WINTER FORAGING ECOLOGY OF MOOSE IN THE TANANA FLATS AND ALASKA RANGE FOOTHILLS

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A

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By

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ABSTRACT

I studied woody browse distribution, production, removal, species composition, twig size, moose diets, and predicted daily intake of resident and migratory moose in the Tanana Flats and adjacent Alaska Range Foothills, Alaska, 1999–2000. Density of moose in these areas was high (1.1 moose/km^2). Moose were experiencing density-dependent effects on reproduction and growth, exhibited by low adult twinning rate (6%) and absence of pregnant yearlings, yet 17.5 kg higher 10-month-old calf body weights in the migratory segment. Of all willow, poplar, and paper birch plants sampled, 74% had a broomed architecture, which I attributed to heavy use by moose. Using a model of daily moose intake based on bite mass and bite density, I estimated that 1) migratory moose met expected intake during winter while intake of resident moose was marginal, 2) moose could not meet their expected daily intake with the mean twig dry mass (0.26 g) remaining unbrowsed at end of winter, and 3) higher predicted intake by migratory moose than resident moose was consistent with their higher 10-month-old calf weights.

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INTRODUCTION

Moose density on the central Tanana River flats (Flats) and adjacent foothills (Foothills) of the Alaska Range (Fig. 1), ranks among the highest recorded for similarly large areas in North America (Gasaway et al. 1992). In 1996 the density was 1.1 moose/km^2 (± 0.17 moose/km^2, 90% CI) in 6,730 km^2 (Boertje et al. 2000). In the surrounding area (Game Management Unit [GMU] 20A; 13,044 km^2), moose density increased from a low level in the late 1970s, and was relatively stable and high from 1992 to 2001 (Fig. 2). In contrast, landscape scale (> 2,000 km^2) moose densities are commonly low (0.04–0.4 moose/km^2) in Interior Alaska (Gasaway et al. 1992).

The goal of this study was to characterize the winter range of a moose population experiencing relatively strong density-dependent effects on reproduction and growth. North American moose populations showing density-dependent effects on reproduction have exhibited adult twinning rates of < 26%, and yearling pregnancy rates of < 41% (Franzmann and Schwartz 1985, Boer 1992, Gasaway et al. 1992). Adult twinning rates of the central Tanana Flats and adjacent Alaska Range Foothills moose population from 1997–2000 were 3–12% (*n* = 210), and yearling pregnancy rates (*n* = 36) were zero (Boertje et al. 2000). Short yearling (10-month-old calves in Mar) weights averaged 163 kg (*n* = 151) versus 207 kg (*n* = 8) in a low-density moose population in Denali National Park (100 km southwest; Adams 1999). These data suggest that the moose in the Flats and Foothills were experiencing relatively strong density-dependent effects on reproduction and growth.

Many moose populations exhibit partial migration (LeResche 1974, Van Ballenberghe 1977, Sweanor and Sandegren 1988, Sweanor and Sandegren 1989, Andersen 1991, Histoe and Hjeljord 1993, Ball et al. 2001). Partial migration is defined as one portion of a population migrating on a seasonal basis, while the remaining portion does not (Ball et al. 2001). Moose in the Flats and Foothills were partially migratory; all spent the summer in the Flats and about half migrated to the Foothills for the winter.

Short yearlings of migratory cows were significantly heavier (*P* = 0.0001) than resident short yearlings (172 kg, SE = 21, *n* = 76 vs 154 kg, SE = 22, *n* = 75) from 1997 through 2000 (Boertje et al. 2000). Since birth weights were not significantly different between Flats and Foothills moose in 1996 and 1997 (Boertje et al. 1999), I assumed that forage may have caused the difference in late-winter short yearling weights between the Flats and Foothills. Since the 2 segments of the moose population shared the same summer range, I assumed that the weight differences arose on the separate autumn or winter ranges from different forage characteristics. I studied characteristics of browse quantity and architecture that might affect moose forage intake rate to elucidate the relationships, if any, between browse characteristics and short yearling weights on the 2 winter ranges.

Moose are selective browsers in winter. Moose preferences for different species of browse can change slightly with changes in habitat (Risenhoover 1985) and distance to cover (Weixelman et al. 1998), but are generally consistent. The broad hierarchy of preference of browse species by moose is willow > aspen > birch > pine > fir > alder = spruce, and is inversely correlated with concentrations of secondary plant defense compounds (Oldemeyer et al. 1977, Bryant and Kuropat 1980). Digestibility and crude protein content of moose winter diets was strongly and positively influenced by the proportion of willow in the diet only 100 km southwest of the central Tanana Flats (Risenhoover 1989). In Interior Alaska, the preference hierarchy among willows (*Salix*) is roughly as follows *S. alaxensis*, *S. planifolia*, *S. interior* > *S. arbusculoides* > *S. scouleriana*, *S. bebbiana* > *S. glauca*, *S. hastata* (Milke 1969, Machida 1979, Wolff and Zasada 1979). Nomenclature follows Hulten (1968).

Daily forage intake rate of moose in winter is a complex process influenced by many factors, including bite rate, bite size, bite spatial density, plant fibrousness, and canopy architecture (Renecker and Hudson 1986, Vivas et al. 1991, Spalinger and Hobbs 1992, Shipley and Spalinger 1995, Moen et al. 1997, Kielland and Osborn 1998, Shipley et al. 1999). Search time between bites can have a large and negative effect on intake rate as forage densities decrease to low levels in a patch (Risenhoover 1987, Moen et al. 1997). A theoretical optimal bite diameter for each species of woody forage in a given area exists for moose (Kielland and Osborn 1998). The smallest twigs provide the most nitrogen gain per unit of mass, but extend rumen fill time, while the largest twigs provide less nitrogen gain per unit mass, but shorten rumen fill time (Shipley and Spalinger 1992). The expected daily intake of dry matter for a 400 kg moose in winter was estimated at 4.6 kg/day (Gasaway and Coady 1974) for Interior Alaska under conditions of normal winter weight loss (24% or 115 kg difference between autumn and spring). Moen et al. (1997) predicted that forage densities of less than 10 bites per square meter dramatically reduced bite rate, due to increased search times.

HYPOTHESES

The general hypothesis was that nutrition had limited the reproduction of adult moose and weight retention of calf moose in GMU 20A, especially in the Tanana Flats. Specifically, I expected:

H1) forage plants to be more likely to be present where moose were currently and historically at high density,

H2) forage production and removal to be higher where moose were currently and historically at high density,

H3) forage bite mass and bite density during winter to be insufficient to meet expected daily intake,

H4) the proportion of preferred forage genera in the diet to decline throughout the winter as preferred forage was consumed, suggesting depletion of forage resources before end of winter,

H5) forage bite mass and bite density remaining at end of winter to be insufficient to meet expected daily intake.

Assuming no differences in either genetic makeup, or summer habitat use between migratory moose and resident moose in GMU 20A, the specific hypotheses addressing the difference in short yearling weights between the Flats and Foothills were:

H6) moose that wintered in the Tanana Flats had reduced forage intake compared to those that wintered in the Foothills, and

H7) the forage species composition in the Foothills had a greater proportion of preferred forage species than the Flats.

OBJECTIVES

To address the hypotheses, my objectives were to:

1) estimate forage production, removal, species composition, plant architecture, twig size, bite mass, and bite density for the shrub and open forest components of the winter ranges of migratory and resident moose, stratified by current and historic relative density of moose, and by winter range

2) estimate diets of moose through winter on both winter ranges, and

3) estimate forage intake during winter and potential forage intake at the end of winter by adapting foraging models developed by Moen et al. (1997) and Spalinger and Hobbs (1992) to estimates of forage bite size and bite density obtained in this study.

STUDY AREA

Moose habitat was studied in the 6,730 km^2 central portion of GMU 20A, Interior Alaska (64°15'N, 147°40'W). The area included portions of the central Tanana Flats and adjacent Foothills of the Alaska Range, between 6 and 104 km south of Fairbanks (Fig. 1) (Gasaway et al. 1983, Gasaway and DuBois 1985). Moose habitat in this area ranged from 130 to 1200 m above sea level (Keech et al. 2000).

The area sampled (2,341 km^2) was the 99% fixed-kernel utilization distribution (Seaman et al. 1998) based on winter locations of radiocollared females from both resident and migratory groups of moose.

Mean minimum daily temperature varied from 5°C to -20°C in winter, but was usually 5–15° warmer in the Foothills than in the Flats during 1976–2000 (National Oceanic and Atmospheric Administration 2001). Mean monthly snow depth ranged from 25 to 50 cm, and was usually 5–8 cm deeper in the Flats than in the Foothills during 1994–2001 (National Resource Conservation Service 2001).

The study area was generally characterized by 2 major landscape types, the Tanana Flats and the Alaska Range Foothills. The Tanana Flats (130–450 m elevation) was poorly drained boreal forest dominated by bogs, shrubs, and spruce (*Picea* sp.), larch (*Larix laricina*), birch (*Betula papyrifera*), and poplar (*Populus tremuloides* and *balsamifera*) forests (Gasaway and DuBois 1985, Keech et al. 2000). The Alaska Range

Foothills (450–1200 m elevation) was high elevation, mostly treeless terrain, with long stretches of dense willow (*Salix* sp.), dwarf birch (*Betula glandulosa* and *B. nana*), and alder (*Alnus*) in the valleys, and alpine tundra interspersed with bare mineral soil on the hilltops above 670 m elevation. Areas below 670 m elevation in the Foothills contain white spruce, aspen, and birch forests (LeResche et al. 1974, Gasaway et al. 1983).

Fires, waterways, and lake margins provide most of the early successional habitat and subsequent high forage biomass in the Flats (LeResche et al. 1974, Gasaway et al. 1989, Keech et al. 2000). Major fires occurred in the central Tanana Flats in 1957, 1958, and 1980. Fires tend to increase the quantity and quality of moose forage by setting succession back to primary stages (Peek et al. 1976, Regelin et al. 1987, Schwartz and Franzmann 1989). However, since the climax stage of succession in the forests of the Flats portion of the study area was typically spruce, fire-initiated, shrub habitats in the Flats were among the least permanent habitats with high biomass moose forage (LeResche et al. 1974, Peek et al. 1976, Schwartz and Franzmann 1989).

High elevation shrub fields and riparian areas produce high forage biomass in the Foothills (Gasaway et al. 1983, Gasaway and DuBois 1985). Fires rarely occur in the open shrublands of the Foothills. These shrub zones were among the most permanent habitats with high biomass moose forage (LeResche et al. 1974).

METHODS

I sampled and analyzed 1) willow (*Salix* spp.), 2) poplar (*Populus* spp.), and 3) paper birch (*Betula papyrifera*). I excluded other deciduous species including alder (*Alnus* spp.), dwarf birch (*Betula nana*), and resin birch (*Betula glandulosa*) because they are not preferred in winter by moose in Interior Alaska (Bryant and Kuropat 1980).

All willows measured in this study were classified with the aid of a winter willow identification key produced by the Alaska Department of Fish and Game for Interior Alaska (Simpson 1986).

A vegetation cover map (U.S. Bureau of Land Management 1997) was used to exclude unvegetated areas (i.e., ice, snow, water, rock, sand) and areas unlikely to contain winter forage (i.e., tundra, aquatic bed, sedge, shrub lower than 0.5 m, and closed, mature forest). The vegetation cover map was used for stratification purposes, decreasing the time spent traveling to nonforage producing habitats. Fifty-two percent of the land area within the study area was excluded in this process, 62% of the Flats and 45% of the Foothills. Closed and mature forests composed 66% of the excluded area in the Flats and 71% of the excluded area in the Foothills.

Landscape Stratification

I stratified the study area on the basis of 1) current relative moose density (CD), 2) historic relative moose density (HD), and 3) winter range, Flats or Foothills (WR).

High and low CD was estimated from fixed-kernel analysis (Seaman et al. 1998) of radiolocations of 32 adult (> 4 yr) cow moose during winters 1998–1999 and 1999–2000 ($n = 261$), using least squares cross validation to select the smoothing parameter. High CD was the contour enclosing observations with greater than average density and low CD was the remainder of the area within the 99% utilization distribution (Seaman et al. 1998). Winter was defined as the last week in September through the first week in April. Resident ($n = 17$) and migratory ($n = 15$) segments of the herd were evenly represented by collared moose. The 32 cows were selected at random and assumed to represent a random sample of the study area population.

High and low HD was based on moose survey unit stratification for GMU 20A (Gasaway et al. 1986). The survey units averaged 31 km^2. HD was estimated during 1988 and was used for moose survey stratification through 1999. The low HD units had an average density of about 0.4 moose per km^2, the high HD units in the Foothills and Flats had an average density of about 2.3 and 1.5 moose per km^2, respectively, during the 1988 survey.

The delineation between migratory WR (Alaska Range Foothills) and resident WR (Tanana Flats) was defined as the approximate 450 m elevational contour. This boundary has been used to delineate resident and migratory moose winter range since moose were first radiocollared in GMU 20A (Gasaway et al. 1980). The line follows existing trails and waterways for ease of identification in the field (Fig. 3).

Forage Plant Distribution and Density

I selected a stratified random sample of 480 points, with each stratum of CD, HD, and WR, equally represented. Forage presence or absence was recorded at these points from aircraft at an altitude of 100–150 ft. A Robertson R-22 helicopter was used to survey 405 of the points and a Piper PA-18 Super Cub was used for the remainder (Peek et al. 1976). Garmin 12XL Global Positioning System (GPS) units were used to navigate to the point.

Forage plant presence or absence and mean distance between forage plants with twigs within the reach of moose were estimated in an imaginary 30×30 m square at the random points (commensurate with pixel size of the vegetation map). Forage plant presence data was used in the analysis of plant distribution with respect to moose density, and mean distance between forage plants was used as a rough estimate of forage plant density in the stratification of production and removal estimates. The location observed was not the exact location of the targeted pixel because position error resulted from movement of aircraft, error in the vegetation map, selective availability of GPS signals, and inherent limitations of the GPS unit used. However, a landscape estimate of forage distribution was obtained.

Forage Collection and Mass vs. Twig Diameter Regressions

Unbrowsed, dormant twigs of variable size (1–10 mm diameter) were collected from forage species in the Flats and Foothills from November through April. The twigs were measured, dried, and weighed to develop regression relationships between diameter and dry mass (Brown 1976, Oldemeyer 1982, Alaback 1986, Kielland and Osborn 1998). Most twigs used in the regression development were current annual growth (CAG), but some diameter-mass pairs included second or third year growth, because CAG twigs of larger diameters (> 6 mm) were rare in some species. Regression equations were developed for 7 species in the Flats (*Betula papyrifera, Populus balsamifera, Populus tremuloides, Salix alaxensis, Salix arbusculoides, Salix bebbiana,* and *Salix planifolia pulchra*) and 6 species in the Foothills (*Betula papyrifera, Populus balsamifera, Populus tremuloides, Salix alaxensis, Salix bebbiana,* and *Salix planifolia pulchra*).

Forage Production and Removal

A stratified (CD, HD, WR) random sample of forage production and removal estimation points (95) was selected randomly from the aerially-surveyed points that had forage present. Aerially-estimated forage densities were split into high and low categories at the median value in each of the 8 strata classes formed by the 2 levels of CD, HD, and WR. In an effort to select areas most likely to contain a measurable quantity of forage, more high forage density sites were randomly selected than low forage density sites, at a ratio of 7:5 except 1 strata which had a ratio of 7:4 (Table 1).

In April 2000 navigation to each of the 95 sample points was conducted with a Rockwell PLGR+96 GPS. Estimated position error was ≤ 25 m (Rockwell International, Cedar Rapids, Iowa). At each plot (radius = 15 m) the number of forage plants was estimated by species. For each species, 3 plants were randomly selected. Ten randomly selected twigs were measured on each of those plants; diameter at point of browsing (DPB), if applicable, and diameter at base of current annual growth (DCAG) were recorded (Lyon 1970). Then, the number of CAG twigs 0.5–3.0 m above ground level on the 3 plants was counted.

This interval represents the normal range in which moose forage in winter. Woody forage below 0.5 m is commonly considered below the minimum foraging height for moose (Wolff and Zasada 1979, Wolff and Cowling 1981, Weixelman et al. 1998), and is often snow covered. The upper limit of 3.0 m was used because preliminary reconnaissance in the study area showed browsing above 3.0 m to be uncommon, and 3.0 m is commonly considered the upper limit in forage surveys (Danell and Ericson 1986, Hjeljord et al. 2000). Further details on forage survey protocol are provided in Appendix A.

The regression coefficients relating diameter to dry mass (Appendix B) and the estimated number of twigs were used to estimate forage production and removal (Telfer 1969) within sampled plots. DCAG was used to predict production and DPB was used to predict removal (Oldemeyer 1982).

Forage Plant Architecture

Forage plants were classified by their history of browsing by moose and the resultant physical characteristics, termed “architecture”. Plant architecture was estimated as 1 of 3 categories based on the evidence of browsing prior to the current year for each plant. The 3 classes were 1) broomed, 2) browsed, and 3) unbrowsed. The definitions of the classes were 1) broomed--more than half of CAG twigs between 0.5 and 3.0 m arose from lateral stems that were produced as a result of browsing; 2) browsed--showed evidence of browsing in past years, but less than half of CAG twigs between 0.5 and 3.0 m arose from lateral stems that were produced from browsing; and 3) unbrowsed--no signs of being browsed by a moose prior to the current year.

Diet Estimation

Fecal pellets were collected monthly from December 1999 to April 2000 along a transect that crossed the wintering areas of both resident and migratory moose. The transect was roughly 140 km in length. The transect extended from the Tanana River south of Fairbanks, into the Alaska Range Foothills, 80 km south of Fairbanks.

The location of the transect within the wintering areas of resident and migratory moose was determined by trail availability. Dense vegetation in the majority of the Flats and Foothills precluded off-trail passage with a motorized vehicle. Trails were selected based on the proximity to radiotelemetry locations of resident and migratory moose in winter.

The same trail was used throughout the winter to collect fecal samples. Fecal collection was performed 1 to 2 weeks after fresh snowfall. Fresh snow was used to determine the age of fecal pellet groups. If fecal pellet groups were on top of the most recent snow, they were collected. I categorized fecal collection sites as Flats or Foothills.

Two pellets from each fecal pellet group were used in composite samples for analysis of each collection period. After sampling from a pellet group, the pellet group was buried with snow so that it could not be sampled again. I avoided sampling multiple pellet groups from the same moose during a sampling period.

Additionally, in March 1999 and March 2000, fecal samples were collected directly from immobilized moose during capture events. Thus, 1 fecal collection event (March 1999) was during a different winter than all other fecal collection events. The locations of the immobilized moose in March were spread more widely across the landscape than the pellets collected from the trail transect.

The percent relative density of forage genera in the feces (Todd and Hansen 1973) was estimated by Washington State University, Habitat Analysis Lab. I estimated percent of each forage genera in the diet (D_g) by correcting for the digestibility (Weixelman et al. 1998) of each genera with the following equation.

$$D_g = \frac{F_g/(1-X_g)}{\sum_g F_g/(1-X_g)}$$

Where F_g was the percent relative density in the feces of genus g and X_g was the proportional digestibility of genus g. For the genera *Salix, Populus, Betula,* and *Alnus* the literature was reviewed to obtain estimates of in vitro dry matter digestibility (Table 2; Oldemeyer et al. 1977, McNay 1983, Steigers and Becker 1986, Schwartz et al. 1988, Risenhoover 1989, Weixelman et al. 1998). All non-Alaskan studies were excluded from this tabulation. Digestibility for the fecal component class "shrub" was estimated as the mean of the 4 genera above. Digestibility for fecal component "other" was estimated by using a digestibility estimate for moss (Steigers and Becker 1986). Class "other" only composed about 1% of the feces. Moss made up the largest portion of class "other" for winter 1999–2000.

For each forage genus, linear regression was used to estimate the slope of the line relating percent composition of the diet to time throughout the winter. An F test statistic was then used to estimate whether the slopes were different from zero.

ANALYSES

All statements of statistical significance were based on an a priori alpha of 0.05.

Mass vs. Diameter Prediction

Dry mass was expected to have an exponential relationship to diameter, $z = ax^b$ (Oldemeyer 1982), where z was dry mass, x was twig diameter, and a and b were parameters. This relationship could be estimated using linear regressions of log transformed dry mass on log transformed twig diameter for the forage plants collected in the study area. After estimating coefficients on the log scale, estimates of dry mass were converted back to the original scale (grams) using the equation

$$\hat{z} = \exp(\hat{a} + \hat{b}\ln(x_0) + \sigma^2 / 2)$$

to correct for approximate bias resulting from skewness (Brown 1976), where $\hat{a}$ was the intercept coefficient and $\hat{b}$ was the slope coefficient on the log scale, σ^2 was the mean square error on the log scale, x_0 was some diameter that I chose, and $\hat{z}$ was the resulting predicted value. Further details are provided in Appendix A.

Forage Plant Distribution

A logistic regression model (Hosmer and Lemeshow 1989, Hastie and Pregibon 1992) was used to estimate the relationships between forage distribution and WR, CD, and HD. This analysis utilized the forage presence/absence data from all 480 aerially-surveyed points. Starting with a full model of main effects and secondary interaction effects, effects were eliminated using a stepwise variable removal procedure (Hosmer and Lemeshow 1989:106). At each step in the process, the factor with the *t* value closest to zero was removed. Then a *P*-value for a log-likelihood ratio statistic was calculated from the following equation,

$$P = 1 - F_{\chi_1^2}(\text{deviance of new model} - \text{deviance old model}),$$

where $F_{\chi_1^2}$ was the cumulative distribution of a chi-square random variable with one degree of freedom. A definition of deviance, as used here, was given by Venables and Ripley (1997:226).

If the *P* value of this equation was greater than 0.05, the elimination process continued. If the *P* value of this equation was less than 0.05, the final model was obtained. Main effects that were included in a significant interaction effect were not eliminated. The *glm*() function in the statistical software *S-PLUS* was used for these analyses.

Forage Production and Removal

I used bootstrap methods (*S-PLUS* statistical software) to test the differences in forage production and removal between the 2 levels of each stratum; WR, CD, and HD. I resampled the differences between classes (high and low) of the strata (WR, CD, and HD) with 10,000 iterations. After building a distribution with the 10,000 resampled differences, I estimated the mean and 95% CI for that distribution. If the high and low limits of the 95% CI included zero, then the difference was deemed not significant. The bootstrapping process is robust to nonnormally distributed data, which was characteristic of most strata.

Proportional Tests

All tests for significant differences between 2 proportions were based on the *Z*-test which uses the normal approximation of the binomial distribution (Moore and McCabe 1993).

Daily Intake

I adapted a model (Moen et al. 1997:510) to estimate daily forage intake for moose based on estimated bite mass and bite density on the study area winter ranges. I used literature estimates of all variables except for bite mass and bite density. The model (Moen et al. 1997:510) was:

$$BiteRate_d = \frac{\left(\dfrac{R\max}{R\max/CropRate + BiteSize}\right)}{1.0 + SearchTimeFrc_d}$$

where…

$SearchTimeFrc_d = 20.0\ BiteDens^{-1.5}$

$SearchTimeFrc_d$ was the fraction of feeding time spent searching, and $BiteDens$ was bite density (number of bites/m^2). To estimate bite density during winter, I divided the average mass of forage removed by moose in each winter range by the average mass of twigs at the mean diameter at point of browsing in the respective winter range. To estimate the bite density of remaining forage at end of winter, I divided the biomass of remaining unbitten CAG twigs in April, in each winter range, by the average mass of twigs at the mean DCAG in the respective winter range.

BiteSize was bite mass in grams. For bite mass during winter I used removal, based on mean DPB observed in the Foothills and Flats winter ranges, estimated by the species specific mass vs. diameter relationships developed in each winter range. For bite mass of unbitten twigs at end of winter, I used the mean mass of twigs at the mean DCAG in the respective winter range.

*R*max was the maximum processing rate in grams per minute ($0.662BM^{0.76}$) where *BM* was body mass in kilograms (Shipley and Spalinger 1992). I used 400 kg body mass based on Gasaway and Coady (1974). *CropRate* was the maximum cropping rate (number of bites per minute) at a sufficient bite density that a moose can maximize intake without the hindrance of searching between bites. I used a maximum cropping rate of 40 bites per minute since Moen et al. (1997) reported a range of 35–45 bites per minute in a review of other literature (Renecker and Hudson 1986, Miquelle et al. 1992, Shipley and Spalinger 1992).

To attain the final product of intake per day (kg), bite rate (number of bites/min) was multiplied by bite mass (grams) and time spent foraging (min/day), then divided by 1,000. Time spent foraging was set at 400 minutes, which was within the range observed for adult moose on winter forage in Alaska and Norway (Risenhoover 1986, Saether and Andersen 1990, Vivas et al. 1991).

RESULTS

Mass vs. Diameter Regressions

The coefficients of the regressions of biomass on twig diameter were similar among species on both winter ranges (Table 3). *Salix arbusculoides* in the Flats had the least taper (long thin twigs), while *Populus tremuloides* in the Flats and *Populus balsamifera* in the Foothills had the most taper (thick, short twigs). The slopes of regression lines of biomass on twig diameter were not consistently steeper or shallower by species on either winter range. I used the species specific and winter range specific equations for production and removal estimates. Further details concerning twig characteristics by species and range are provided in Appendix C.

Moose Distribution

A total of 261 monthly winter moose radiolocations were used to estimate CD (Table 4, Fig. 4). The area of the 99% utilization distribution was 2,341 km^2. The Flats area totaled 1,727 km^2, with 1,641 km^2 in low CD, and 85 km^2 in high CD. The Foothills area totaled 615 km^2, with 530 km^2 in low CD and 84 km^2 in high CD. Five percent of the Flats was high relative moose density, while 15% of the Foothills was high relative density. This was consistent with ADF&G moose survey data which suggested about half of the cows in the study area were in the Foothills in winter, in an area about one-third the size of the Flats (J. Ver Hoef, Alaska Department of Fish and Game, unpublished data).

Of the 2,341 km^2, low HD comprised 1,304 km^2, while high HD comprised 1,037 km^2. The Flats had 1,143 km^2 in low HD and 584 km^2 in high HD. The Foothills area had 161 km^2 in low HD and 453 km^2 in high HD (Fig. 3). The proportion of area with high HD was about 2 times greater in the Foothills (74%) than the Flats (34%), consistent with results obtained from CD.

Forage Distribution

Forage plants were observed at 289 of the 480 stratified random points. Of points sampled in the Flats, 79% (± 4%, 95% CI) had forage present. Of the Foothills sample points 41% (± 4%, 95% CI) had forage present. When multiplied by the proportion of the area sampled after vegetation map exclusions, an estimated 30% (± 4%, 95% CI) of the total Flats land area had forage present and 22.5 % (± 4%, 95% CI) of the total Foothills land area had forage present.

The final logistic regression model of forage distribution included WR ($P < 0.001$), HD ($P = 0.018$), an interaction between CD and HD ($P = 0.017$), and an interaction between HD and WR ($P = 0.048$) as significant effects on the presence or absence of forage at random points in the study area (Table 5). Specifically, the chances of finding any preferred forage (willow, poplar, and paper birch with twigs within the reach of moose) were significantly higher in areas that had high moose density in the late 1980s, high moose density during this study, and in the Flats.

Forage Production and Removal

The mean CAG forage biomass (for sites that had forage present) tended to be higher in the Foothills (235 kg/ha [± 95, 95% CI]) than in the Flats (190 kg/ha [± 64, 95% CI]), but the difference was not significant ($P > 0.05$; Table 6). The mean in the Foothills was greatly influenced by 3 very high biomass (> 1500 kg/ha) sites (Fig. 5).

Mean forage removal by moose tended to be higher in the Foothills (105 kg/ha [± 15, 95% CI]) than in the Flats (64kg/ha [± 5, 95% CI]), but the difference was not significant ($P > 0.05$; Table 6). The Foothills also had 3 very high biomass removal sites (> 700 kg/ha; Fig. 6). The proportion of biomass removed tended to be higher ($P = 0.12$) in the Foothills (45%) than in the Flats (33%).

The average bite diameter across all forage species differed between Flats and Foothills (3.0 and 3.3 respectively, $P < 0.001$). These mean bite diameters implied bite masses in the Flats and Foothills of 0.81 g and 1.10 g, respectively. Bite mass in the Foothills was about one-third larger than in the Flats. The mean bite diameters varied by species (Fig. 7). Further details on mean twig and bite characteristics by range and species are provided in Appendix C.

Willow composed 84% of estimated forage production for the study area. The Foothills had a higher (94 % vs. 8 %; $P < 0.001$) proportion of production from the 2 most preferred (*Salix alaxensis* and *Salix planifolia pulchra*) forage species (Fig. 8). The species composition of removal was similar to production (Fig. 9). Mean DCAG of willow twigs was larger ($P < 0.001$) in the Foothills (3.1 mm ± 0.08 [95% CI]) than in the Flats (2.3 mm ± 0.06 [95% CI]). This difference in willow twig diameter translates to a 2.4 times larger mean mass of willow twigs in the Foothills (0.90 g vs. 0.38 g) than in the Flats, using the species and winter range specific diameter to dry mass regressions. Concurrently, the Foothills had 34% of CAG willow twigs larger than mean willow bite diameter compared to 22% in the Flats (Table 7).

Areas that had burned in the last 50 years were located only in the Flats, and composed 73% of the sites sampled there. Burned sites had approximately 5 times higher forage production (243 kg/ha ± 85 [95% CI] vs. 49.0 kg/ha ± 7 [95% CI]) and removal by moose (82 kg/ha ± 38 [95% CI] vs. 15 kg/ha ± 3 [95% CI]) than other Flats habitats.

Daily Intake

During winter the simulated daily dry matter intake for a 400 kg moose in the Flats and Foothills was 4.5 and 6.2 kg, respectively. If moose were to continue feeding on the mean DCAG-sized stems remaining at end of winter, the model predicted that a 400 kg moose could only consume 3.1 or 4.4 kg per day in the Flats or Foothills, respectively.

Forage Architecture

In the Flats, 72% of forage plants were broomed, 26% were browsed, and 2% were unbrowsed ($n = 325$). In the Foothills, 77% of forage plants were broomed, 21% were browsed, and 2% were unbrowsed ($n = 219$). Confidence intervals (95%) overlapped between Foothills and Flats for each of the architecture classes (Fig. 10). In the entire study area, 74% of forage plants were broomed, 24% were browsed, and 2% were unbrowsed.

Winter Diet

The number of pellet groups sampled in each wintering area during each monthly sampling event varied from 8 to 22 with a total of 221 (Table 8). There were no significant temporal trends in the proportion of forage genera in the diet ($P > 0.05$) for either resident or migratory WR strata throughout the winter, so data were pooled over the entire study area.

The winter diet of moose in the study area was composed almost entirely (99%) of woody forage species. Willow, birch, poplar, and alder composed 43, 25, 22, and 6% of the diet, respectively (Fig. 11). Shrubs that could not be identified taxonomically composed 3% of the diet. The remainder of the diet (1%) was composed of mosses, grasses, sedges, and forbs. Willow decreased ($P = 0.002$) throughout the winter from

56% in December to 35% in March (Fig. 12), but no other species had a significant temporal trend ($P > 0.05$).

DISCUSSION

I chose the habitats most likely to contain woody forage based on my observations during moose surveys and radiotracking in the study area and the vegetation map descriptions. Exclusion of closed and mature forests from my sampling may have reduced my estimates of forage distribution and biomass in the study area. Closed and mature forested areas of the same type as those excluded in my study area were sampled in a Kuskokwim valley (400 km southwest) forage study. The Kuskokwim valley (Seaton, unpublished data) sites with the same satellite vegetation classes as my excluded sites averaged only 8 kg forage/ha ($n = 39$) with 24 of the sites having no forage at all. Conversely, the sites in the Kuskokwim valley that had the same satellite vegetation class as my sampled sites averaged 281 kg forage/ha ($n = 26$) with only 1 site having no forage at all. Thus, any negative bias in forage biomass estimates at the study area scale was relatively small (< 3%) and my methods enabled me to survey forage biomass and distribution as efficiently as possible.

Because alder composed about 6% of the diet, excluding it from the forage production and removal sampling might have caused a slight underestimate of production and removal at the study area scale. Similarly, because browsing was occasionally observed on dwarf birch and resin birch at some sampling sites, not sampling production and removal of these species may have biased my estimates downward. However, the species I sampled composed at least 90% of the diet, and the small downward bias that may have resulted from not sampling some species was expected to be relatively uniform among strata.

Forage was more likely to be present in areas with high current and historical moose density and in the Flats. Although forage was more likely to be found in the Flats, the species composition, smaller bite diameters, and lower bite density suggested that these foraging sites were less desirable than foraging sites in the Foothills. Since 73% of the sample plots of the Flats were in burns < 50-years old, and these age burns had approximately 5 times higher biomass than other Flats sites, the burns may have increased forage presence, production, and removal in the Flats.

The daily intake model predicted intake during winter of 4.5 and 6.2 kg/day in the Flats and Foothills, respectively. These model predictions suggested that moose in the Foothills achieved their expected daily intake of 4.6 kg (Gasaway and Coady 1974), but moose in the Flats may have had difficulty. About 60% of the difference between Flats and Foothills in estimated daily intakes was due to differences in bite mass and 40% was due to differences in bite density. Since bite mass varied by species (Fig. 13), species composition of forage patches in the Flats and Foothills may have had a greater effect on daily intake by moose than forage density in those patches. This difference in predicted daily intake based on observed bite density and bite mass in the 2 ranges was consistent with the differences in short yearling weights between the 2 ranges. Since mean biomass removed per hectare was not significantly different between the Flats and Foothills, the difference between predicted daily intake in the 2 ranges is consistent with the concept that small differences in estimated forage characteristics may have large nutritional consequences for ungulates (White 1983).

The best indication of the condition of range at the end of winter may be the diameter of remaining potential bites. If available bites are too small to allow moose to attain expected intake, then the range may be considered overutilized or suboptimal. In the Flats and Foothills the average twig not bitten by moose had a DCAG of 2.0 mm (± 0.03, 95% CI, estimated mass of 0.23 g) and 2.3 mm (± 0.04, 95% CI, estimated mass of 0.38 g) respectively. The daily intake model predicted that if moose consumed 0.23 or 0.38 g bites in the Flats or Foothills, the end-of-winter daily intake would have been only 3.1 or 4.4 kg/day respectively. This predicted intake was less than the normal winter weight loss intake of 4.6 kg dry mass (Gasaway and Coady 1974).

In this end-of-winter (April) example, moose could potentially increase foraging time per day to compensate to some degree. However, the amount of foraging time required to intake 4.6 kg dry forage was 1,100 and 630 min in the Flats and Foothills, respectively, using mean late winter CAG twig sizes in the model. The maximum time spent foraging per day in winter, reported by Risenhoover (1986), was 559 min/day for late April. Increases of winter daily foraging time beyond 600 min may be physiologically impossible for wild moose in Interior Alaska. Thus, the small diameters of remaining forage in the study area at end of winter at least accelerated the rate of winter weight loss for moose at that time.

Plant architecture, the browsing history of a plant throughout its lifetime and resultant canopy structure, may also affect intake rate of moose. Plants that have been browsed heavily for long periods of time can experience mortality (Andrews 1998), twig die-off, smaller twigs (Peek 1998), more chemical defense in twigs and leaves (Bryant et al. 1993), and structure that makes it harder for moose to reach CAG twigs (Kielland and Osborn 1998, Mallek 1999). Of forage plants sampled, 75% were broomed, 22% were browsed, and only 2% were unbrowsed. This large percentage of broomed plants in the study area, across all species of forage measured, suggests intense use of the forage. Without more architecture data of this type from other moose ranges for comparison, the implications of these architecture class proportions were undetermined. However, the heavily broomed architecture of forage plants on this range indicates heavy forage use.

In Norway, a winter range that was deemed to have heavily browsed plants (23.5% biomass removed per year) and poorly preferred species composition resulted in decreased daily intake by moose compared to a winter range with lightly browsed plants (3.1% forage biomass removed per year) and more preferred species composition (Saether and Andersen 1990). Perhaps the observed differences in intake rate of moose were influenced by the long-term browsing pressure on the plants (architecture) in their 2 study areas. One of the potential mechanisms for the reduced intake was the transition of growth allocation from a few large twigs to many smaller twigs by the heavily browsed plants and the resulting smaller bite diameters for moose (Bergstroem and Danell 1987a). The Tanana Flats and Foothills moose may have experienced similarly decreased intake compared to other moose populations with higher twinning rates, which may have led to reduced physical condition. It has been shown that twinning rate of cow moose in the Flats and Foothills is affected by maternal body condition (Keech et al. 2000). Thus, the low twinning rate in the Flats and Foothills moose populations may be related to the high proportion of broomed plants, and estimates of plant architecture may be an important, easily monitored index to forage intake and condition of moose.

Willow significantly decreased in the diet of moose throughout the winter across the study area. This may be a result of selection for this most preferred forage genus, and depletion of willow as winter progressed. However, less preferred genera such as birch and poplar appeared to compensate for the decrease in willow. As the percent use of willow declined in the diet, I assume that moose spent more time searching for forage, and when they found it, it was more likely to be composed of less preferred species. This assumed increase in search time may have increased rumen fill time and decreased daily intake rates, consistent with the general hypothesis that nutrition had limited the reproduction of adult and weight retention of calf moose in GMU 20A.

Plant architecture and diet composition through winter suggested that moose had a history of depleting forage during winter. However, the low removal rate (40%) of forage CAG did not. Since GMU 20A moose have maintained high density and exhibited the assumed density-dependent effects of reduced twinning and low yearling pregnancy rates, I expected a higher proportion of forage removal. However, even optimally foraging moose may leave substantial amounts of forage, even when food supply is very low (Vivas et al. 1991). Additionally, the high proportion of broomed plants in the study area may have reduced the proportion of biomass that moose could remove, because twigs on broomed plants were commonly small and may have been difficult to consume.

A higher proportion of annual production is removed on plants with a growth form exhibiting a few, large twigs than plants exhibiting many, smaller twigs (Bergstroem and Danell 1987b, Saether 1990). Brooming of plants increases branching and transfers growth from fewer, larger twigs to more, smaller twigs (Bergstroem and Danell 1987a). This change in growth form (architecture) may be an adaptation to reduce the impact of further browsing (Vivas et al. 1991). Since repeated browsing can reduce the proportion of forage removed by moose (Bergstroem and Danell 1987a), estimates of the proportion of forage biomass removed alone were insufficient to assess the relationship between moose populations and their forage resources.

Landscape averages of forage biomass and removal may be important, but not sufficient for assessing forage characteristics important to moose. Average forage biomass tended to be higher in the Foothills than in the Flats, but 3 very high biomass sampling sites made the data nonnormal (Fig. 5). I observed large variation in biomass data between sites due to the wide variability of forage plant species, densities, and growing conditions in the study area. Very high forage biomass patches may be quite important to moose intake yet cause high variability that reduces the probability of detecting significant differences in mean biomass.

Future research is needed to better understand how brooming of forage plants by moose affects succession and the resultant bite density and bite mass of browse over longer time periods than the scope of this study. Specific topics include 1) degradation of the quality and quantity of broomed plants (McInnes et al. 1992, Kielland et al. 1997), 2) decreasing the rate of succession by reducing height growth of shrubs through brooming (Kielland et al. 1997, Andrews 1998), and 3) increased encroachment of alder in shrub lands when the competing willow is broomed by moose (Kielland and Bryant 1998).

MANAGEMENT IMPLICATIONS

In 2000 the moose in the central Tanana Flats and adjacent Alaska Range Foothills had consumed nearly all the browse of usable bite diameter by the end of winter. This conclusion is consistent with the low twinning rates, low yearling pregnancy rates, heavily broomed plant architecture, small twig diameters remaining at end of winter, and significant diet change through winter. Managers wishing to assess moose population proximity to maximum forage utilization should monitor all of these indicators. It appears that a moose population of this density can be supported by a range where about 25% of the landscape had an average of 213 kg/ha forage production. With the average forage density of the Flats and Foothills combined, and the species composition I observed, an average bite diameter of about 3.0 mm would provide a moose with the ability to meet its expected daily forage intake of 4.6 kg dry mass. A small reduction in mean bite diameter to 2.2 mm would only allow a moose to intake half of its expected daily intake (2.3 kg).

I recommend against twig counts (e.g., percent twigs browsed estimates). Over a 9-year period (1981–1992), moose increased 8-fold on a study area in the Koyukuk River drainage of Alaska. During that time, the percent of twigs browsed only increased from 68% to 73% (Knut Kielland and Tim Osborne, unpublished data). In my study area, only 40% of CAG biomass was removed by moose, but the remaining 60% had characteristics that precluded efficient use by moose. Twig count data would not have provided the information needed to separate functionally available forage from other forage.

In all, I used many comparisons as tools to characterize the study area and the differences between Flats and Foothills (Table 7). However, bite diameters and bite density estimates were sufficient to indicate near complete utilization of available forage during winter and to explain the difference in calf weights in March. The degree of usefulness of these measures for future forage studies on other moose ranges will be validated and enhanced if this type of study is repeated on other ranges with variable forage production and moose productivity.

While this population showed signs of nutritionally-limited reproduction and growth, it has been stable and has supported a yearly harvest of 500–600 moose from 1990 to 2000 (Boertje et al. 2000), which is a greater harvest per land area than any other equivalent-sized area in Alaska.

LITERATURE CITED

ADAMS, L. G. 1999. Population dynamics of wolves and their prey in Denali National Park, Alaska: progress report. Alaska Biological Science Center, Anchorage, Alaska, USA.

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

ANDERSEN, R. 1991. Habitat deterioration and the migratory behaviour of moose (*Alces alces* L.) in Norway. Journal of Applied Ecology 28:102–108.

ANDREWS, J. H. 1998. The impact of moose browsing on *Populus* in the Susitna valley, southcentral Alaska. Thesis, University of Alaska Fairbanks, Fairbanks, Alaska.

BAIN, L. H., AND M. ENGLEHARDT. 1987. Introduction to probability and mathematical statistics. Doxbury Press, Boston, Massachusetts, USA.

BALL, J. P., C. NORDENGREN, AND K. WALLIN. 2001. Partial migration by large ungulates: characteristics of seasonal moose *Alces alces* ranges in northern Sweden. Wildlife Biology 7:39–47.

BERGSTROEM, R., AND K. DANELL. 1987a. Effects of simulated winter browsing by moose on morphology and biomass of two birch species. Journal of Ecology 75:533–544.

———, AND K. DANELL. 1987b. Moose winter feeding in relation to morphology and chemistry of six tree species. Alces 22:91–112.

BOER, A. H. 1992. Fecundity of North American moose (*Alces alces*): a review. Alces Supplement 1:1–10.

BOERTJE, R. D., M. A. KEECH, C. T. SEATON, AND B. W. DALE. 1999. Factors limiting moose at high densities in Unit 20A. Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Research Progress Report. Grants W-27-2. Study 1.51. Juneau, Alaska, USA.

———, C. T. SEATON, D. D. YOUNG, M. A. KEECH, AND B. W. DALE. 2000. Factors limiting moose at high densities in Unit 20A. Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Research Progress Report. Grants W-27-3. Study 1.51. Juneau, Alaska, USA.

BROWN, J. K. 1976. Estimating shrub biomass from basal stem diameters. Canadian Journal of Forestry Research 6:153–158.

BRYANT, J. P., AND P. J. KUROPAT. 1980. Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. Annual Review of Ecology and Systematics 11:261–285.

———, P. B. REICHARDT, CLAUSEN T. P., AND R. A. WERNER. 1993. Effects of mineral nutrition on delayed inducible resistance in Alaska paper birch. Ecology 74:2072–2084.

CRESSIE, N. 1993. Statistics for spatial data, revised edition. John Wiley and Sons, New York, USA.

DANELL, K., AND L. ERICSON. 1986. Foraging by moose on two species of birch when these occur in different proportions. Holarctic Ecology 9:79–84.

DORFMAN, R. 1938. A note on the δ-method for finding variance formulae. Biometric Bulletin 4:129–137.

FRANZMANN, A., AND C. SCHWARTZ. 1985. Moose twinning rates: A possible population condition assessment. Journal of Wildlife Management 2:394–396.

GASAWAY, W. C., AND J. W. COADY. 1974. Review of the energy requirements and rumen fermentation in moose and other ruminants. Naturaliste Canadien 101:227–262.

———, AND S. D. DUBOIS. 1985. Initial response of moose (*Alces alces*) to a wildfire in Interior Alaska. Canadian Field-Naturalist 99:135–140.

———, S. D. DUBOIS, AND K. L. BRINK. 1980. Dispersal of subadult moose from a low density population in Interior Alaska. Proceedings of the North American moose conference and workshop 16:314–337.

———, S. D. DUBOIS, D. J. REED, AND S. J. HARBO. 1986. Estimating moose population parameters from aerial survey. Biological Paper 22, University of Alaska Fairbanks, Fairbanks, Alaska, USA.

———, S. D. DUBOIS, R. D. BOERTJE, D. J. REED, AND D. T. SIMPSON. 1989. Response of radiocollared moose to a large burn in central Alaska. Canadian Journal of Zoology 67:325–329.

———, R. STEPHENSON, J. DAVIS, P. SHEPHERD, AND O. BURRIS. 1983. Interrelationships of wolves, prey, and man in Interior Alaska. Wildlife Monographs 84.

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

HASTIE, T. J., AND D. PREGIBON. 1992. Generalized Linear Models. Pages 195–247 *in* J. M. Chambers, and T. J. Hastie, editors. Statistical Models in S. Wadsworh & Books/Cole Advanced Books & Software. Pacific Grove, California, USA.

HISTOE, T., AND O. HJELJORD. 1993. Winter feeding strategies of migrating and nonmigrating moose. Canadian Journal of Zoology 71:1421–1428.

HJELJORD, O., E. RONNING, AND T. HISTOL. 2000. Yearling moose body mass: importance of first year's growth rate and selective feeding. Alces 36:53–59.

HOSMER, D. W., AND S. LEMESHOW. 1989. Applied Logistic Regression. John Wiley and Sons, New York, USA.

HULTEN, E. 1968. Flora of Alaska and Neighboring territories. Stanford University Press, Stanford, California, USA.

KEECH, M. A., T. R. BOWYER, J. M. VER HOEF, R. D. BOERTJE, B. W. DALE, AND T. R. STEPHENSON. 2000. Life-history consequences of maternal condition in Alaskan moose. Journal of Wildlife Management 64:450–462.

KIELLAND, K., AND J. BRYANT. 1998. Moose herbivory in taiga: Effects on biogeochemistry and vegetation dynamics in primary succession. Oikos 82:377–383.

———, AND T. OSBORN. 1998. Moose browsing on feltleaf willow: optimal foraging in relation to plant morphology and chemistry. Alces 34:149–155.

———, J. BRYANT, AND R. RUESS. 1997. Moose herbivory and carbon turnover of early successional stands in Interior Alaska. Oikos 80:25–30.

LERESCHE, R. E. 1974. Moose migrations in North American. Naturaliste Canadien 101:393–415.

LERESCHE, R. E., R. H. BISHOP, AND J. W. COADY. 1974. Distribution and habitats of moose in Alaska. Naturaliste Canadien 101:143–178.

LYON, J. L. 1970. Length- and weight-diameter relations of serviceberry twigs. Journal of Wildlife Management 34:456–460.

MACHIDA, S. 1979. Differential use of willow species by moose in Alaska. Thesis, University of Alaska Fairbanks, Fairbanks, Alaska, USA.

MALLEK, E. J. 1999. Plant architecture and forage selection by moose. Thesis, University of Alaska Fairbanks, Fairbanks, Alaska.

MCINNES, P. F., R. J. NAIMAN, J. PASTOR, AND Y. COHEN. 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. Ecology 73:2059–2075.

MCNAY, M. 1983. Alaska Department of Fish and Game. Moose habitat assessment on the Alaska Peninsula. Unpublished.

MILKE, G. C. 1969. Some moose–willow relationships in the interior of Alaska. Thesis, University of Alaska Fairbanks, Fairbanks, Alaska, USA.

MIQUELLE, D. G., J. M. PEEK, AND V. VAN BALLENBERGHE. 1992. Sexual segregation in Alaskan moose. Wildlife Monographs 122.

MOEN, R., J. PASTOR, AND Y. COHEN. 1997. A Spatially explicit model of moose foraging and energetics. Ecology 78:505–521.

MOORE, D. S., AND G. P. MCCABE. 1993. Introduction to the Practice of Statistics. Second edition. W. H. Freeman and Company, New York, USA.

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION. 2001. http://www.wrcc.dri.edu/cgi-bin/cliRECtM.pl?akfair [Web Page]. Accessed 2001.

NATIONAL RESOURCE CONSERVATION SERVICE. 2001. http://aksnow.akanchorag.fsc.usda.gov/ambcs/pub/sc_sum_ak [Web Page]. Accessed 2001.

OLDEMEYER, J. L. 1982. Estimating production of paper birch and utilization by browsers. Canadian Journal of Forestry Research 12:52–57.

———, A. W. FRANZMANN, A. L. BRUNDAGE, P. D. ARNESON, AND A. FLYNN. 1977. Browse quality and the Kenai moose population. Journal of Wildlife Management 41:533–542.

PEEK, J. M. 1998. Habitat relationships. Pages 351–376 *in* A. W. Franzmann, and C. C. Schwartz, editors. Ecology and Management of North American Moose. Wildlife Management Institute. Washington D.C., USA

———, D. L. URICH, AND R. J. MACKIE. 1976. Moose habitat selection and relationships to forest management in northeastern Minnesota. Wildlife Monographs 48.

REGELIN, W. L., C. C. SCHWARTZ, AND A. W. FRANZMANN. 1987. Effects of forest succession on nutritional dynamics of moose forage. Swedish Wildlife Research Supplement 1:247–263.

RENECKER, L. A., AND R. J. HUDSON. 1986. Seasonal foraging rates of free-ranging moose. Journal of Wildlife Management 50:143–147.

RISENHOOVER, K. L. 1985. Intraspecific variation in moose preference for willows. Pages 58-63 *in* F. D. Provenza, J. T. Flinders, and E. D. McArthur, compilers. Proceedings--Symposium on plant-herbivore interactions, snowbird, Utah, 7–9 August 1985. pp. 58–63.

———. 1986. Winter activity patterns of moose in Interior Alaska. Journal of Wildlife Management 50:727–734.

———. 1987. Winter foraging strategies of moose in subarctic and boreal forest habitats. Dissertation, Michigan Technical University, Houghton, Michigan, USA.

———. 1989. Composition and quality of moose winter diets in Interior Alaska. Journal of Wildlife Management 53:568–577.

SAETHER, B. E. 1990. The impact of different growth pattern on the utilization of tree species by a generalist herbivore, the moose *Alces alces*: implications of optimal foraging theory. Pages 323–340 *in* R. N. Hughes, editor. Behavioral basis for food selection. Springer Verlag. Heidelberg.

———, AND R. ANDERSEN. 1990. Resource limitation in a generalist herbivore, the moose *Alces alces*: Ecological constraints on behavioural decisions. Canadian Journal of Zoology 68:993–999.

SCHWARTZ, C. C., AND A. W. FRANZMANN. 1989. Bears, wolves, moose, and forest succession, some management considerations on the Kenai Peninsula, Alaska. Alces 25:1–10.

———, W. L. REGELIN, AND A. W. FRANZMANN. 1988. Estimates of digestibility of birch, willow, and aspen mixtures in moose. Journal of Wildlife Management 52:33–37.

SEAMAN, D. E., B. GRIFFITH, AND R. A. POWELL. 1998. KERNELHR: a program for estimating animal home ranges. Wildlife Society Bulletin 26:95–100.

SHIPLEY, L. A., AND D. E. SPALINGER. 1992. Mechanics of browsing in dense food patches: effects of plant and animal morphology on intake rate. Canadian Journal of Zoology 70:1743–1752.

———, AND D. SPALINGER. 1995. Influence of size and density of browse patches on intake rates foraging decisions of young moose and white-tailed deer. Oecologia 104:112–121.

———, A. ILLIUS, K. DANELL, N. HOBBS, AND D. SPALINGER. 1999. Predicting bite size selection of mammalian herbivores: A test of a general model of diet optimization. Oikos 84(1):55–68.

SIMPSON, D. T. 1986. Key for winter identification of *Salix* in Interior Alaska. Alaska Department of Fish and Game, Division of Wildlife Conservation, Fairbanks, Alaska, USA.

SNEDECOR, G. W., AND W. G. COCHRAN. 1980. Statistical methods, Seventh edition. Iowa State University Press, Ames, Iowa.

SPALINGER, D. E., AND N. T. HOBBS. 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. American Naturalist 140:325–348.

STEIGERS, W. D., AND E. F. BECKER. 1986. Moose food habits and nutritional quality forage in the middle Susitna River basin, Alaska. LGL, Anchorage, Alaska, USA.

SWEANOR, P. Y., AND F. SANDEGREN. 1988. Migratory behavior of related moose. Holarctic Ecology 11:190–193.

———. 1989. Winter-range philopatry of seasonally migratory moose. Journal of Applied Ecology 26:25–33.

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

TODD, J. W., AND R. M. HANSEN. 1973. Plant fragments in the feces of bighorns as indicators of food habits. Journal of Wildlife Management. 37:363–365.

U.S. BUREAU OF LAND MANAGEMENT. 1997. Military operational area mitigation effectiveness study - habitat phase (Tanana Flats). U.S. Bureau of Land Management, Anchorage, Alaska, USA.

VAN BALLENBERGHE, V. 1977. Migratory behavior of moose in southcentral Alaska. Transactions of the 13th International Congress of Game Biologists 13:103–109.

VENABLES, W. N., AND B. D. RIPLEY. 1997. Modern applied statistics with S-PLUS, Second edition. Springer, New York, USA.

VIVAS, H., B. E. SAETHER, AND R. ANDERSEN. 1991. Optimal twig-size selection of a generalist herbivore, the moose *Alces alces* : Implications for plant herbivore interactions. Journal of Animal Ecology 60:395–408.

WEIXELMAN, D. A., R. T. BOWYER, AND V. VAN BALLENBERGHE. 1998. Diet selection by Alaskan moose during winter: Effects of fire and forest succession. Alces 34:213–238.

WHITE, R. G. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. Oikos 40:377–384.

WOLFF, J., AND J. COWLING. 1981. Moose browse utilization in Mount McKinley National Park, Alaska. Canadian Field-Naturalist 95:85–88.

———, AND J. C. ZASADA. 1979. Moose habitat and forest succession on the Tanana River floodplain and Yukon–Tanana upland. Proceedings of the North American moose conference and workshop 15:213–244.

Table 1. Number of sites where forage biomass production and removal was estimated, stratified by winter range (WR), historic relative moose density (HD) and current relative moose density (CD), central Tanana Flats and adjacent Alaska Range Foothills, Alaska, 2000.

WR	HD	CD	Forage density	*n*
Resident	Low	Low	Low	5
		Low	High	7
		High	Low	5
		High	High	7
	High	Low	Low	5
		Low	High	7
		High	Low	5
		High	High	7
Migratory	Low	Low	Low	5
		Low	High	7
		High	Low	5
		High	High	7
	High	Low	Low	4
		Low	High	7
		High	Low	5
		High	High	7
			Total:	95

Table 2. Mean digestibility of forage groups used to correct percent relative density in fecal pellets to proportional forage intake, central Tanana Flats and adjacent Alaska Range Foothills, Alaska, 2000. Sample sizes were the number of literature-based estimates used to calculate the mean.

	Forage groups					
	Betula	*Salix*	*Alnus*	*Populus*	All shrubs	Moss
IVDMD[a]	29.6	35.9	33.1	43.4	35.3	20.3
(*n*)	12	18	3	8	41	1

[a] IVDMD was in vitro dry matter disappearance (digestibility)

Table 3. Regression coefficients relating twig diameter to dry mass for forage species in resident and migratory winter ranges, central Tanana Flats and adjacent Alaska Range Foothills, Alaska, 2000.

Species	Winter range	a	b	*n*	σ^2	R^2
Betula papyrifera	migratory	0.02	3.33	105	0.093	0.98
	resident	0.02	3.30	154	0.140	0.97
Populus balsamifera	migratory	0.03	2.77	117	0.068	0.96
	resident	0.04	2.83	100	0.095	0.95
Populus tremuloides	migratory	0.04	2.80	147	0.092	0.98
	resident	0.06	2.44	112	0.098	0.95
Salix alaxensis	migratory	0.01	3.44	526	0.248	0.90
	resident	0.02	3.28	225	0.177	0.95
Salix arbusculoides	resident	0.03	3.28	123	0.158	0.96
Salix bebbiana	migratory	0.03	3.00	178	0.099	0.96
	resident	0.02	3.36	167	0.140	0.97
Salix planifolia pulchra	migratory	0.04	3.03	363	0.248	0.93
	resident	0.04	2.99	274	0.195	0.94

a and b were the intercept and slope used in the curvilinear relationship of log transformed diameter used to predict dry mass (y) as $y = ax^b$.

n was the sample size of (diameter, dry mass) pairs used in the regression.

σ^2 was mean square error and was used in the conversion of logarithmic estimates to arithmetic estimates.

R^2 was the correlation coefficient of the arithmetic scale regressions of diameter and dry mass.

Table 4. Number of winter radiolocations of adult female moose used to estimate current relative density of moose (CD), Tanana Flats and adjacent Alaska Range Foothills, Alaska, 1998–2000.

Year	Month	Flats	Foothills	Total
1998	Late Sep	17	13	30
	Oct	5	4	9
	Nov	15	14	29
1999	Jan	17	12	29
	Feb	17	10	27
	Mar		4	4
	Early Apr	16	13	29
	Late Sep	15	13	28
	Oct	14	12	26
	Nov/Dec	13	14	27
2000	Jan/Feb	10	13	23
	Total:	139	122	261

Table 5. Forage plant presence/absence model, central Tanana Flats and adjacent Alaska Range Foothills, Alaska, 2000.

Final logistic regression model components		
Variable	Coefficient	SE
Intercept	0.99	0.25
WR[a]	-1.32	0.28
CD[b]:HD[c]	-0.98	0.41
HD	0.93	0.39
HD:WR	-0.83	0.42
CD	0.31	0.28

[a] WR was winter range (migratory/resident).

[b] CD was current moose density (high/low).

[c] HD was historic moose density (high/low).

Table 6. Mean forage biomass, mean differences, and 95% CI for mean differences for all strata classes, central Tanana Flats and adjacent Alaska Range Foothills, Alaska, 2000.

Strata	Level	Mean	Mean difference	Low 95% CI difference	High 95% CI difference
Production:					
WR	Foothills	235	45	-165	305
	Flats	190			
CD	High	296	168	-40	420
	Low	128			
HD	High	147	-129	-379	87
	Low	276			
Removal:					
WR	Foothills	105	42	-48	160
	Flats	64			
CD	High	118	69	181	-22
	Low	49			
HD	High	65	-39	-147	62
	Low	103			

Table 7. Summary of comparisons between central Tanana Flats and adjacent Alaska Range Foothills winter ranges, Alaska, 2000

Comparison	Flats	Foothills	Significance
Short yearling weight	154 kg	172 kg	($P < 0.0001$)
Percent of sample points with forage	79%	41%	($P < 0.001$)
Percent of land area with forage present	30%	22.5%	($P < 0.001$)
Mean forage biomass	190 kg/ha	235 kg/ha	($P > 0.05$)
Mean forage removal	64 kg/ha	105 kg/ha	($P > 0.05$)
Percent biomass removed	33%	45%	($P = 0.12$)
Mean bite diameter	3.0 mm	3.3 mm	($P < 0.001$)
Mean bite mass	0.81 g	1.10 g	($P < 0.05$)
Proportion of most preferred willow species in biomass	8%	94%	($P < 0.001$)
Mean DCAG[a] of willow twigs	2.3 mm	3.1 mm	($P < 0.001$)
Mean mass of willow twigs	0.38 g	0.90 g	($P < 0.05$)
Percent of willow twigs larger than mean willow bite size	22%	43%	($P < 0.001$)
Predicted daily dry matter intake, during winter	4.5 kg	6.2 kg	N/A
Predicted daily dry matter intake, end of winter	3.1 kg	4.4 kg	N/A
Percent plants with broomed architecture	72%	77%	($P > 0.05$)

[a] DCAG was the diameter at the base (bud scar) of current annual growth.

Table 8. Number of moose fecal pellet groups collected during various time periods throughout the winter of 1999–2000, central Tanana Flats and adjacent Alaska Range Foothills winter ranges, Alaska.

	Winter Range	
Date(s)	Migratory	Resident
5-Dec-00	20	12
7-Jan-00		10
Late Jan-00	20	16
12-Feb-00	8	22
Late Feb-00	20	
Mar-00	21	19
8-Apr-00	10	
Mar-99	22	21
Totals:	121	100

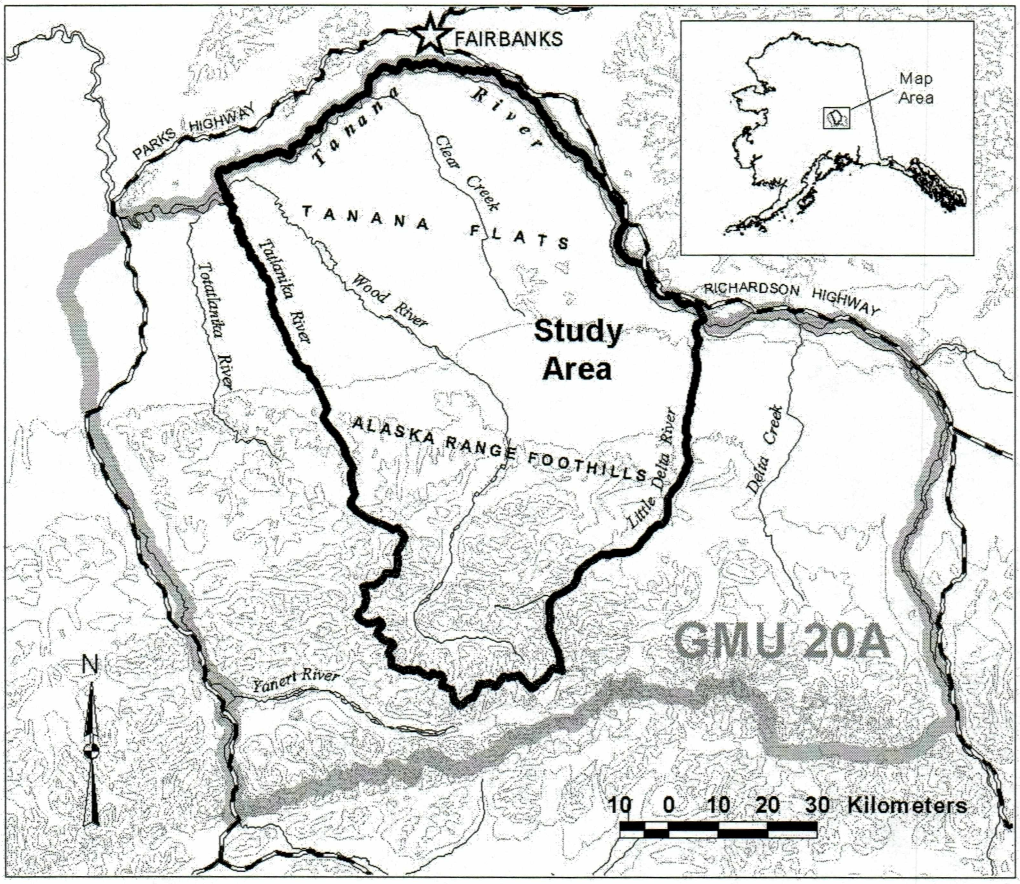


Fig. 1. The study area (6,730 km^2) contained the central Tanana Flats and adjacent Foothills of the Alaska Range, within Game Management Unit (GMU) 20A, Alaska (Boertje et al. 1999).

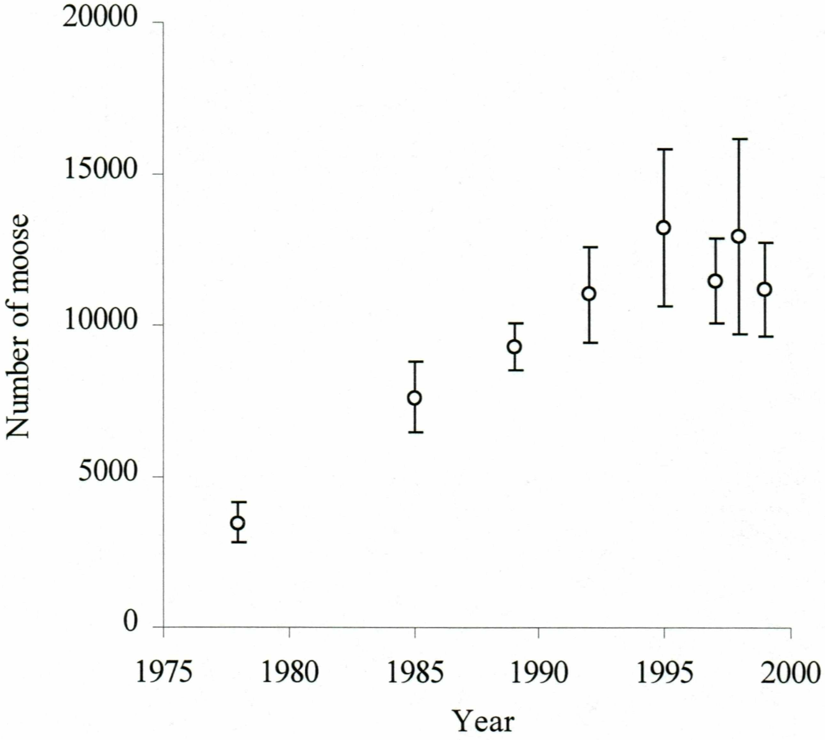


Fig. 2. Moose population estimates (± 90% CI) in 13,044 km^2 of moose habitat in Game Management Unit 20A, Tanana Flats and adjacent Alaska Range Foothills, Alaska 1977–1999 (Boertje et al. 1999).

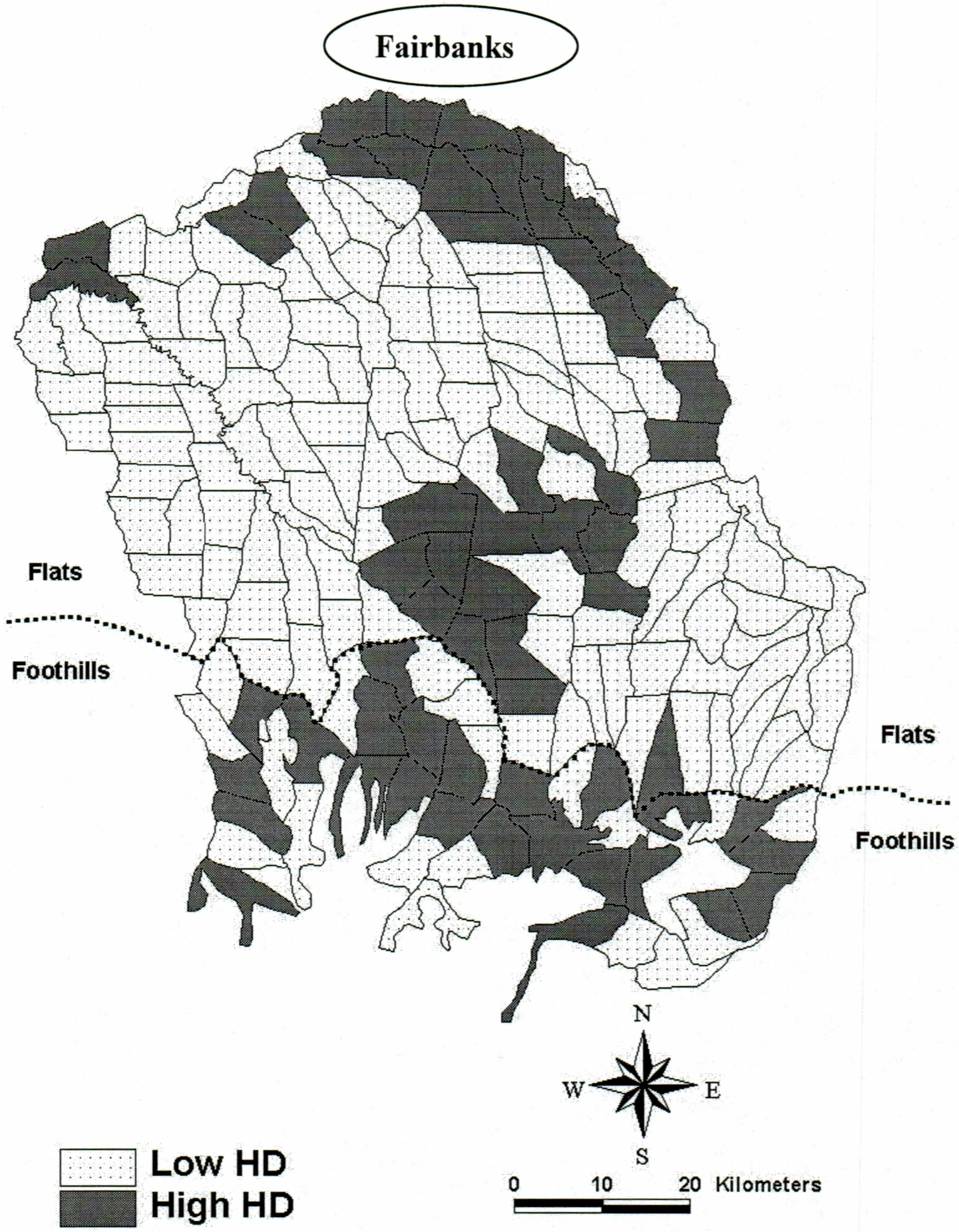


Fig. 3. Historic moose distribution (HD) from aerial survey stratification, collected by Alaska Department of Fish and Game, 1988, central Tanana Flats and adjacent Alaska Range Foothills. Low HD had an average moose density of 0.4 moose per km^2, and high HD had an average moose density of 2.3 and 1.5 moose per km^2 in the Foothills and Flats, respectively.

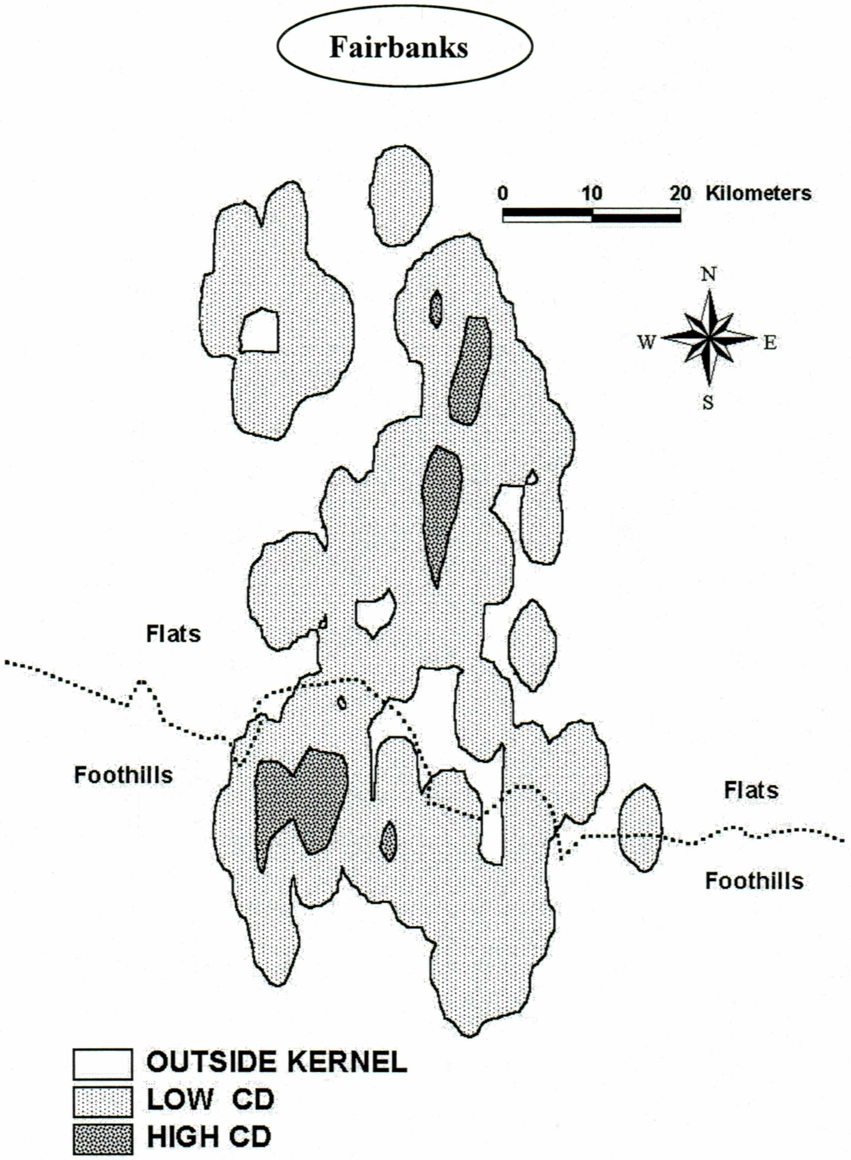
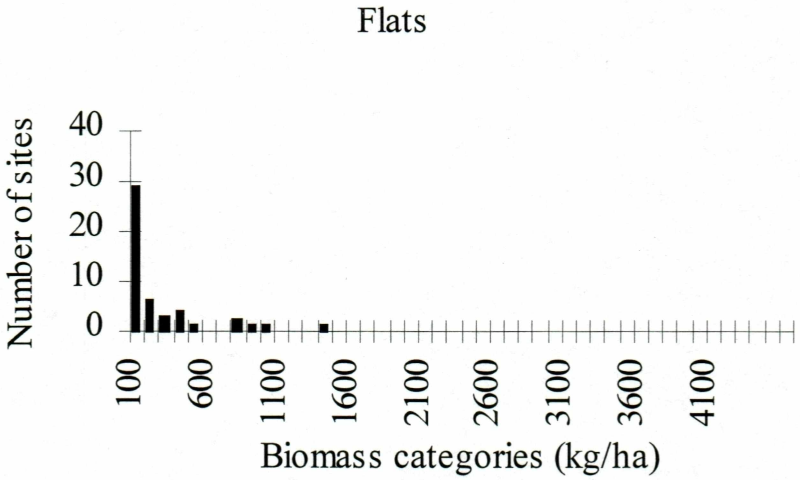


Fig. 4. Current moose distribution (CD) stratification from fixed-kernel analysis of monthly radiolocations of 32 moose evenly sampled in the central Tanana Flats and adjacent Alaska Range Foothills, winter 1999–2000. The low-density area contained 2,171 km^2 of moose habitat and the high-density area contained 170 km^2.



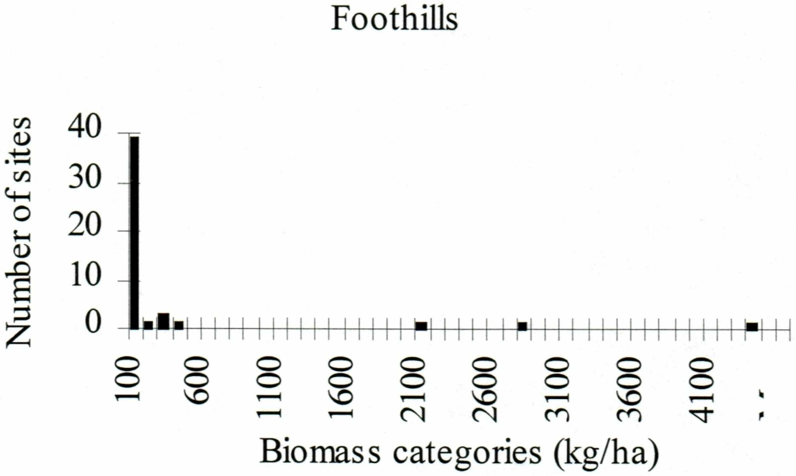
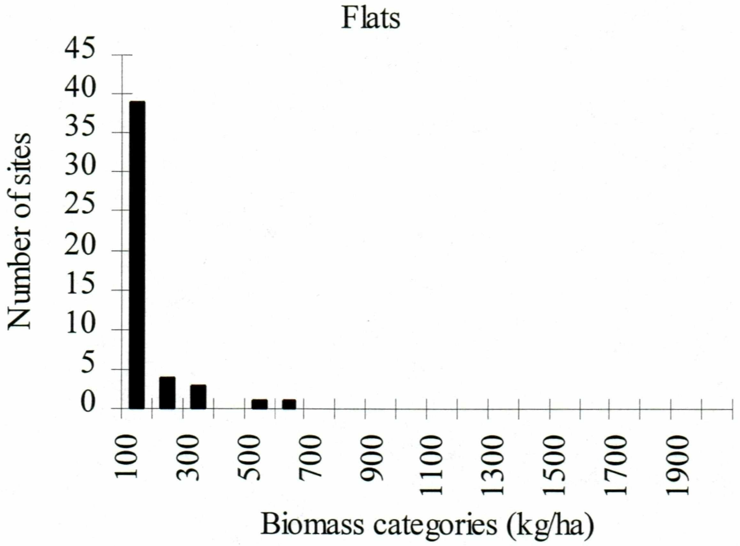


Fig. 5. Forage production estimates in the central Tanana Flats and the adjacent Alaska Range Foothills, Alaska, 2000.



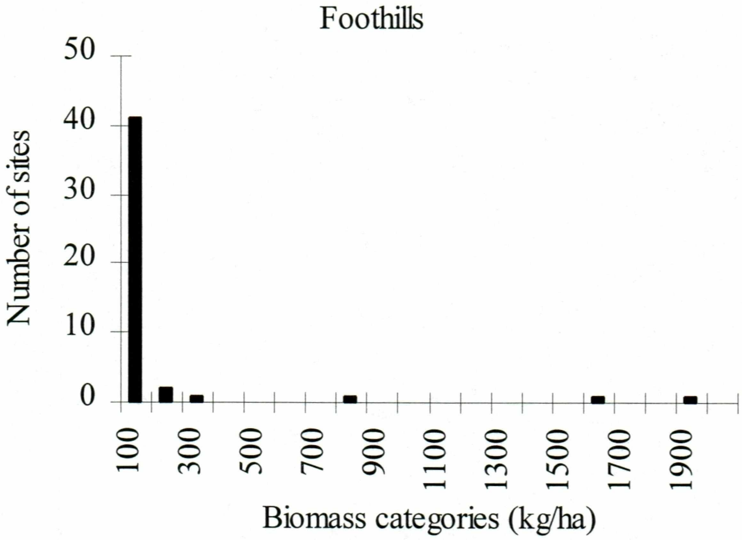


Fig. 6. Forage removal estimates in the central Tanana Flats and the adjacent Alaska Range Foothills, Alaska, 2000.

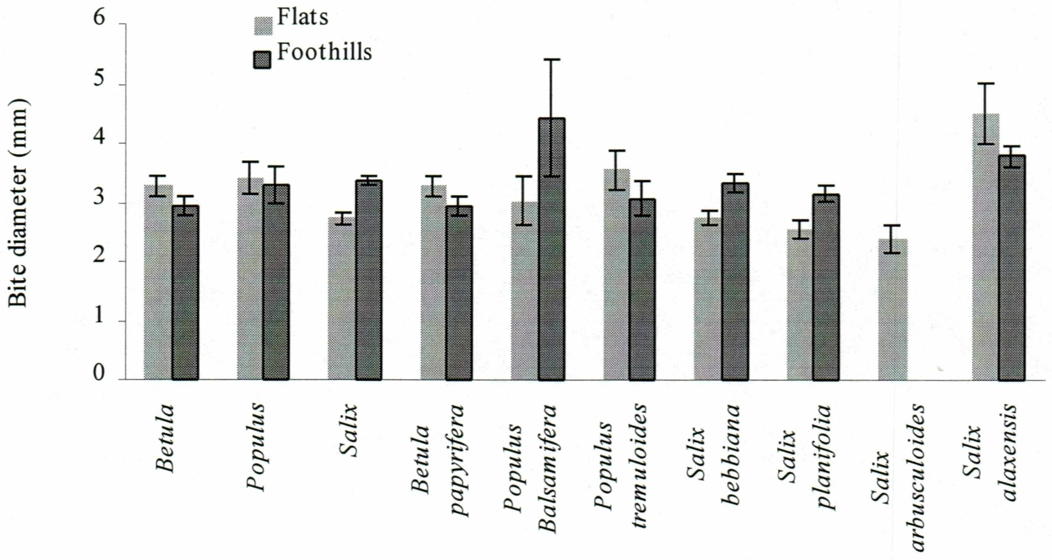


Fig. 7. Mean bite diameters with 95% CI, by species and winter range for the central Tanana Flats and adjacent Alaska Range Foothills, 2000

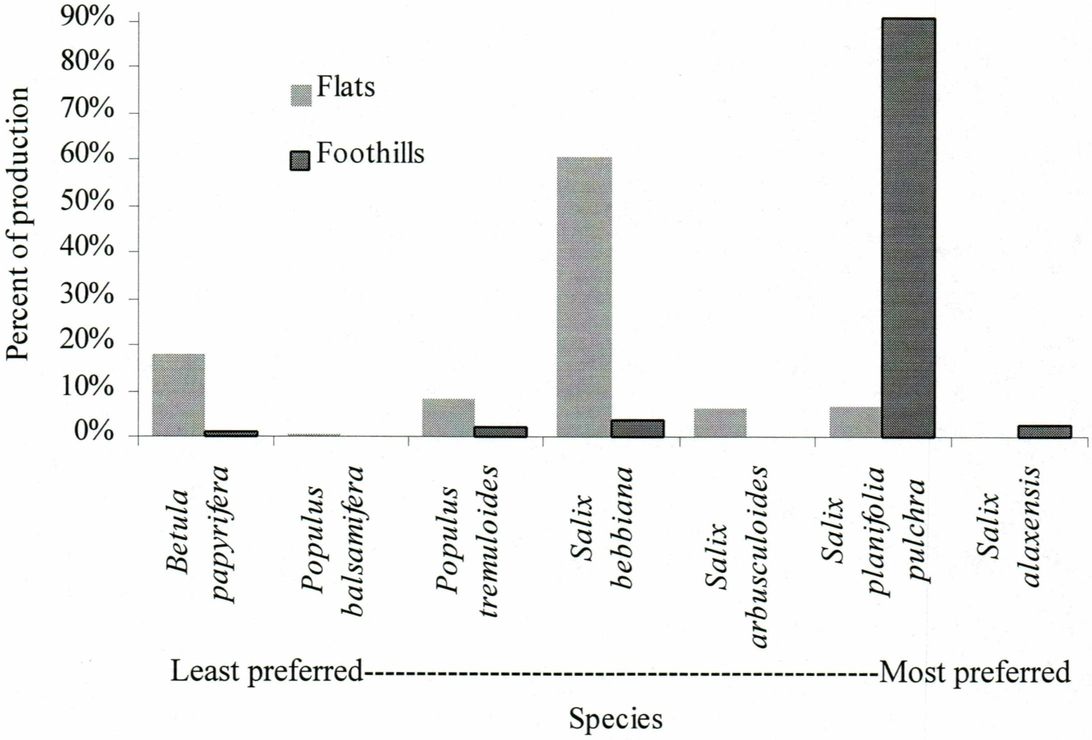


Fig. 8. Forage production by species in the winter range of resident and migratory moose, central Tanana Flats and adjacent Alaska Range Foothills, Alaska, 2000. Preference was derived from the literature (Milke 1969, Oldemeyer et al. 1977, Machida 1979, Wolff and Zasada 1979, Bryant and Kuropat 1980).

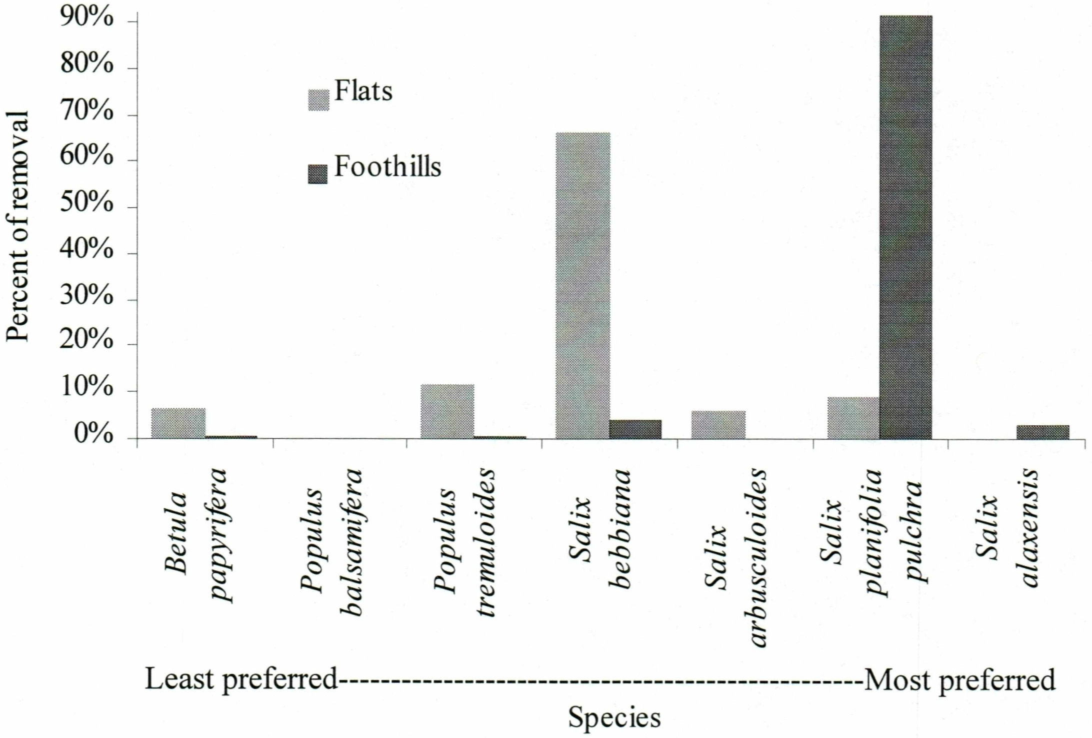


Fig. 9. Forage removal by species in the winter range of resident and migratory moose, central Tanana Flats and adjacent Alaska Range Foothills, Alaska, 2000. Preference was derived from the literature (Milke 1969, Oldemeyer et al. 1977, Machida 1979, Wolff and Zasada 1979, Bryant and Kuropat 1980).

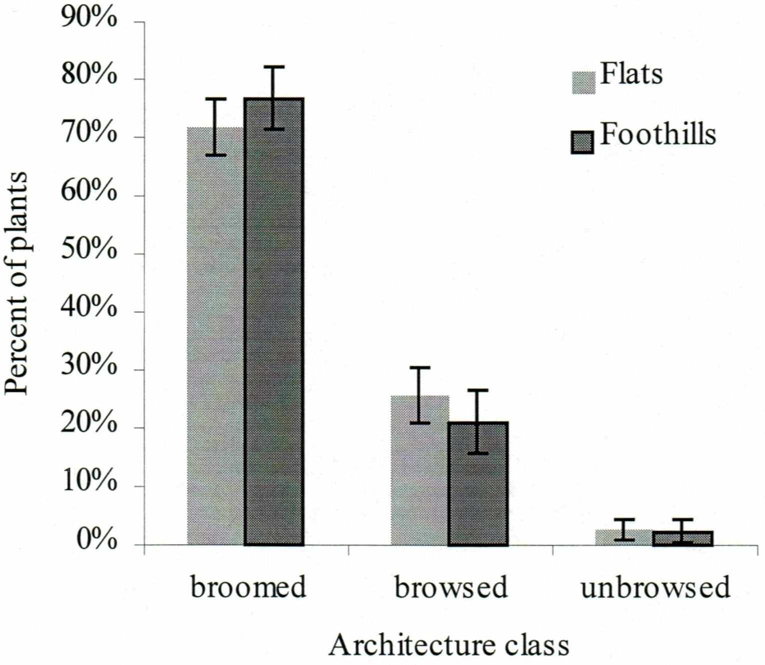


Fig. 10. Forage plant architecture for the central Tanana Flats and adjacent Alaska Range Foothills with 95% CI, 2000.

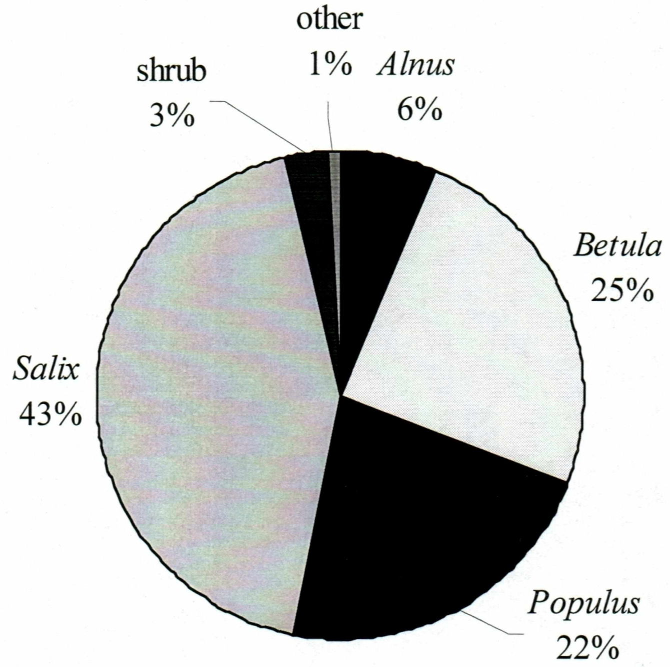


Fig. 11. Pooled winter diets of moose in the Tanana Flats and adjacent Alaska Range Foothills by genus, 1999 and 2000.

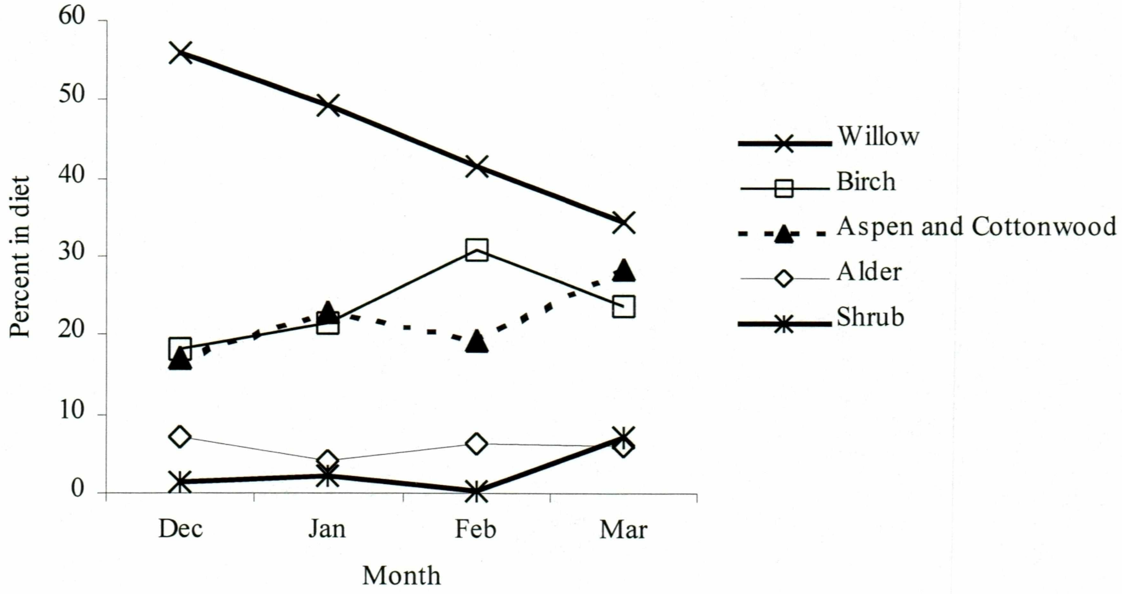


Fig. 12. Winter diets of moose in the Tanana Flats and adjacent Alaska Range Foothills, 1999 and 2000.

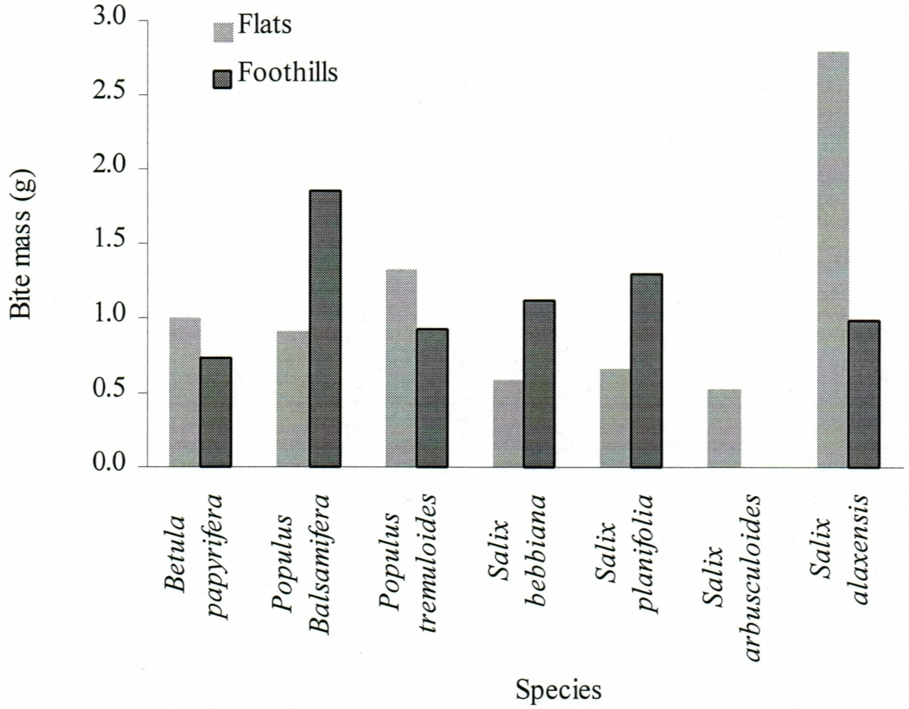


Fig. 13. Mean bite mass by species and range, estimated from mean bite diameter and diameter to mass regressions, central Tanana Flats and adjacent Alaska Range Foothills, Alaska, 2000.

APPENDIX A. BROWSE SURVEY PROTOCOL

Landscape

The method was designed for large areas (Game Management Unit or watershed level, rather than 1 acre, 1 stand level).

Plots should be distributed in a stratified random fashion. Any number of strata levels can be used. Examples include:

- Burn/nonburn
- Closed forest, Open forest, Shrubland
- Riparian/Upland
- Vegetation map cover types
- Elevation classes
- Forest species types

Timing of Sampling

Sampling should be done before leaf-out in the spring, but as late as possible in the winter so that browsing by moose throughout the winter is fully represented. In Interior Alaska, the month of April is an acceptable time-period. During and after leaf-out, vision is often hindered in the sample site. Growth and swelling of twigs during leaf-out renders regression relationships developed from fully-ormed dormant twigs useless.

Tools Needed

- A 2 m pole marked in 0.1 m increments.

- Dial Calipers (mm units).
- Winter browse key - available from ADF&G and written by Dot Simpson.
- Clipboard - closable type.
- Data sheets - contact Tom Seaton (ADF&G, Fairbanks)
- Pencils
- Marker - to label collected plants. Plants can be collected for identification in the lab, or for building mass/diameter regressions in the lab.
- Bags for collecting browse (if desired).
- Flagging tape - to mark the center of the plot for easy visibility while determining the boundary.
- GPS, extra batteries
- Compass
- Clinometer
- Tape measure or range finder

Training Required

At least 1 person in the crew should be familiar with winter browse classification to the species level. For consistency, at least 1 person should have used the method before.

Crew Size

Optimum crew size is 3–4 people, but the method may be done with 1–5 people. With 4 people, 1 person marks the boundary, 1 person counts plants, 1 person measures diameters, and 1 person records data.

Time Per Site

Time at a site can range from 10 minutes to 90 minutes. With 4 people and 0.5 m snow conditions, average time at a site is 30–40 minutes. With 2 people, average time will be 40–60 minutes. With 1 person, sites will average over an hour. Another factor that influences time at a site is diversity of woody browse species. A site with 6 species of woody browse will take about double the time a site with 2 species takes.

At the site, follow these steps

1. Locate the center of the plot. Record the following;

- Coordinates
- Plot ID
- Date
- Crew
- Stratum (however you set up your sampling scheme)
- Slope
- Aspect
- Snow depth

2. Determine the boundary of the plot (radius 15 m). This can be done with an electronic range finder, rope, pole range finder, etc.

3. Locate preferred species. If there are no preferred species in the plot, fill out a data form and state such. Then select an alternate random plot in the same strata class. Preferred species are defined as willow, aspen, birch, cottonwood with CAG leaders above 0.5 m and under 3 m.

4. Measure the snow depth. I only measure browse above the snow, so if the snow is 1 m deep, I know that my estimate missed some CAG between 0.5 and 1.0 m.

5. Look for bark stripping. Record species and how many plants. Include stripping from past years. This is an index to browsing intensity

6. Estimate the number of preferred species plants. Observe the preferred species (*Salix* spp., *Betula papyrifera, Populus* spp.). For all the preferred species plants, estimate the number of plants. The definition of a plant is a stem or group of stems that appear to enter the ground no farther than 10 cm from the nearest stem. If you find 10 stems that enter the ground in a line all less than 10 cm from each other, that is 1 plant. Be observant on taller birch, aspen, and cottonwood. These plants may have live twigs below 3.0 m that do not possess any current annual growth. If they have no current annual growth below 3.0 m, classify them as nonpreferred.

7. Count the number of broken main stems on preferred plants in the plot (i.e., 3 m *Bepa* that have been broken by moose to get at the top). Record only plants broken by moose, not snow or wind.

8. Estimate number of nonpreferred plants (spruce, tamarack, alder, *Betula glandulosa*, *Betula nana*, mature aspen, mature birch, mature cottonwood). Estimate the number of nonpreferred plants by species, along with a mean height. This includes preferred species plants that don't have CAG leaders below 3 m (i.e., mature birch and aspen). You may wish to record dead snags. Provide a mean height for all.

9. Randomly choose 3 plants of each preferred species.

10. Measure plants. On those 3 plants of each preferred species, record the following for each plant:

- Height above ground.
- Number of CAG stems between 0.5 m and 3.0 m that were present before browsing (above snow).
- Proportion of dead material of the plant by volume between 0.5 m and 3.0 m.
    - X = no or very little dead material < 5% by volume of live material
    - L = less dead than live material
    - M = more dead than live material
- Randomly choose a stem (a stem is a portion of the plant to which young twigs are attached) of the plant and measure 10 twig diameters at the base of CAG, as well as DPB measurement if the twig was browsed.
    - Measure consecutively along a stem from apical terminus toward ground. If you cannot find enough twigs on a stem, randomly select another stem and continue.
    - If the bite diameter (DPB) is suspected to be below this years growth, then circle the DPB measurement (i.e., if the moose bit the twig down to 2 year of 3-year-old tissue). When difficult to tell, use the unbrowsed twigs of the plant for comparison.
    - The goal is 30 CAG leaders per species per plot. If you cannot get 30 twigs from 3 plants, continue to select plants. If there are not 30 twigs in the whole plot, measure all there are.

11. Architecture class - this is a measure of browsing intensity over the visible history of the plant.

- Broomed - any of the following conditions:
    - (sapling type plants) the main apical stem has been broken by moose. Look back through the history of the plant, this may have happened 2–10 years before you measured it.
    - (bushy type plants) more than half of the CAG stems arise from lateral stems that were produced as a result of browsing. Look back through stems that are many years old.
- Browsed
    - Has been browsed some in the past, but browsing has not significantly affected its growth.
    - Less than half of CAG twigs between 0.5 and 3.0 m arise from lateral stems that were produced from browsing.
- Unbrowsed
    - There is no visible evidence that moose have ever browsed this plant.

12. Observe nonpreferred species for evidence of browsing. If so, repeat Step 10 and 11 on 1 representative plant of each species. Choose a plant that represents the average size and use for that species in the plot. Detailed notes may be required.

13. Record Notes

- Record evidence that the site has burned, and estimate an age if possible. Charred stumps and young, even-aged stands are clues. A burn map from your local land management agency may help you estimate the age of the burn.

- If the snow was drifted, record the range of depths in the plot.
- Record the successional stage of the site.

  Examples include:

    - Willow shrub transitioning to spruce sapling
    - Birch sapling transitioning to mature birch forest
    - Climax black spruce forest
    - Climax white spruce forest
    - Marsh land with willow pockets
    - Primary succession willow on river bar, young alder sprouting underneath
    - Mature spruce/birch forest transitioning to spruce forest
    - Aspen forest transitioning to spruce forest
    - Climax high elevation shrub land
    - etc.
- Record if moose appear to have preferred a species on the plot.
    - Example: ‘cottonwood CAG was heavily browsed while aspen was untouched’.

Species Abbreviations Used on Data Sheet

With CAG between 0.5 m and 3.0 m

Poba	*Populus balsamifera*	Cottonwood
Potr	*Populus tremuloides*	Aspen
Bepa	*Betula papyrifera*	Paper birch
Saal	*Salix alaxensis*	Felt-leaf willow
Sapu	*Salix planifolia pulchra*	Diamondleaf willow
Sabe	*Salix bebbiana*	Bebb willow
Sala	*Salix lanata*	Richardson willow
Sain	*Salix interior*	Sandbar willow
Sano	*Salix novae-angliae*	Tall Blueberry willow
Saar	*Salix arbusculoides*	Littletree
etc.		

Without CAG between 0.5 m and 3.0 m

Mpoba	Cottonwood with no CAG below 3 m
Mpotr	Aspen with no CAG below 3 m
Msaal	Feltleaf willow with no CAG below 3 m
Msabe	Bebb willow with no CAG below 3 m
etc.	

14. Data entry. For a Microsoft ACCESS database entry program, contact Tom Seaton (ADF&G, Fairbanks).

APPENDIX B. ANALYSIS EQUATIONS

Estimated Dry Mass Based on Twig Diameter

Dry mass on the log scale was predicted using linear regression,

$$y_i = a + bx_i + \varepsilon_i , \tag{1}$$

where y_i is the natural logarithm of dry mass (in grams), x_i is the natural logarithm of diameter (in mm), and ε_i is an independent random error. The estimate of the intercept $\hat{a}$ and the slope $\hat{b}$ can be used to predict a new value of dry mass based on an arbitrary diameter x_0,

$$\hat{y} = \hat{a} + \hat{b}x_0 . \tag{2}$$

Thus the predicted dry mass on the original scale is, from Cressie (1993:135),

$$\hat{z} = \exp(\hat{y} + \sigma^2 / 2) , \tag{3}$$

where $\hat{y}$ is given by (2) and σ^2 is the mean square error of the random errors in (1).

Variance

The variance of prediction of new values in linear regression is given by Snedecor and Cochran (1980) as,

$$\operatorname{var}(\hat{y}) = \sigma^2 \left(1 + \frac{1}{n} + \frac{(x_0 - \bar{x})^2}{\sum (x_i - \bar{x})^2} \right),$$

where n is the number of (y_i , x_i) pairs in the regression analysis (1), and thus the approximate variance of predicted dry mass on the original scale is, from Cressie (1993:137),

$$\mathrm{var}(\hat{z}) = \left(e^{\hat{y}}\right)^2 \mathrm{var}(\hat{y})\,. \tag{4}$$

Estimated of Site Level Biomass

Let the following indices *hijk* denote the h^{th} twig for the i^{th} plant for the j^{th} species at the *k*th site. Then site biomass is estimate by,

$$\hat{B}_k = \sum_j \frac{M_{jk}}{m_{jk}} \sum_i \frac{N_{ijk}}{n_{ijk}} \sum_h \hat{z}_{hijk}\,, \tag{5}$$

where $\hat{z}_{hijk}$ is the predicted biomass (3) n_{ijk} is the number of sampled branches, N_{ijk} is the total number of branches with CAG stems on plant *i* between 0.5 m and 3.0 m, m_{jk} is the number of sampled plants, M_{kj} is the total number of plants, and $\hat{B}_k$ is the estimated biomass for the *k*th site.

Variance

Using rules of variance (e.g., Bain and Englehardt 1987:178), the variance of (5) is,

$$\mathrm{var}(\hat{B}_k) = \sum_j \frac{M_{jk}^2}{m_{jk}^2} \sum_i \frac{N_{jk}^2}{n_{jk}^2} \sum_h \mathrm{var}(\hat{z}_{hijk})\,, \tag{6}$$

where $\mathrm{var}(\hat{z}_{hijk})$ is given by (4).

Estimated Proportion of Biomass Removed Per Strata

The estimation of proportion of biomass removed is based on the ratio of removal to availability. Estimates of availability and removal were made for each site using (5).

Let R_k be the removal estimate (5) for the k^{th} site, and let A_k be the availability estimate (5) for the k^{th} site. The range-wide proportion was estimated with,

$$\hat{p}_{range} = \frac{\sum_{k\in range} R_k}{\sum_{k\in range} A_k}. \tag{7}$$

Variance

Because (7) is a ratio of random variables, the delta method (Dorfman 1938) was used to approximate the variance,

$$Var(\hat{p}) = \frac{\sum_k Var(\hat{R}_k)}{\left(\sum_k \hat{A}_k\right)^2} + \frac{\left(\sum_k \hat{R}_k\right)^2}{\left(\sum_k \hat{A}_k\right)^4} \sum_k Var(\hat{A}_k),$$

where $Var(\hat{R}_k)$ and $Var(\hat{A}_k)$ are given by (6).

APPENDIX C. TWIG AND BITE CHARACTERISTICS

Index

List of Tables

List of Figures

Introduction

The data and analyses provided in Appendix C provide some insight into moose browsing ecology that could not be addressed in the main body of the thesis. The frequency distributions of twig and bite size show what size twig moose were selecting compared to randomly selected twigs, and how various species influence that choice. The diameter to mass regression lines show how plants of the same and different species have variable shapes, which influence the ability for moose to intake browse, and influence the impact a moose can have on a particular plant. The mean twig and bite diameters found in Appendix C can be of use to managers and researchers for comparisons to other winter ranges.

Frequency Distributions of Twig and Bite Sizes

The 3 divisions of CAG in the following figures are defined as follows. CAG0 represents the basal diameter of twigs that were not bitten by moose, CAG1 represents the basal diameter of twigs that were bitten by moose, and CAG ALL represents the basal diameter of all twigs, bitten, and unbitten.

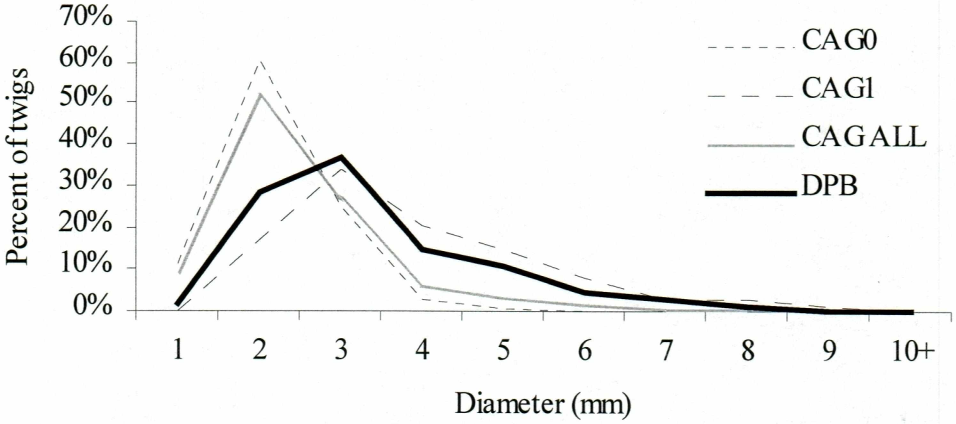


Fig. C1. Frequency distribution of *Betula papyrifera* in the Flats winter range, Game Management Unit 20A, Alaska, 2000.

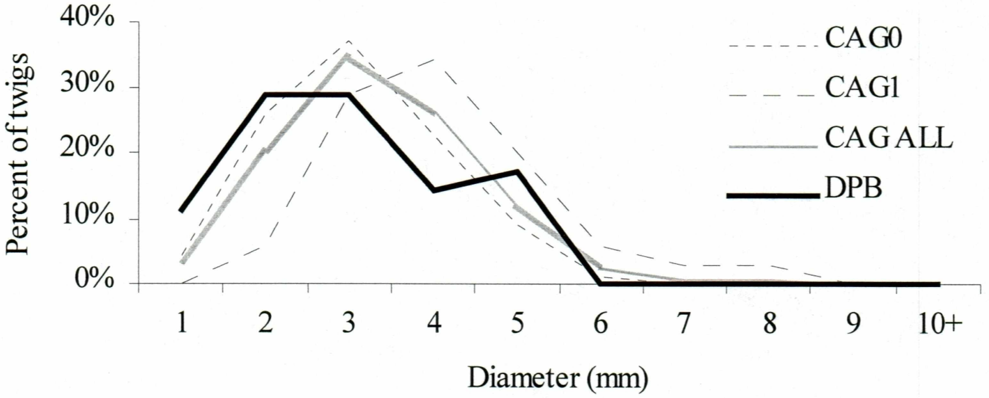


Fig. C2. Frequency distribution of *Populus balsamifera* in the Flats winter range, Game Management Unit 20A, Alaska, 2000.

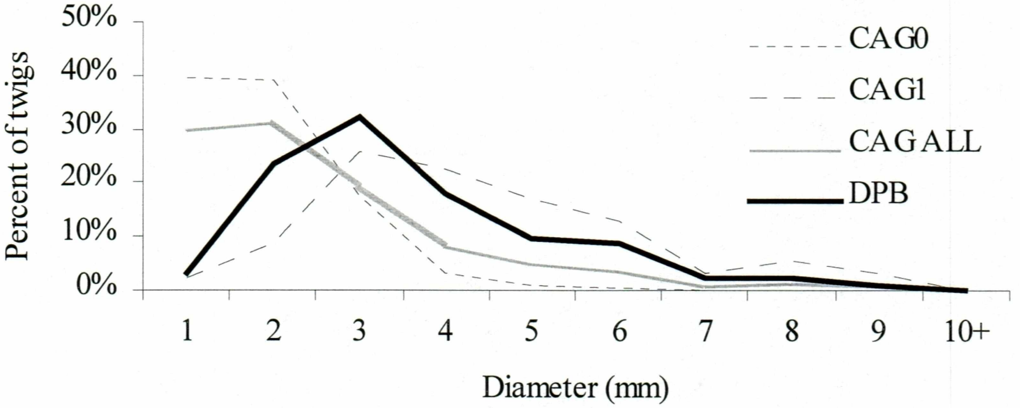


Fig. C3. Frequency distribution of *Populus tremuloides* in the Flats winter range, Game Management Unit 20A, Alaska, 2000.

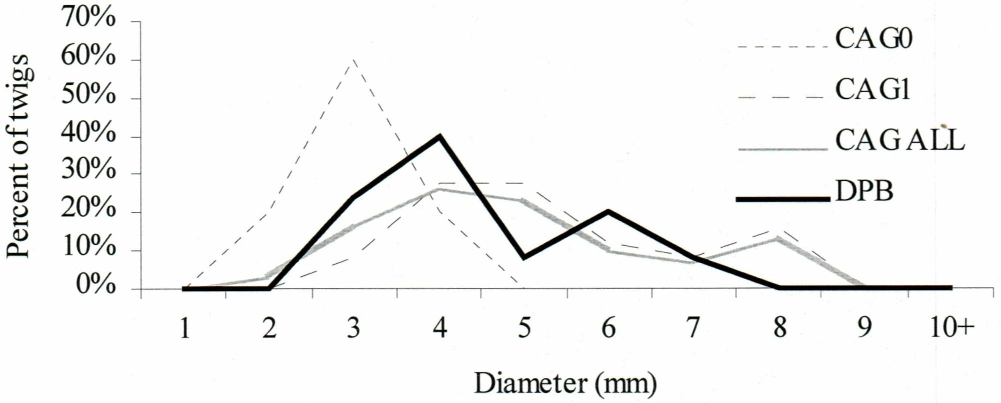


Fig. C4. Frequency distribution of *Salix alaxensis* in the Flats winter range, Game Management Unit 20A, Alaska, 2000.

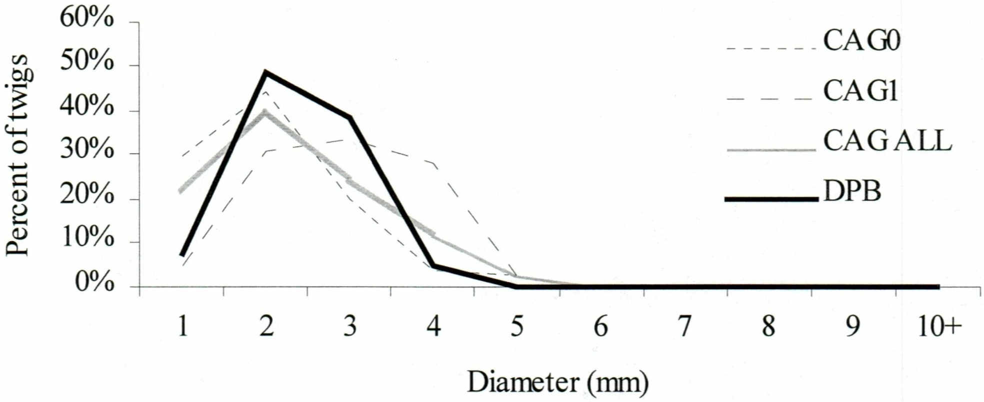


Fig. C5. Frequency distribution of *Salix arbusculoides* in the Flats winter range, Game Management Unit 20A, Alaska, 2000.

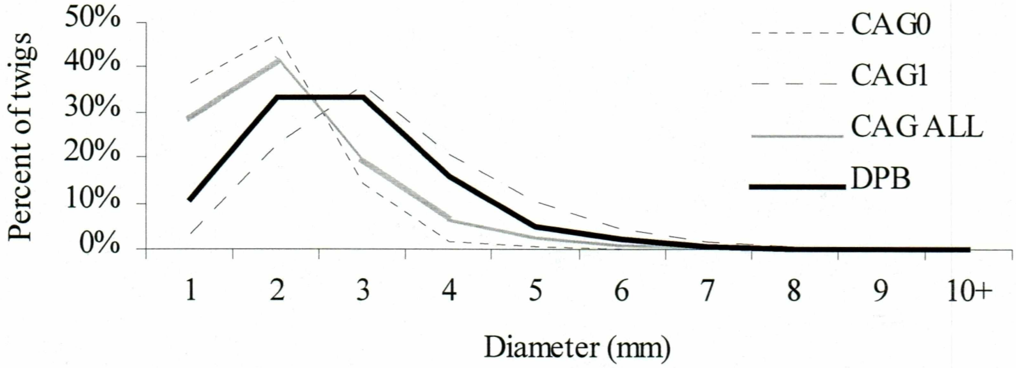


Fig. C6. Frequency distribution of *Salix bebbiana* in the Flats winter range, Game Management Unit 20A, Alaska, 2000.

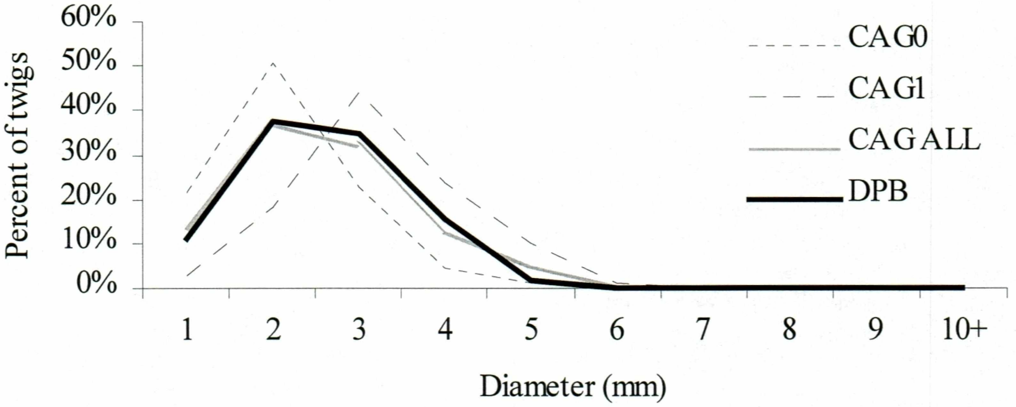


Fig. C7. Frequency distribution of *Salix planifolia pulchra* in the Flats winter range, Game Management Unit 20A, Alaska, 2000.

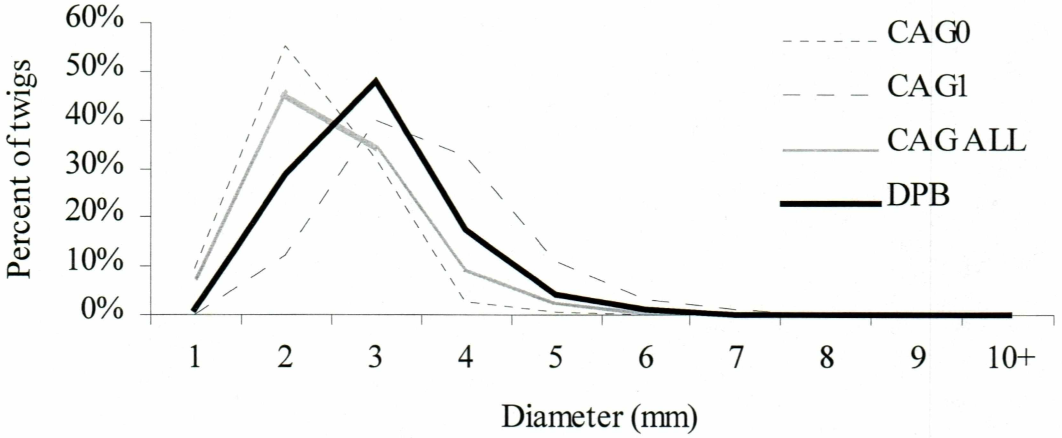


Fig. C8. Frequency distribution of *Betula papyrifera* in the Foothills winter range, Game Management Unit 20A, Alaska, 2000.

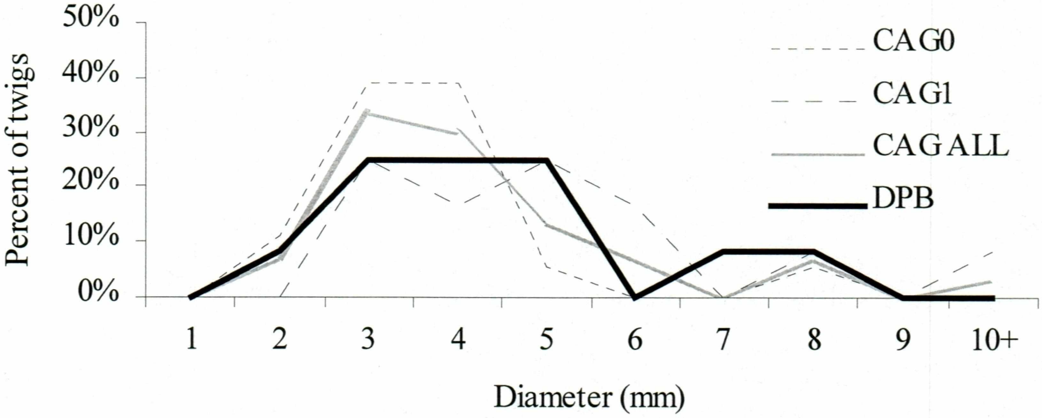


Fig. C9. Frequency distribution of *Populus balsamifera* in the Foothills winter range, Game Management Unit 20A, Alaska, 2000.

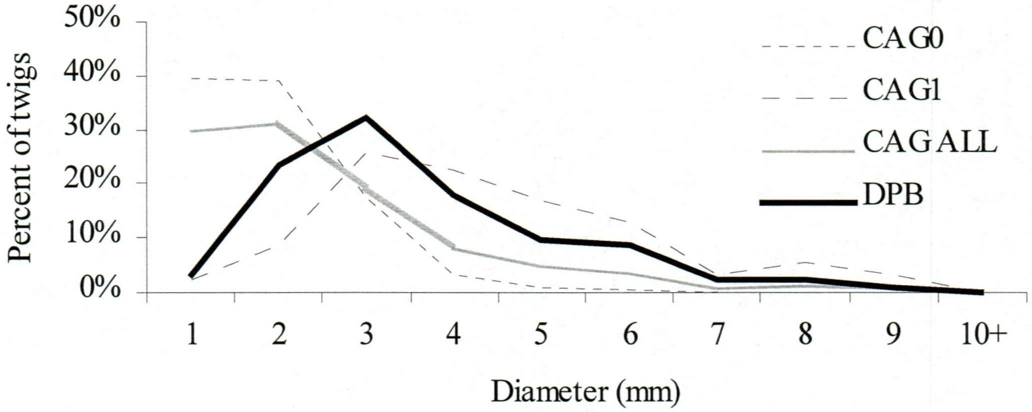


Fig. C10. Frequency distribution of *Populus tremuloides* in the Foothills winter range, Game Management Unit 20A, Alaska, 2000.

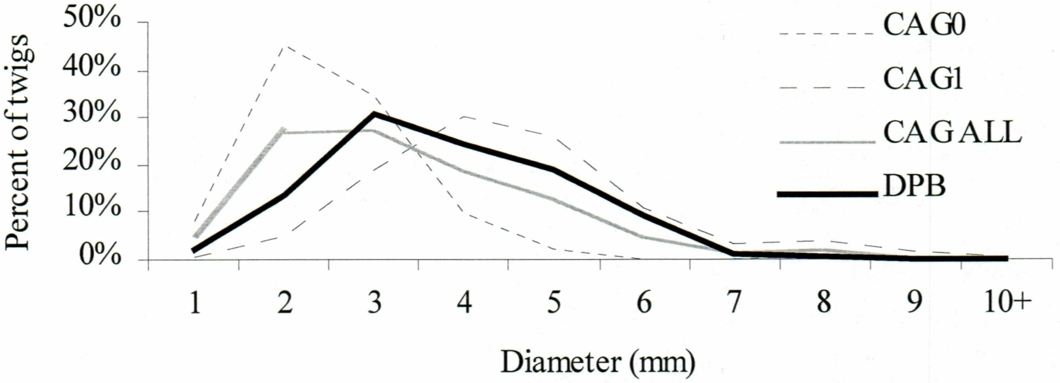


Fig. C11. Frequency distribution of *Salix alaxensis* in the Foothills winter range, Game Management Unit 20A, Alaska, 2000.

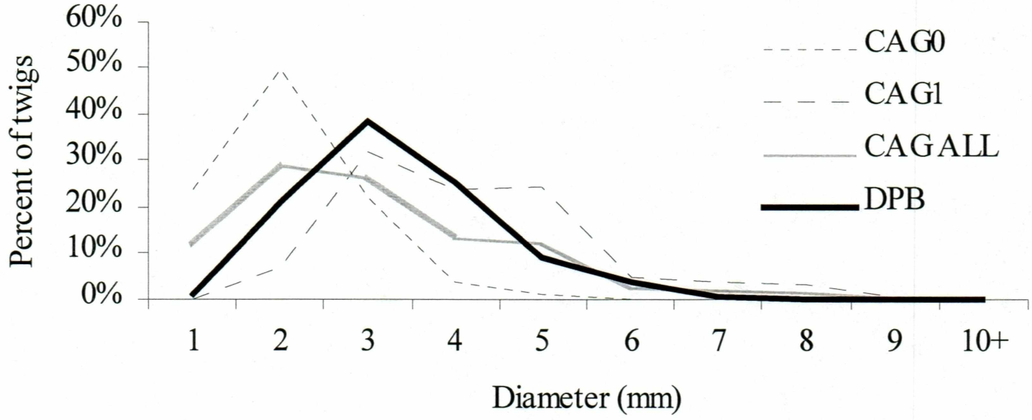


Fig. C12. Frequency distribution of *Salix bebbiana* in the Foothills winter range, Game Management Unit 20A, Alaska, 2000.

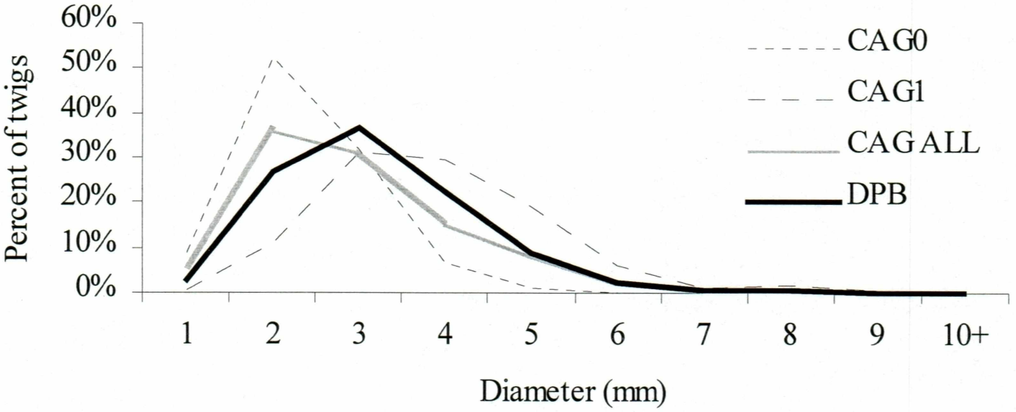


Fig. C13. Frequency distribution of *Salix planifolia pulchra* in the Foothills winter range, Game Management Unit 20A, Alaska, 2000.

Table C1. Sample sizes of twig diameters at point of browsing (DPB) and twig diameters at base of current annual growth (CAG) used in this study, Game Management Unit 20A, Alaska, 2000.

Species	Type of diameter	Flats	Foothills
Betula papyrifera	CAG	1147	418
	DPB	236	98
Populus balsamifera	CAG	124	30
	DPB	35	12
Populus tremuloides	CAG	360	249
	DPB	94	60
Salix bebbiana	CAG	1257	363
	DPB	319	176
Salix pulchra	CAG	365	866
	DPB	158	338
Salix alaxensis	CAG	30	412
	DPB	25	186
Salix arbusculoides	CAG	120	0
	DPB	39	0

Diameter to Dry Mass Regressions

Dry mass varied by twig diameter, species, and range in the study area. Abbreviations for species can be found in Appendix A. The suffix of F or H denotes Flats or Foothills, respectively.

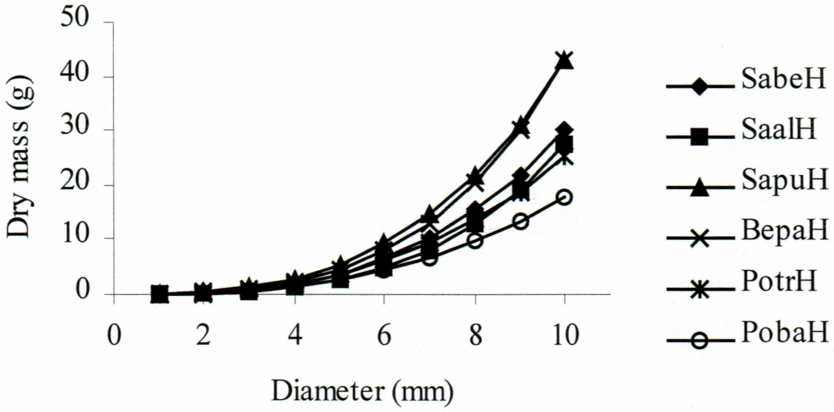


Fig. C14. Diameter to dry mass regressions for the Foothills range, Game Management Unit 20A, Alaska, 2000.

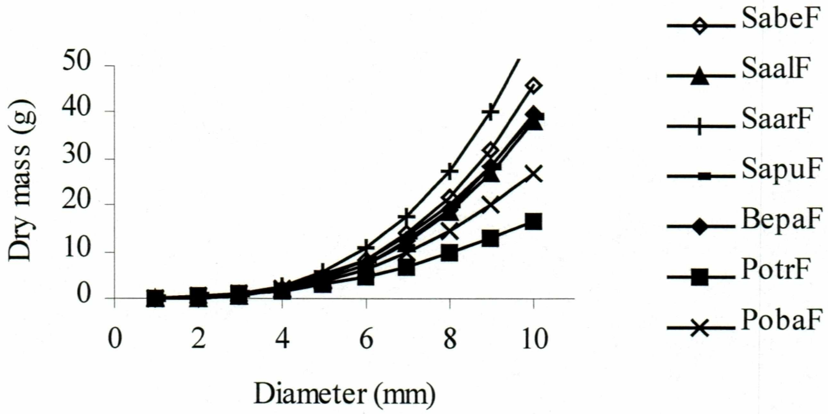


Fig. C15. Diameter to dry mass regressions for the Flats range, Game Management Unit 20A, Alaska, 2000.

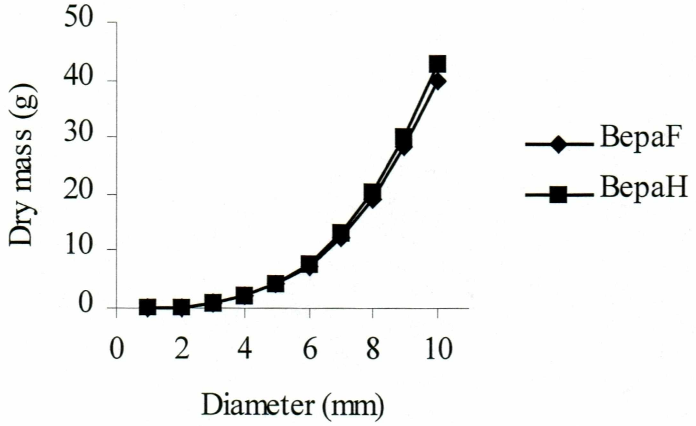


Fig. C16. Diameter to dry mass regressions for *Betula papyrifera*, Game Management Unit 20A, Alaska, 2000.

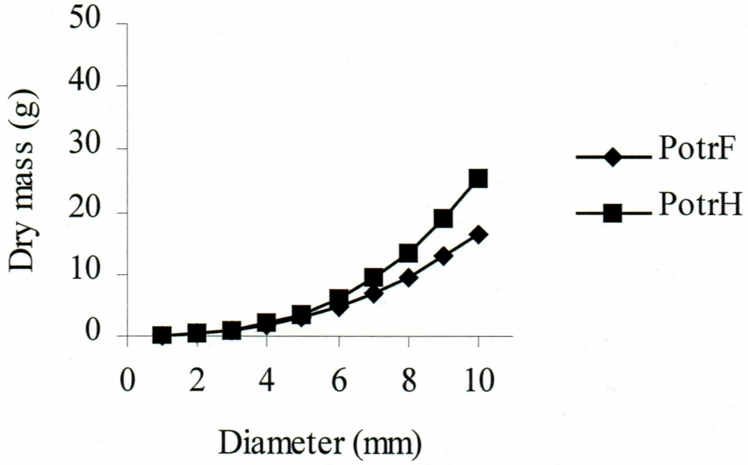


Fig. C17. Diameter to dry mass regressions for *Populus tremuloides*, Game Management Unit 20A, Alaska, 2000.

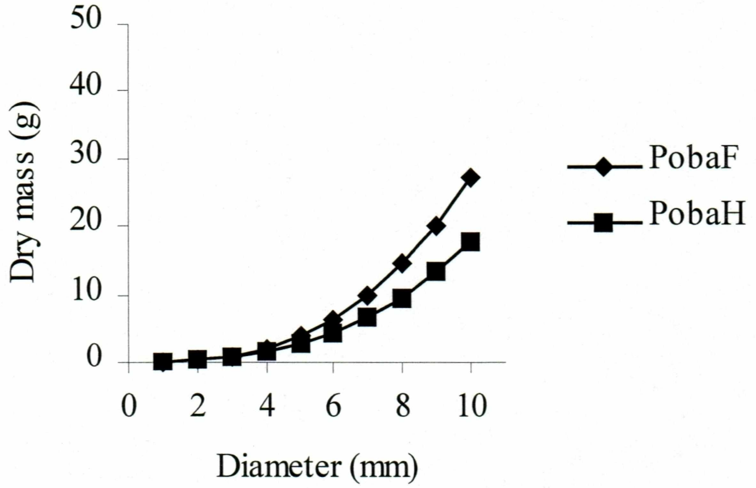


Fig. C18. Diameter to dry mass regression lines of *Populus balsamifera*, Game Management Unit 20A, Alaska, 2000.

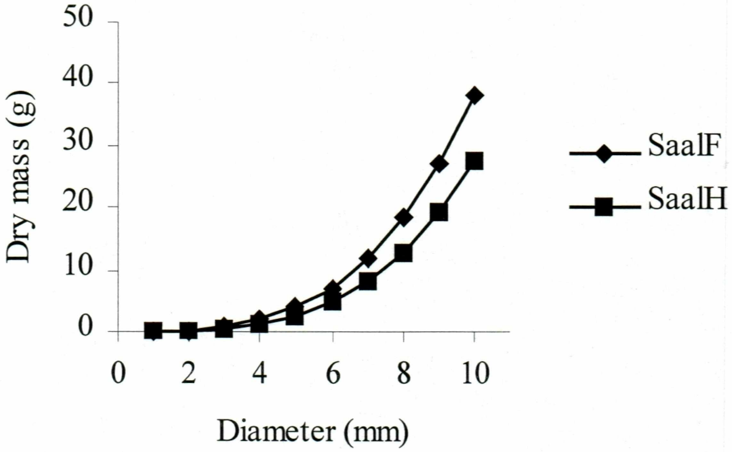


Fig. C19. Diameter to dry mass regression lines for *Salix alaxensis*, Game Management Unit 20A, Alaska, 2000.

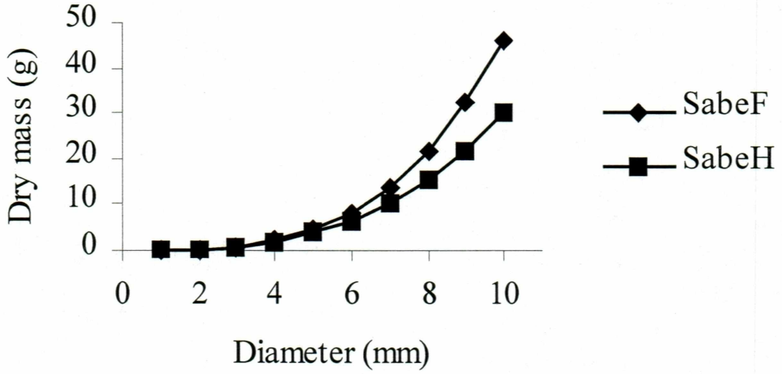


Fig. C20. Diameter to dry mass regression lines for *Salix bebbiana*, Game Management Unit 20A, Alaska, 2000.

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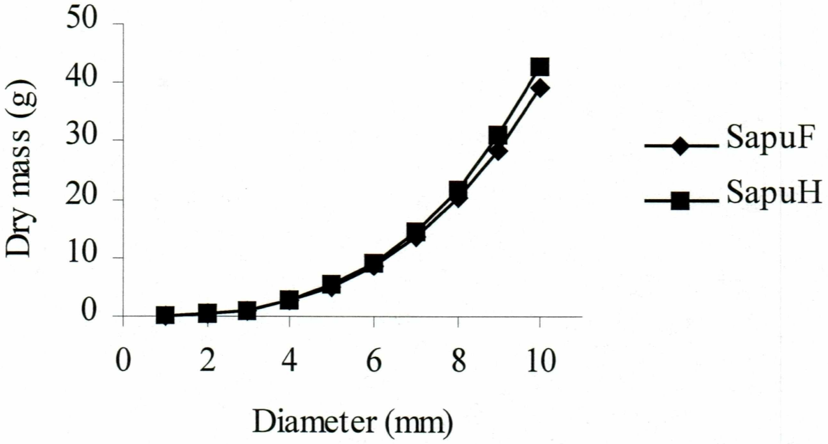

Fig. C21. Diameter to dry mass regression lines for *Salix planifolia pulchra*, Game Management Unit 20A, Alaska, 2000.

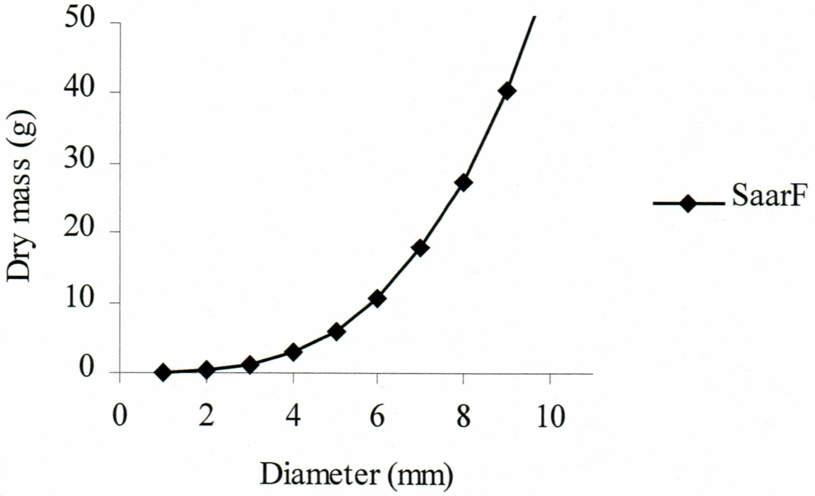

Fig. C22. Diameter to dry mass regression line for *Salix arbusculoides*, Game Management Unit 20A, Alaska, 2000.

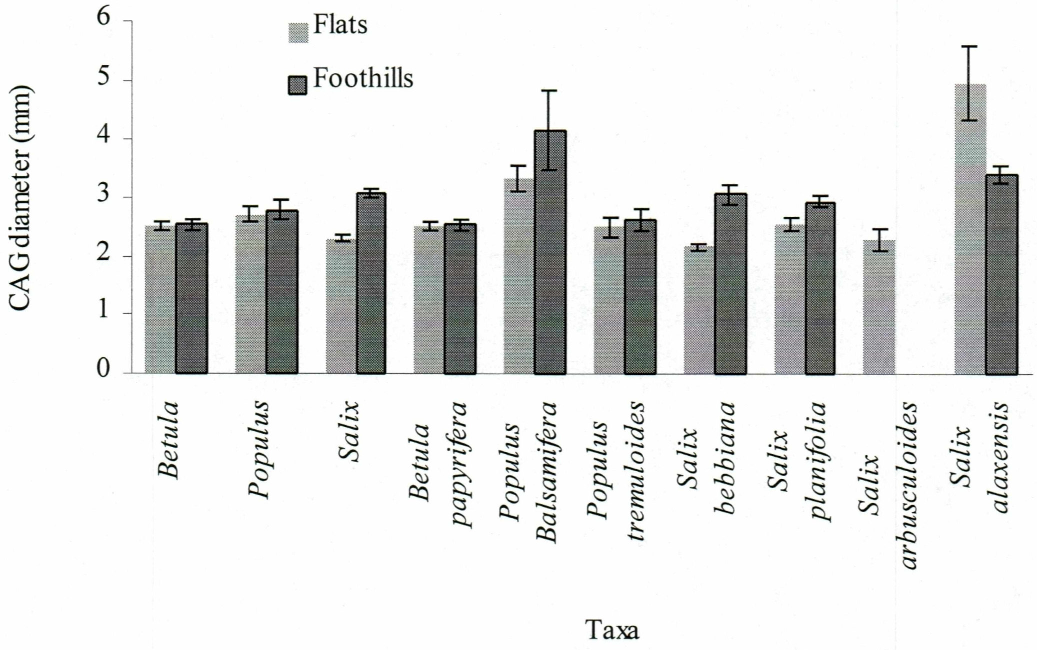

Fig. C23. Mean twig diameters at base of current annual growth (CAG) with 95% CI by genera and species for the study area, Game Management Unit 20A, Alaska, 2000. Sample sizes can be found in Table C1.