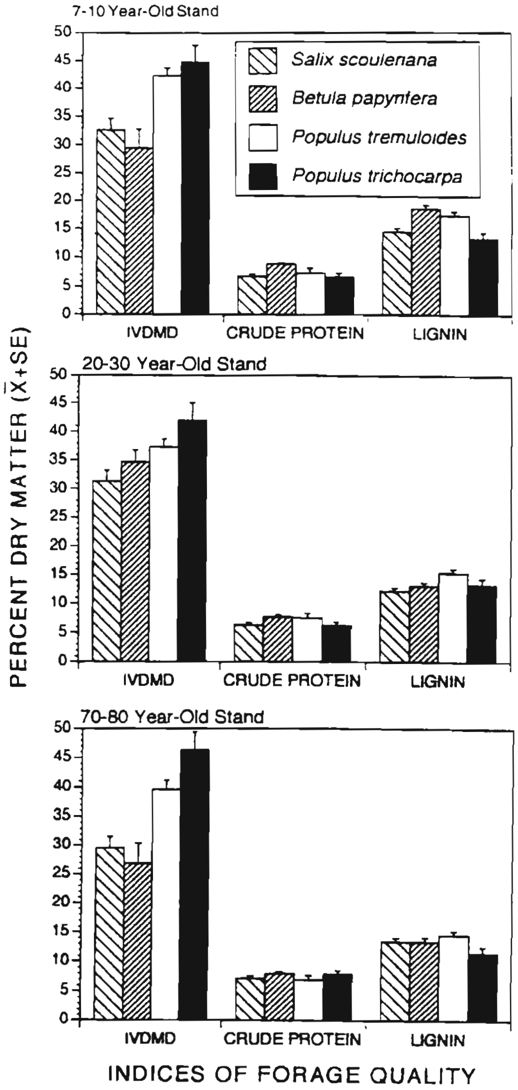

Fig. 5. Indices of forage quality for browse species eaten by Alaskan moose by age of stand, Kenai Mountains, Alaska, USA, mid-winter 1990.

**Use of Browse and Abundance of Moose**

Analysis of variance indicated that age classes of stands differed in forage use (twigs browsed/m$^2$) for all periods of winter ($F = 36.5$; 2,7 df; $P < 0.0001$; Fig. 8). Scheffe's multiple comparison indicated that more forage was browsed ($P < 0.001$) in 20-30 year stands than in 7-10 year stands; use of forage in 7-10 year stands was greater ($P < 0.001$) than in 70-80 year stands (Fig. 8). Diameter at point of browsing varied little across species or periods of winter (Table 4).

Numbers of moose tracks counted differed between periods of winter when stands were pooled ($F = 13.0$; 2,7 df; $P = 0.002$; Fig. 9). In early winter, numbers of moose tracks were highest in the early successional habitats, but by mid-winter, numbers of moose were relatively constant for all age classes of stands as indicated by multiple comparisons. When periods of winter were pooled, counts of moose tracks were higher ($P = 0.05$) in 20-30 year stands than in 70-80 year stands. No difference ($P >$

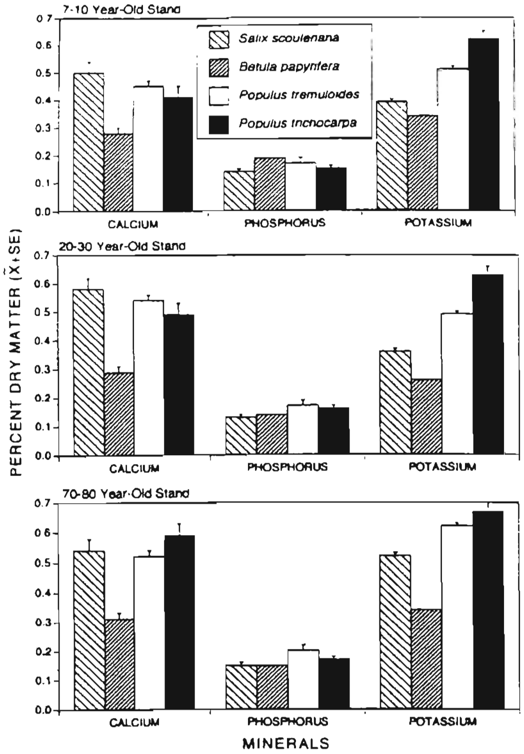

Fig. 6. Mineral composition of browse species eaten by Alaskan moose by age of stand, Kenai Mountains, Alaska, USA, mid-winter 1990.

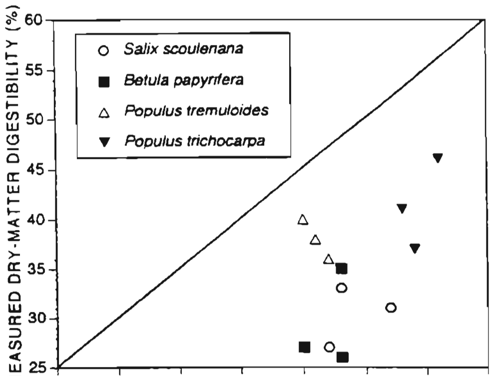

Fig. 7. Relationship between measured dry-matter digestibility (IVDMD) and predicted digestibility for woody plants eaten by Alaskan moose, Kenai Mountains, Alaska, USA, mid-winter, 1990. Predicted dry-matter digestibility (PDMD) was calculated according to Van Soest (1965): PDMD = 0.98 (100 - NDF) + NDF (1.473 - 0.789 $\log_{10}$ [(L/ADF)100]) - 12.9.

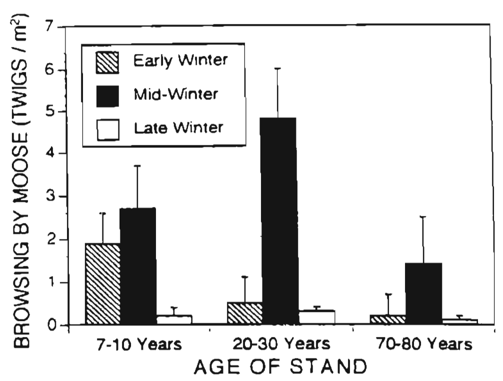

Fig. 8. Use of twigs of current annual growth ($\overline{X}$ + SE) by Alaskan moose by age of stand and period of winter, Kenai Mountains, Alaska, USA, 1989-1990. Note the heavy use of twigs in 20-30 year-old stands during mid winter.

0.7) existed in tracks between the 20-30 and 7-10 year stands, or between 7-10 and 70-80 year stands ($P > 0.4$).

Differences in use of browse species among age classes of stands were still detected when the number of moose tracks, an index to moose density (Fig. 9), was included as a covariate in the model ($P < 0.001$). Forage use did not differ among periods of winter with all age classes of stands pooled ($F = 1.15$; 2,7 df; $P > 0.05$).

There were significant differences in the use (browsed twigs/m$^2$) of individual browse species as determined by ANOVA within stands for all periods of winter ($F = 16.6$; 3,7 df; $P < 0.0001$; Table 5). In 20-30 year-old stands, scouler willow and Kenai birch were used more than black cottonwood and aspen (multiple comparisons; $P < 0.05$). In the 7-10 year-old stands, scouler willow, Kenai birch, and aspen were used more than black cottonwood ($P < 0.05$). In the 70-80 year-old stands, scouler willow was used most often, followed by black cottonwood, aspen, and Kenai birch. Relative proportions of twigs browsed for each species within age classes did not change during winter ($F = 0.3$; 3,7 df; $P = 0.9$). Use and availability of twigs was compared for

Table 4. Diameter at point of browsing (mm) for woody plants eaten by moose by age of stand and period of winter, Kenai Mountains, Alaska, USA, 1989-1990. Stands ($n = 8$) are sampling units for summary statistics.

| | Age of Stand | | | | | |
|---|---|---|---|---|---|---|
| | 7-10 years | | 20-30 years | | 70-80 years | |
| Period and Species | $\bar{X}$ | SE | $\bar{X}$ | SE | $\bar{X}$ | SE |
| Early Winter | | | | | | |
| *Salix scouleriana* | 3.2 | 0.4 | 3.0 | 0.1 | 3.1 | 0.1 |
| *Betula papyrifera* | 2.4 | 0.1 | 2.6 | 0.2 | na[1] | na |
| *Populus tremuloides* | 2.8 | 0.3 | 2.5 | 0.2 | na | na |
| *Populus trichocarpa* | 3.2 | 0.4 | 3.7 | 0.1 | 3.3 | 0.1 |
| Mid-Winter | | | | | | |
| *Salix scouleriana* | 3.0 | 0.2 | 3.4 | 0.6 | 3.2 | 0.3 |
| *Betula papyrifera* | 2.3 | 0.1 | 2.1 | 0.2 | 1.8 | 0.1 |
| *Populus tremuloides* | 3.0 | 0.2 | 2.5 | 0.2 | 2.9 | 0.5 |
| *Populus trichocarpa* | 3.7 | 0.4 | 3.4 | 0.1 | 2.2 | 0.4 |
| Late Winter | | | | | | |
| *Salix scouleriana* | 3.0 | 0.4 | 3.0 | 0.1 | 3.8 | 0.1 |
| *Betula papyrifera* | 2.4 | 0.4 | 2.3 | 0.1 | 2.0 | 0.1 |
| *Populus tremuloides* | 2.8 | 0.1 | 2.8 | 0.1 | 3.6 | 0.2 |
| *Populus trichocarpa* | 3.3 | 0.2 | 4.0 | 0.3 | 3.6 | 0.4 |

[1] na = not available on subplots

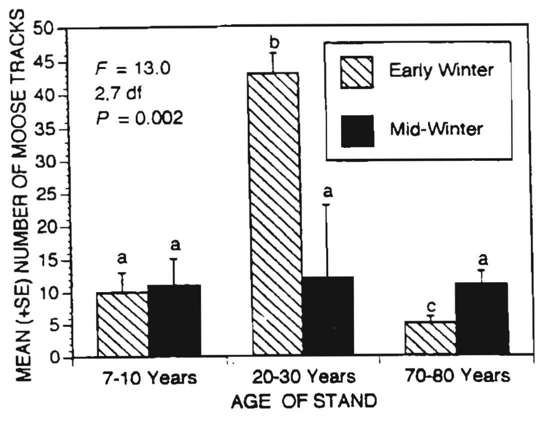

Fig. 9. Number of tracks of Alaskan moose crossing transects by age of stand and period of winter, Kenai Mountains, Alaska, USA, 1989-1990. Different letters above error bars indicate significant ($P \leq 0.05$) differences.

the different height classes of browse (i.e., seedling, sapling, and tree; Fig. 4). Use was not different from availability for height classes when all periods of winter and stands were pooled ($F = 0.5$; 3,7 df; $P = 0.6$).

Stepwise multiple regression was used to determine if percent use of a browse species was related to its availability or nutrient content. In this analysis, percent use was the dependent variable, the independent variables were availability (twigs/m$^2$), IVDMD, the difference between IVDMD and predicted digestibility, protein, NDF, and cellulose. The analysis indicated that percent use for a browse species was not related significantly ($P > 0.05$) to any of the independent variables. Percent use was most closely correlated with availability ($r^2 = 0.39, n = 32$), but this relationship was not significant ($P > 0.10$).

Table 5. Summary statistics for woody plants browsed by moose ($\bar{X}$ ± SE twigs browsed/$m^2$ and kg/ha) by age of stand and period of winter, Kenai Mountains, Alaska, USA, 1989-1990. Stands ($n = 8$) are sampling units for summary statistics.

| | Age of Stand | | | | | |
|---|---|---|---|---|---|---|
| | 7-10 years | | 20-30 years | | 70-80 years | |
| Period and Species | Twigs/$m^2$ | kg/ha | Twigs/$m^2$ | kg/ha | Twigs/$m^2$ | kg/ha |
| Early Winter | | | | | | |
| *Salix scouleriana* | 0.20±0.10 | 2.4 | 2.48±1.62 | 27.8 | 0.01±0.01 | <0.1 |
| *Betula papyrifera* | 0.15±0.05 | 1.0 | 0.94±0.45 | 7.2 | na[1] | — |
| *Populus tremuloides* | 0.00±0.00 | 0.0 | 0.07±0.05 | 0.8 | na | — |
| *Populus trichocarpa* | 0.02±0.00 | <0.1 | 0.03±0.03 | 0.4 | na | — |
| Mid-Winter | | | | | | |
| *Salix scouleriana* | 0.33±0.13 | 3.7 | 2.86±0.71 | 35.8 | 0.21±0.04 | 1.4 |
| *Betula papyrifera* | 0.16±0.06 | 1.1 | 1.61±0.31 | 10.1 | na | — |
| *Populus tremuloides* | 0.11±0.04 | 1.1 | 0.01±0.00 | 0.1 | na | — |
| *Populus trichocarpa* | 0.02±0.01 | 0.3 | 0.39±0.39 | 4.9 | 0.02±0.02 | 0.2 |
| Late Winter | | | | | | |
| *Salix scouleriana* | 0.89±0.46 | 10.0 | 2.71±1.73 | 30.4 | 0.08±0.10 | 1.1 |
| *Betula papyrifera* | 0.61±0.23 | 4.4 | 1.91±0.27 | 13.2 | na | — |
| *Populus tremuloides* | 0.32±0.11 | 2.9 | 0.10±0.04 | 0.9 | 0.36±0.20 | 0.1 |
| *Populus trichocarpa* | 0.10±0.04 | 1.2 | 0.02±0.02 | 0.3 | na | — |

[1] na < 0.01 twigs/$m^2$

Results from microhistological analysis of moose fecal pellets indicated that forage consumed by moose consisted of woody deciduous browse in all age classes of stands during all periods of winter (Fig. 10). When corrected for digestibility, Kenai birch and scouler willow composed 83% of all plant fragments identified in moose feces for all age classes of stands. Percent of woody plant fragments identified in decreasing order were (average for all stands and periods): Kenai birch (45%), *Salix* spp. (38%), alder (9%), *Populus* spp. (black cottonwood and aspen) (5%), and *Vaccinium* (2%). Nonbrowse forages composed only 4% of identified plant fragments for all stand ages and periods combined. In general, results confirmed our analysis from twig counts. Willows and Kenai birch dominated diets in winter; white spruce was not eaten by moose. Alder, which moose consumed (Fig. 10), did not occur on our sampling plots but on hillsides above them, and *Vaccinium* was covered by snow when we sampled.

## Diet Selection

Relative use of browse species was compared with relative availability to determine diet selection using twig-count data (Fig. 11). Black cottonwood was avoided ($t = 11.60$, 35 df, $P = 0.002$) scouler willow, Kenai birch, and aspen were browsed in proportion to availability ($P > 0.09$) when data from all age classes of stands and periods of winter were pooled (Fig. 11). These results suggest that browsing of scouler willow, Kenai birch, and aspen was nearly, but not significantly different, from availability. Figure 11 indicates that use of scouler willow was greater than its avail-

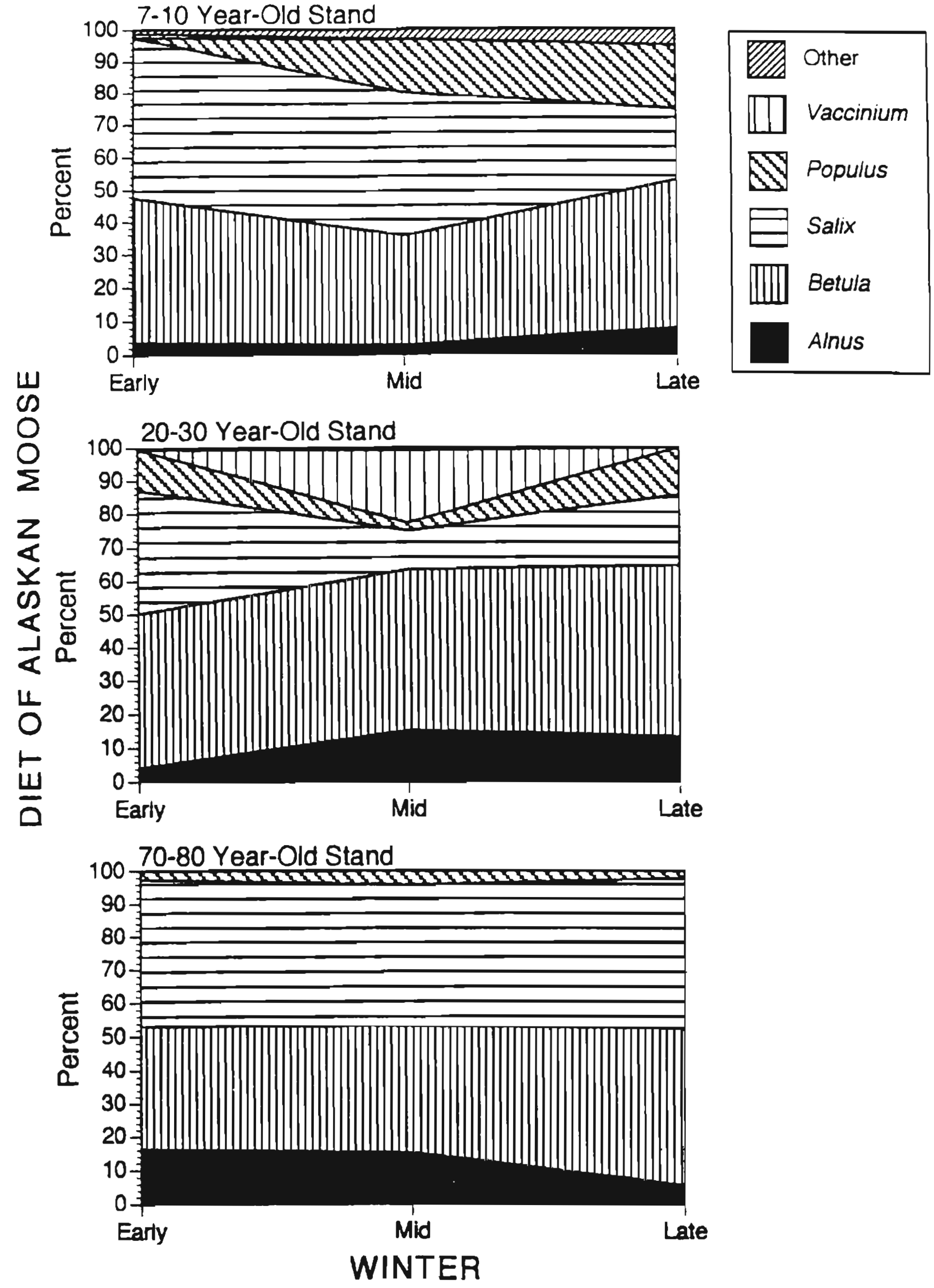

Fig. 10. Diet of Alaskan moose estimated from microhistological analysis of feces by period of winter and age of stand, Kenai Mountains, Alaska, USA, 1989-1990. Data from microhistological analysis was corrected by digestibility of each forage to calculate diet.

ability for all stands and periods of winter; however, the difference was not significant ($P > 0.12$) due to high variability in these data. Kenai birch was marginally nonsignificant ($t = 1.30$, 35 df, $P > 0.09$) in use being less than availability when stands and periods were pooled.

Selection for individual species as de-

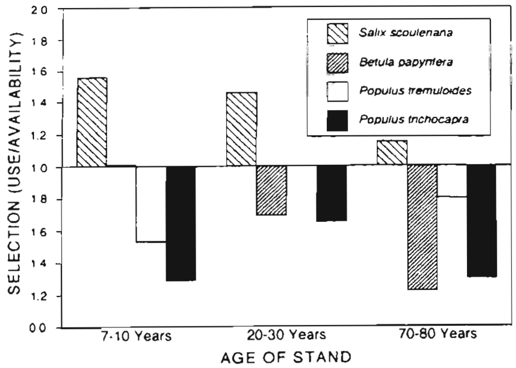

Fig. 11. Selection (use/availability) of browse by Alaskan moose in differing age classes of stands during winter, Kenai Mountains, Alaska, USA, 1989-1990. Species with values >1 are selected, whereas species with values <1 are avoided.

termined by MANOVA varied by age class of stand ($F = 3.4$; 3,7 df; $P < 0.04$). Use of black cottonwood was significantly different from availability in the 7-10 year ($t = 3.37$, 16 df, $P < 0.004$) and 70-80 year ($t = 2.48$, 16 df, $P < 0.05$) age classes, but not in the 20-30 year age class ($t = 0.60$, 16 df, $P > 0.6$). Period of winter had no effect on diet selection ($F = 1.9$; 3,7 df; $P = 0.09$). There was no significant interaction between diet selection, age class of stand, and period of winter ($F = 1.10$; 4,6 df; $P = 0.35$). The importance of willow to moose, however, increased with the age of the stand (Fig. 12).

Analysis of relative use versus relative availability using MANOVA on ranked data for mass of twigs (kg/ha) (Table 5) showed a similar pattern. Black cottonwood was avoided ($F = 4.8$; 3,7 df; $P = 0.004$), scouler willow, Kenai birch, and aspen were browsed in proportion to availability when all periods of winter and stands were pooled. Black cottonwood was browsed in proportion to availability in the 20-30 year-old stands ($t = 0.66$, 5 df, $P = 0.5$), and less than availability in the 7-10 ($t = 4.27$, 16 df, $P = 0.001$) and 70-80 ($t = 4.0$, 16 df, $P = 0.0001$) year-old stands.

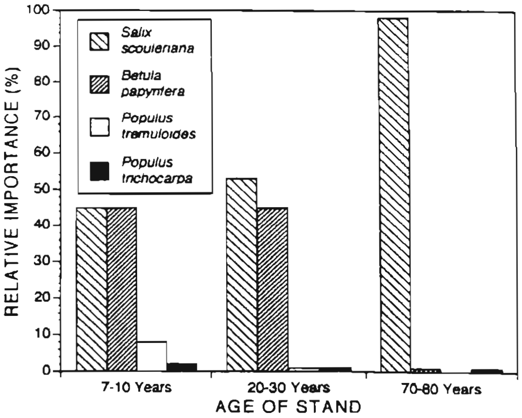

Fig. 12. Relative importance (use x availability) of woody plants to Alaskan moose by age of stand during winter, Kenai Mountains, Alaska, USA, 1989-1990.

Stepwise multiple regression was used to determine if relative availability and nutrient variables could be used to predict selection (use/availability). In this analysis, selection was the dependent variable and the independent variables were relative availability, IVDMD, the difference between observed and predicted DMD, protein, cellulose, and NDF. Results indicated that relative availability was highly correlated with selection of browse species ($r^2 = 0.89$, $n = 32$). No other variables, however, entered ($P > 0.05$) the multiple regression. Caution should be used in interpreting this outcome, because availability is used to calculate selection (e.g., use/availability).

Multivariate ANOVA indicated that distance from cover in the 7-10 year-old stands had a significant effect on use of cottonwood ($F = 5.0$; 1,24 df; $P = 0.034$). Cottonwood was utilized in proportion to availability at a distance of 40-60 m from the forest edge, and less than availability at 0-20 m from the forest edge (Fig. 13). Use was proportional to availability at these distances from cover for willow, birch, and aspen. Availability of browse at 0-20 m from cover, however, was not different than at 40-60 m ($P = 0.6$).

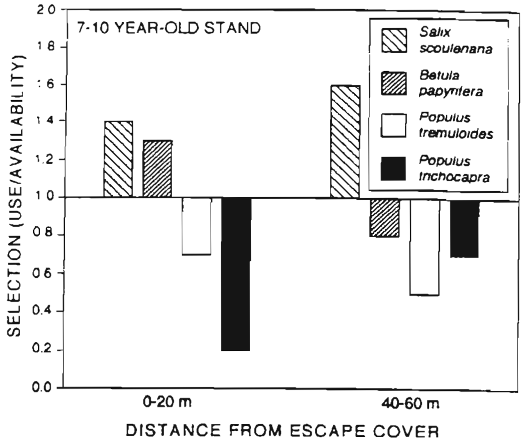

Fig. 13. Effects of distance from cover on the selection (use/available) of browse by Alaskan moose on 7-10 year-old stands during winter, Kenai Mountains, Alaska, USA, 1989-1990. Values >1 indicate selection, whereas values <1 show avoidance.

## DISCUSSION

### Fire, Forest Succession, and Moose-Habitat Relationships

We documented that, within the age classes we sampled, forest succession following fire provided the most abundant forage for moose 20-30 years postburn; early successional stands possessed more browse than those in late succession (Table 2, Fig. 2). These outcomes were not unexpected—effects of fire on vegetation composition and structure have been known for many years (Cowan *et al.* 1950, Dewitt and Derby 1955). Moreover, fire and subsequent patterns of forest succession have been linked with productivity of moose populations on the Kenai Peninsula (Spencer and Hakala 1964, Oldemeyer *et al.* 1977, Loranger *et al.* 1991).

Care should be taken, however, in extrapolating lessons learned about forest succession and populations of moose on the Kenai Peninsula to other regions of Alaska where ecological conditions differ. Clearly, fire holds the potential to affect the forage of moose in interior Alaska (Wolff 1978, MacCracken and Viereck 1990). Nevertheless, where fires burn vast areas of open tundra or black spruce (*Picea mariana*) forest without an understory of willow, increases in moose populations would be unlikely because such areas traditionally support few moose. Jandt (1992) reported that fire had little effect on population density of moose in interior Alaska, although other aspects of habitat were influential in predicting density. Likewise, Gasaway *et al.* (1989) noted that burns in the interior did not increase productivity of moose.

Differences in the response of moose to fire on the Kenai Peninsula and in interior Alaska may relate to several factors. Climatic extremes are most pronounced in interior Alaska, but severe weather alone as an explanation for differences between areas is unsatisfying because productivity (twinning rate) of moose in the interior can be high (55%) even following severe winters (Bowyer *et al.* 1998).

The most obvious difference, however, between moose on the Kenai Peninsula and in interior Alaska relates to population density; many populations of moose in the interior are held at low density by extremely heavy predation and experience particularly high mortality of young (Gasaway *et al.* 1992, Van Ballenberghe and Ballard 1994, Bowyer *et al.* 1998). Moose on the Kenai Peninsula have responded favorably to fire and subsequent successional changes in forage because they are nearer to carrying capacity (*K*) of the habitat than moose in the interior. Indeed, habitat manipulation by fire or other means to enhance moose populations held at low density by predation are unlikely to succeed because moose are not food limited in such systems, and the production of more browse will have little effect on their populations.

Likewise, it is tempting to categorize the successional stages of forest we sampled with respect to their value to moose based on the density or biomass of forage available (Table 5, Fig. 4). For populations of moose on the Kenai Peninsula, this approach may be reasonable. Our crude index to population density corresponded with the availability of browse, particularly during early winter (Fig. 9). Moreover, Loranger *et al.* (1991) reported a linear, inverse relationship between moose density and years postfire on the Kenai Peninsula. Nonetheless, a low-density population (i.e., not food limited) might have done equally well in all three successional stages we sampled (i.e., willows became relatively more available and important to moose in 70-80 year-old stands). Thus moose density plays a critical role in the interpretation of habitat quality relative to productivity of moose populations.

### Diet Selection

Nudds (1980) suggested that northern cervids should adopt a generalist foraging strategy during winter in response to low availability and quality of food. With such a strategy, the relative use of foods is approximately equal to their availability. He argued that energy acquisition should become the critical factor for survival, and optimization of the diet for other nutrients should be relaxed. Thus, according to this hypothesis, availability of browse species should predict use of these resources.

Relative abundance of food items best explained diet selection of moose in this study. Stepwise multiple regression showed that selection for a species was based largely on relative availability ($r^2 = 0.89$), rather than on measures of nutrients. This argument, however, is somewhat circular because availability is used to calculate selection. Moreover, the patterns of forage selection by moose in the Kenai Mountains suggest that there are important differences among the 4 species of browse we studied in their relative value to moose. Although moose selected much of their winter diet based primarily on availability, they avoided black cottonwood. In addition, Alaskan moose on the Kenai Peninsula (Fig. 10) or elsewhere in Alaska (Bowyer *et al.* 1997) do not consume white spruce, although they do eat white spruce and other conifers in eastern North America (Ludewig and Bowyer 1985, Renecker and Schwartz 1998). Thus, predictions of diet selection based on optimal foraging were not met.

Avoidance of a particular forage may be due to relatively low palatability (Longhurst *et al.* 1969) or the presence of toxic secondary compounds (Freeland and Janzen 1974, Bryant and Kuropat 1980, Bryant 1981, Bryant *et al.* 1983), which limit the amount of a species that may be consumed. Additionally, palatability of browse can be affected by local soil conditions or age of the stand (Longhurst *et al.* 1969, Short 1975).

Because of the relationship between forage digestibility, retention time in the rumen, and rate of intake (Owen-Smith 1982, Van Soest 1982), digestibility is likely to be an important factor in forage selection by ruminants. Persons *et al.* (1980) argued that reductions in IVDMD below the level expected from Van Soest (1965) predictions provided an index to the effects of plant secondary compounds on *in vitro* digestibility of forages. The bulk forages consumed by moose on the Kenai Peninsula fell well below expected values (Fig. 7), but the actual digestibility of black cottonwood was closer to that predicted than for either Kenai birch or scouler willow. Thus, browsing on black cottonwood may be deterred by mechanisms other than inhibition of digestion. Bryant *et al.* (1989) documented that Alaskan woody plants have evolved substantial chemical defenses that deter browsing by mammalian herbivores, some of which may operate by affecting the animal by pathways other than digestion. Moose may avoid plants that are too heavily defended. For instance, Alaskan moose did not eat white spruce (Fig. 10), which occurred on or near the stands we sampled, and avoid black cottonwod on most age-classes of stands.

If moose employed a nutrient-mixing strategy for selecting a winter diet, they should utilize more of a less-preferred plant in stands with an abundance of preferred forage. In this study, black cottonwood, a less-preferred species, was browsed in proportion to availability in stands with the most forage (i.e., the 20-30 year stands), but less than its availability in stands with less forage (i.e., the 7-10 and 70-80 year stands; Fig. 11). Even correcting for density of moose, the use of a plant with low preference was not significantly related to the abundance of surrounding forage; thus, we reject the nutrient-mixing hypothesis for moose on our study area.

Nudds (1980) argued that foraging by northern cervids during winter should most closely follow an energy-maximization strategy. Reduced food availability, quality, and digestibility, combined with the increased energetic costs of foraging during severe weather, should force animals to maximize caloric return per unit of energy expended. The necessity to maximize this benefit:cost ratio favors a generalist diet. Thus, moose should adopt a generalist feeding strategy, especially in stands with the least amount of available forage. With this strategy, use of food types should be approximately equal to availability regardless of stand age. The 70-80 year-old stands contained the least amount of forage, yet moose avoided black cottonwood in those stands. Again, a prediction from optimal foraging theory was not met.

Optimal foraging theory predicts that species should be added to the diet only if the advantages of eating it outweigh the disadvantages of not doing so. Our data indicate that moose avoided (use < availability) black cottonwood in 70-80 year-old stands even at the expense of reduced caloric intake. Consequently, our results are contrary to predictions of optimal foraging theory, and suggest that this hypothesis should be modified to accommodate the role of plant secondary compounds in determining diet selection by large herbivores in northern environments.

Our data do not provide a critical test of the satisfying hypothesis of Bunnell and Gillingham (1985). The depressed IVDMD of browse (Fig. 7) and the avoidance of black cottonwood in their diet suggests this pattern of feeding may occur. Further research is needed in this area.

Distance from cover in 7-10 year-old stands had a significant effect on diet selection by moose. Plant species in these young stands averaged about 1 m in height and, consequently, provided little concealment cover for moose. Moose in those stands were more exposed to predators (primarily wolves). Presence of predators has been suggested as an important factor influencing the foraging behavior and habitat use of their prey (Hirth 1977, Pyke *et al.* 1977, Edwards 1983, Berger 1991, Molvar and Bowyer 1994, Bowyer *et al.* 1997). When moose are more vulnerable to predation (Ballard and Van Ballenberghe 1998), a time-minimizing strategy of diet selection should be employed. With such a strategy, fitness is maximized when time spent feeding to gather a given energy requirement is minimized (Schoener 1971). Less-valued foods should not be passed by in the interest of time. By using a time-minimizing strategy, vulnerability to predators is minimized. Indeed, moose foraged less selectively as they moved farther away from concealment cover in seasons other than winter (Molvar and Bowyer 1994). Results of our study indicate that moose likely used a time-minimizing strategy when away from cover.

Moose at 40-60 m from cover utilized all species in proportion to their availability—including cottonwood, a less-palatable forage (Fig. 13). This outcome was consistent with a time-minimizing pattern of feeding. Moose at 0-20 m from cover, however, used most species in proportion to availability but avoided cottonwood. Thus, when assessing diet selection for large herbivores, behavior due to vulnerability to predation may influence foraging strategy and play an important role in the winter ecology of moose.

### Winter Ecology of Moose

Availability and quality of forage are critical factors in the winter ecology of moose (Schwartz *et al.* 1984, 1988). The forage obtained by moose (Figs. 5, 6, 8) is a function of the age of the stand (Fig. 4), the density of moose (Fig. 9), and the depth of snow (Fig. 3), which can cover forage and affect the energy balance of moose by impeding movements. In addition, the foraging activities of large herbivores affects the quality of diet obtained as winter progresses (Hodgman and Bowyer 1986), as well as the availability of browse. Depth of snow also can force moose to use less-preferred habitats with poorer forage resources (Hundertmark *et al.* 1990). Too often, forage availability and use by herbivores are measured at the end of winter. This provides insights into the effects of moose on their forage, but not the effects (or value) of forage to moose.

Likewise, the quality of forage should affect diet selection, but we were unable to correlate use of forage by moose with any measure of quality we collected. Plant secondary chemistry is no doubt involved (moose avoided black cottonwood and did not forage on white spruce), but understanding the mechanisms involved requires further study. Our results indicate that a simple summation of browse availability per hectare (even when controlled for its variation through winter) is inappropriate. Moose exhibited selectivity in their winter diets, and some knowledge of quality is necessary to estimate *K* (i.e., abundance x quality). Likewise, distance to cover influenced diet selection by moose (Fig. 13) and needs to be considered in estimating *K* or in determining the size of habitat patches of value to moose. Moreover, these potential shortcomings of nutritional-based models for *K* point out the need to obtain measures of physical condition and reproduction in moose (Schwartz and Hundertmark 1993) to accompany data on forage. One important aspect of the winter ecology of moose we cannot address is the differential use of space and habitat by the sexes; we do not know which sex used the plots we sampled. Sexual segregation is common among polygynous ungulates (Bowyer 1984; Bleich *et al.* 1997). For moose, the spatial separation of the sexes in winter is pronounced with adult males and females selecting habitats differently (Miquelle *et al.* 1992, MacCracken *et al.* 1997). Both sexes occur at differing densities while segregated, and large males have dissimilar nutrient requirements to females (Miquelle *et. al.* 1992, Bowyer *et al.* 1997). Thus, it is not advisable to manipulate habitat for polygynous ungulates without understanding the habitat requirements of both sexes (Bleich *et al.* 1997). A more complete understanding of diet selection and habitat use by the sexes is necessary to further understand moose-habitat relationships in winter.

Finally, moose have the ability to alter the vegetative composition of some communities they inhabit (Risenhoover and Maass 1987), and to strongly influence rates of nutrient cycling and regrowth of browse in others (Molvar *et al.* 1993). Moose change the architecture of shrubs they feed on (Bergstrom and Danell 1987, Molvar *et* *al.* 1993), and show a strong preference for individual stems that have regrown from ones that were browsed previously (Bowyer and Bowyer 1997). Inputs of feces and urine from large herbivores enhance vegetative growth of plants (Ruess and McNaughton 1987), and these herbivores often defecate at feeding sites (Etchberger *et al.* 1988). Such relationships may be responsible for moose concentrating in traditional areas during particular seasons, including winter (Bowyer *et al.* 1997). How these factors relate to diet selection and the *K* of winter range for moose need more study.

The importance of winter range to moose should to be viewed in a broad perspective. The nutritional requirements necessary for reproduction cannot be obtained during winter (Schwartz *et al.* 1988). Moose are in a negative energy balance, and foraging activities serve principally to slow the rate of loss of body reserves (*sensu* Mautz 1978). Consequently, moose in better physical condition (and hence with more reserves) at the start of winter might do well on marginal winter range, whereas a moose in poor condition might perish on even the best winter habitats. Thus, a productive moose population requires year-round habitat of high quality. Although the needs of moose in winter play a major role in their reproduction and survivorship, managing habitat for moose only in that season is short sighted and may be ineffective. Likewise, the physical condition of moose may influence their diet selection in winter; this topic clearly is deserving of further study.

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