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Original article

Browse biomass removal and nutritional condition of moose *Alces alces*

C. Tom Seaton, Thomas F. Paragi, Rodney D. Boertje, Knut Kielland, Stephen DuBois & Craig L. Fleener

We present methodology for assessing browse removal to help evaluate resource limitation among moose *Alces alces* populations in large, potentially remote areas of boreal forest. During 2000-2007, we compared proportional removal (ratio of browse consumption to browse production) in eight areas of Interior Alaska, USA, with multi-year twinning rates of the respective moose populations. Several prior studies concluded that twinning rate provided an index of the nutritional condition of moose. We theorized that a plant-based sampling of proportional use of browse by moose in late winter would inversely correlate with the nutritional condition of moose. We sampled willow *Salix* spp., quaking aspen *Populus tremuloides*, balsam poplar *P. balsamifera* and Alaska paper birch *Betula neoalaskana*, i.e. plants with current annual growth (CAG) between 0.5 and 3.0 m above ground. We estimated the biomass of CAG and biomass removed by moose based on bite diameters and diameter-mass regressions specific to each browse species. Mean browse removal by moose varied among study areas from 9 to 43% of CAG. Moose twinning rate (range: 7-64%) was inversely correlated with proportional browse removal by moose (Spearman's rho = -0.863, $P < 0.005$). Proportional browse removal appeared useful in linking foraging ecology and population dynamics of moose in Alaska, and the technique may be used to quantify resource limitation in moose populations inhabiting boreal forest in a broader geographic region.

Key words: Alces alces, browse, forage, Interior Alaska, moose, moose density, twinning, willow

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Northern ungulates exhibit large seasonal variation in food intake, metabolic rate, body mass and activity patterns (Renecker & Hudson 1986, Sæther & Andersen 1990, Holand 1992, Hjeljord et al. 1994). Snow is an important factor influencing winter habitat selection and foraging behaviour (Mysterud et al. 1997), as well as spring body condition (Pettorelli et al. 2005). Despite seasonal and annual variability in nutrition, wildlife managers are often required to estimate the nutritional status of wild ungulate populations to predict harvestable surplus. In Alaska, predicting harvestable surplus is particularly important to wildlife managers because state law requires that ungulate populations be managed on a sustained yield basis for the maximum benefit to the public (Alaska Statutes 2009).

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The most established means of evaluating nutritional status of moose populations in Interior (non-coastal) Alaska is measuring twinning rate (Boer 1992, Gasaway et al. 1992:24, Keech et al. 2000, Boertje et al. 2007). Ages at first reproduction and yearling body mass have also been used to rank nutritional status of moose populations (Boertje et al. 2007). However, a change in each of these demographic indices generally indicates that the forage base, and thus nutritional condition of the animals, has already changed. This lack of predictive power renders direct measurements of food availability and food consumption relevant. We examine a direct browse-based index (the ratio of browse consumption to browse production), which has potential to corroborate alternative nutritional indices. Our goal was to provide a direct quantitative assessment of a moose range's ability to support additional moose. Ideally, we would gain the ability to anticipate changes in demographic parameters relevant to management decisions.

Ranking of the sustainability of habitats and thus moose nutrition (i.e. forage consumption relative to forage production) is prerequisite to implementing controversial management practices. For example, public requests to increase a low-density moose population may involve considering population control of bears *Ursus americanus* and *U. arctos* or wolves *Canis lupus* (Gasaway et al. 1992). However, managers must first address whether a population has adequate food resources to support population growth. Conversely, proposals to slow or halt growth of a moose population through harvest of antlerless moose (females or calves; Young et al. 2006) or to enhance the habitat require evidence of notably reduced nutritional condition of a population (Boertje et al. 2007).

Our work with browse biomass removal began with a study to address potential resource limitation in a growing moose population at high density (Seaton 2002). Subsequently, we conducted similar surveys in areas with lower moose density where predator control was being considered (Keech 2007), and in several additional areas to understand index performance among moose populations that differed in density and nutritional status (Boertje et al. 2007). To characterize range use, we chose a landscape measurement of plant use by moose in relation to biomass produced by plants. Our objective was to further evaluate the browse biomass removal as a standardized method of assessing forage resources for moose populations in boreal forests.

Methods

Study areas

Our eight study areas were located in Interior Alaska (Fig. 1) and referenced hereafter by game management unit (GMU). Vegetation was generally mixed boreal forest with canopy dominated by spruce *Picea* spp., Alaska paper birch *Betula neoalaskana*, balsam poplar *Populus balsamifera*, quaking aspen *Populus tremuloides*, and eastern larch *Larix laricina* grading into shrub communities at higher elevations and included active floodplains of large rivers. Disturbances such as wild-land fire and flooding dynamics created a mosaic of successional habitats. Aside from portions of GMUs 20B and 20D, our study area habitats were typically unsettled and uncultivated wild-lands. Terrain elevation ranged from 30 m a.s.l. in lowland river corridors to 1,400 m a.s.l. in subalpine areas. Peak snow depth in late winter increased with proximity to the coast from northeast (< 70 cm) to southwest (> 90 cm; average for the years 1975-2005; National Weather Service). Differences in snow depth and density likely influenced energetic requirements and habitat selection by moose (Coady 1974). Vegetative taxonomy followed Collet (2004) for willows *Salix* spp. and Viereck & Little (2007) for trees and other shrubs.

We sampled the portion of GMU 20A (Tanana Valley) between 5 and 105 km south of Fairbanks, Alaska, which was characterized by wetlands and uplands. The area contained winter range for migratory and resident moose, both of which shared a common summer range (Boertje et al. 2009). We sampled the portion of GMU 20B (Tanana Valley) along roadways within 75 km of Fairbanks area. This area was primarily in forested uplands with low density housing and development outside the urban footprint. The southwestern portion of GMU 20D (Tanana Valley) varied from canopy forest and agricultural fields near Delta Junction to subalpine terrain 50 km to the south, and contained several upland areas that had burned in the last 20 years. GMU 25D (Yukon Valley) was comprised of floodplain and uplands within 25 km of Beaver. GMU 19D (Kuskokwim Valley) was floodplain and uplands within 40 km of McGrath. GMU 19A

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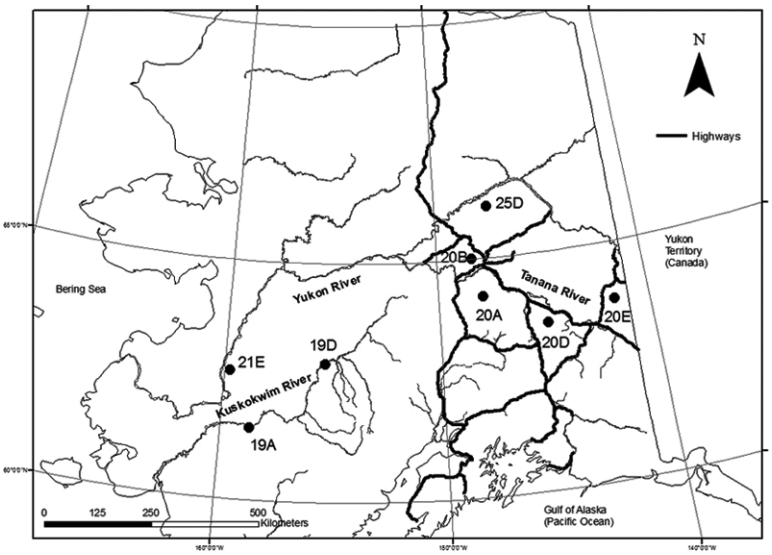


Figure 1. Location of our eight browse study areas in Interior Alaska, USA, identified by game management unit, 2000-2007. For more geographic detail see Paragi et al. (2008: Appendix A) and http://www.adfg.alaska.gov/index.cfm?adfg=wildliferegulations.hunting.

(Kuskokwim Valley) contained floodplain and uplands between Aniak and Lime Village. GMU 20E (uplands between Tanana and Yukon Valleys) was uplands, primarily within the Fortymile drainage between 25 and 100 km north and east of Tok. GMU 21E (Yukon Valley) was floodplain and uplands within 30 km of the lower Innoko River.

Selection of plot locations

Our selection of browse sampling locations differed among our eight study areas because of funding limitations, the availability of data on moose and habitat characteristics. However, in all instances we focused on known moose range and attempted to minimize sampling bias. Most of our study areas had current or prior telemetry studies to verify correspondence of winter range and calving areas by marked individuals. For areas without telemetry data, we utilized empirical knowledge obtained by managers on moose distribution from population surveys of unmarked animals in different seasons and from general knowledge of seasonal movements.

Seaton (2002) sampled 2,340 km^2 of GMU 20A in April 2000 by selecting plots in a stratified random manner based on available moose radio-locations, moose density from aerial surveys and vegetative classification. He used the vegetation classification to remove all non-browse habitats, such as rock, ice and water, in order to focus logistical effort on the habitats most likely to contain browse (Seaton 2002). After a preliminary visit by helicopter to exclude sites without browse, he used helicopter and snowmobile access to visit 97 plots in which he sampled 561 plants. The analysis by Seaton (2002) excluded two plots with extremely high browse production that we included in our analysis.

In May 2000, we sampled 130 km^2 of moose winter range in GMU 25D by boat and ATV at 2.5-km intervals from the village of Beaver, Alaska, along the Yukon River, including islands and main banks, and along two trails leading northeast and northwest from Beaver, Alaska. At each route interval we walked a random distance of up to 400 m perpendicular from the shoreline or trail to access 40 plots (234 plants).

We sampled browse on 1,350 km^2 in GMU 19D during March 2003. We systematically sampled 23 plots (190 plants) by snowmobile in floodplain stands and willow bars that moose were known to visit frequently in winter along the Kuskokwim River. We accessed another 16 plots (108 plants) by helicopter from the river corridor. Helicopter access sites were uniformly selected from rectangular cells used in moose surveys (ca 15 km^2; Kellie & DeLong 2006), with sampling allocated equally among cover types known to contain browse (tall shrub, open forest and closed forest; Viereck et al. 1992). We identified these cover types from a digital classification of Landsat imagery (Ducks Unlimited 2000). We considered an area of 2 ha (block of five 30-m pixels square) to be the minimum size useful for stratifying habitat to choose a specific type on the ground with reasonable accuracy (D. Fehringer,

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Ducks Unlimited, pers. comm.). The helicopter pilot navigated to the center of chosen polygons by global positioning system (GPS) and hovered so we could confirm browse. If we observed browse, we landed at the nearest available location for snowshoe access. When we observed no current annual growth (CAG) of browse species during the hover (N = 35; 69% of sites), we flew to the nearest alternate site among the cover type identified beforehand.

In April 2006, we used the rectangular cells from recent moose surveys stratified as high or low moose density by local biologists (Kellie & DeLong 2006:16) to divide the browse sampling area into a grid for GMUs 19A, 20E and 21E. Based on variance of estimated parameters from previous browse sampling in GMU 20A, we desired browse biomass data from $\geq$ 30 plots per study area. We recognized that only 20-50% of randomly sampled plots (15-m radius) likely contained CAG of the height and species we desired. Thus, we randomly chose 150 cells at a 3:2 ratio of high:low moose density (Kellie & DeLong 2006:21) to focus plot sampling where browse production and browse foraging likely occurred. Plot selection within each chosen cell was based on proximity of helicopter landing sites for access on snowshoes. The helicopter pilot flew a northwest heading from the southeast corner of the cell (up to ca 5.5 km from the southeastern to the northwestern corner). We placed a coloured dot on the helicopter windows near each passenger seat to indicate a lateral distance of 100 m on the ground when flying at 30 m above ground level (above the tallest trees typically encountered). At the first safe landing spot encountered within 100 m perpendicular to the heading, the pilot hovered over the landing spot while a GPS location point was marked. We then flew a random distance (30-100 m) and bearing (0-359°) to hover over the potential sampling site. If browse CAG was observed, we collected a GPS fix and then visited the site on foot. If no browse CAG was visible within a 15-m radius of the potential sampling site, we noted community type based on vegetation above snow cover, took a digital photo from the air, collected a GPS fix and flew to the next cell. We assigned browse community type as forest (trees $>$ 3 m, $>$ 10% canopy cover), tall scrub (shrubs $>$ 1.5 m, $>$10% canopy cover) or dwarf scrub (shrubs 0.2-1.5 m, $>$ 25% canopy cover; Level II; Viereck et al. 1992). If the general area around the landing zone was vegetated, but the potential sampling site was not (e.g. at the edge of a frozen lake or river), we continued choosing alternate potential sampling sites from the landing zone until a vegetated community was selected. We failed to sample a few cells because solid forest cover (or snags in burns) prevented landing, or because no vegetation occurred above the snow within 100 m of the landing site. In these instances we moved on to the next selected cell. We recognized that in dense forest habitats this sampling scheme had some bias toward edge habitats at the stand scale, but we considered it a necessary compromise for feasible access at the landscape scale in remote forested environments. We sampled 27 plots and 134 plants (48 additional sites were visited but contained no browse) from 21,000 km^2 in GMU 19A, 30 plots and 136 plants from 14,300 km^2 in GMU 20E (41 additional sites were visited but contained no browse), and 32 plots and 210 plants from 17,500 km^2 in GMU 21E (44 additional sites were visited but contained no browse).

In April 2007, we again used stratified sampling of rectangular cells by helicopter to sample 41 plots (167 plants, 13 additional sites contained no browse) over 4,550 km^2 in southwestern GMU 20D. We also sampled 76 plots (437 plants) from the road system in 20D. For road access we identified chosen cells near a highway or forest road, drove to the nearest point perpendicular to the GPS location of the cell corner by truck or snowmobile, and walked a randomly chosen 15-100 paces perpendicular toward the cell corner to establish the plot center (two plots contained no browse).

Finally, in April 2007, we used stratified sampling of rectangular cells near highways and forest roads surrounding Fairbanks (3,900 km^2) in central GMU 20B. We used the same plot selection method from the road system as in GMU 20D, and sampled 37 plots (255 plants) in GMU 20B. Further details of browse sampling on all study sites were noted in Paragi et al. (2008:Table 1).

Estimating proportional browse biomass removal

We defined *Salix* spp., *Populus* spp. and Alaska paper birch as browse species. These taxa are important to moose throughout their continental range (Peek et al. 1976, Risenhoover 1989, Weixelman et al. 1998). We also included red osier dogwood *Cornus stolonifera* in our analysis since this widely distributed but rare shrub was usually heavily browsed. We excluded other deciduous woody plants such as *Alnus* spp., Dwarf birch *B.*

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nana and American dwarf birch *B. glandulosa* because these plants were less important food items on moose winter range in Interior Alaska (Bryant & Kuropat 1980), and we observed comparatively little use of these species.

We sampled only plants with CAG between 0.5 and 3.0 m above ground level. Woody forage < 0.5 m is commonly considered below the minimum foraging height for moose (Wolff & Zasada 1979, Wolff & Cowling 1981, Weixelman et al. 1998) and is often snow covered. We used the upper limit of 3.0 m because preliminary reconnaissance in Interior Alaska showed higher browsing to be uncommon, and 3.0 m is commonly considered the upper limit in forage surveys (Danell & Ericson 1986, Hjeljord et al. 2000). We sampled all plants in late winter before leaf emergence in spring. We chose a 15-m radius plot to correspond with Landsat pixel size of the Ducks Unlimited cover classifications (Ducks Unlimited 2000). Our preliminary reconnaissance in 1999 indicated that this large plot size would reduce the number of plots with no browse in the vegetation types typical of moose winter range in Interior Alaska.

At each sample plot, we randomly selected three plants from each browse species present, and 10 twigs on each of the selected plants. For each twig we recorded the diameter at base of CAG (Lyon 1970) and diameter at point of browsing, if applicable. Starting in 2001, we noted if browsing appeared to have occurred beyond CAG. We counted the number of CAG twigs 0.5-3.0 m above ground level on the three plants per species and noted snow depth. We collected unbrowsed reference twigs of variable sizes (1-10 mm diameter) from each forage species sampled for biomass (Seaton 2002). In the lab we measured, oven dried and weighed these twigs to develop regression relationships between live diameter and dry mass (Brown 1976, Oldemeyer 1982, Alaback 1986, Kielland & Osborne 1998). We used the regression coefficients relating diameter to dry mass (Appendix I) and the number of twigs per plant to estimate forage production and removal (Telfer 1969) for plants within our eight study areas. We used diameter at base of CAG to predict production and diameter at point of browsing to predict removal (Oldemeyer 1982). In cases where moose may have removed the CAG bud scar, we used the next visible bud scar to predict production. In some study areas for certain species, unbrowsed specimens of many size categories were relatively rare at the plots we visited, so we augmented samples or used the regression coefficients from the nearest study area to predict biomass. Proportional removal of browse biomass in a study area was estimated by the following equation:

$$\text{Proportional browse biomass removal} = \left(\frac{\sum \text{biomass removed from plants sampled}}{\sum \text{CAG biomass produced on all plants sampled}} \right)$$

Analysis of proportional browse biomass removal

Dry biomass of browse has an exponential relationship to diameter, $z = ax^b$, where z is dry mass and x is live twig diameter (Oldemeyer 1982). We estimated this relationship using linear regressions of log-transformed dry mass on log-transformed twig diameter for the forage plants collected in our study areas. After we estimated coefficients on the log scale, we converted estimates of dry mass back to the original scale (g) 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). Here $\hat{a}$ is the intercept coefficient , $\hat{b}$ the slope coefficient on the log scale, σ^2 the mean square error on the log scale, x_0 the diameter input and $\hat{z}$ is the resulting predicted value. We averaged the predicted twig weights for a given plant and multiplied that average by the total number of twigs observed on that plant. We extrapolated variance of $\hat{z}$ to the plant level using the delta method (Bain & Engelhardt 1987:178) and constructed 95% confidence intervals on biomass estimates.

We contracted development of software in R (R Development Core Team 2008) to read the Microsoft® (Microsoft Corporation, Redmond, WA) Access™ database unique to each study area that contained twig, plant and plot data and the reference twig data used to predict twig dry mass (http://www.adfg.alaska.gov/index.cfm?adfg=librarycollections.wildliferesearch#habitat). We used the software to estimate mass-diameter relationships, biomass produced by plants, biomass removed by moose and proportional browse removed for all sampled plants in our study area. Alternately, we could have extrapolated production and removal to the plot level, but this introduced bias through variation in the proportion of total plants sampled per species in a plot and variability in

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plant counts. Previously, Seaton (2002:73) estimated production and removal at the plot level for GMU 20A to allow modeling of forage intake by moose relative to estimated forage production. We used the software to estimate mean and 95% confidence limits using bootstrap techniques (Efron & Tibshirani 1993). The bootstrap technique allows calculation of asymmetric confidence limits, which is important as proportion of browse removal approaches zero. At each bootstrap iteration, we drew a bootstrap sample of size N (total number of plots sampled per study area). We estimated mean and standard error of mean for production, removal and proportion removed as the sample standard deviation of 1,000 bootstrap samples. We obtained confidence intervals by applying the basic percentile method (Davison & Hinkley 1997). To examine how the number of plots sampled in a study area affected the estimate of proportional browse removal and its variance, for GMUs 20A and 20D we chose random samples with replacement of 5, 10, 15... to N plots, and performed 1,000 replicate calculations with each sample to estimate mean proportional browse removal and sample standard deviation.

Sensitivity of proportional browse biomass removal

To evaluate whether the proportional browse biomass removal technique can distinguish spatial variation in moose populations, we used moose distribution to subdivide GMU 19D. Moose were more concentrated in the riparian floodplain than in off-river areas during winter. This observation was based on a November moose survey in 2001 (Seavoy 2006), locations of radio-marked moose and winter moose observations. The data from November 2001 show that survey biologists observed approximately twice as many moose in sample units containing riparian floodplains (0.5 moose/km^2, N = 28) than they did in non-floodplain units (0.2 moose/km^2, N = 59). We tested whether browse removal differed between these two habitats of different winter moose density in GMU 19D.

Twinning rates

Boertje et al. (2007) described how twinning rates of moose populations were estimated from the proportion of parturient females with twin calves. Aerial surveys occurred shortly after peak of calving in late May, usually from a sample of unmarked individuals. Moose density and sample size for twinning rate for six of our study areas (GMUs 19D, 20A, 20D, 20E, 21E and 25D) were reported in Table 1 of Boertje et al. (2007). We added two more years of twinning data (2006 and 2007) for GMUs 20D (N = 102 unmarked females) and 20E (N = 69). In GMU 19A, the twinning rate was estimated from aerial surveys in 2002 and 2005 (N = 63; Seavoy 2006). In central GMU 20B, twinning rate was estimated in 2006, 2007 and 2008 (N = 120; Young 2006).

We estimated mean twinning rate for each study area, weighting equally among years in a study area. Further details on twinning rates for all study sites are found in Paragi et al. (2008:Table 4). Standard errors and 95% confidence intervals for each study area were estimated using bootstrap techniques (Efron & Tibshirani 1993). Within each study area, twinning rate for each of N years (where N = number of years of twinning rate data for that study area) was modeled as a binomial using the total number of parturient females observed and observed numbers of twins. At each bootstrap iteration, we drew a bootstrap sample of size N from these N modeled twinning rates, and we calculated the mean of this bootstrap sample. We estimated the standard error of mean twinning rate as the sample standard deviation of 10,000 bootstrap samples. We obtained confidence intervals by applying the basic percentile method (Davison & Hinkley 1997). We tested for an inverse relationship (one-tailed) between proportional browse biomass removal and twinning rate using Spearman's rank correlation coefficient (Conover 1980:252-255).

Results

Not all browse species occurred at each sample plot. *Salix* spp. composed the majority (range: 60-92%) of the plants sampled for biomass in our eight study areas (Fig. 2). The bootstrap estimate of CAG biomass removed by browsing was stable at $\geq$ 15 plots and not different from the deterministic estimate in GMUs 20A and 20D, whereas the variance around the mean declined with further increases in sample size (Fig. 3). Little relative gain in precision for each additional five plots occurred after the confidence limits in GMU 20A decreased to 13% of the mean at N = 30 plots (see Fig. 3A). A similar rate of change in precision occurred at N = 30 plots in GMU 20D

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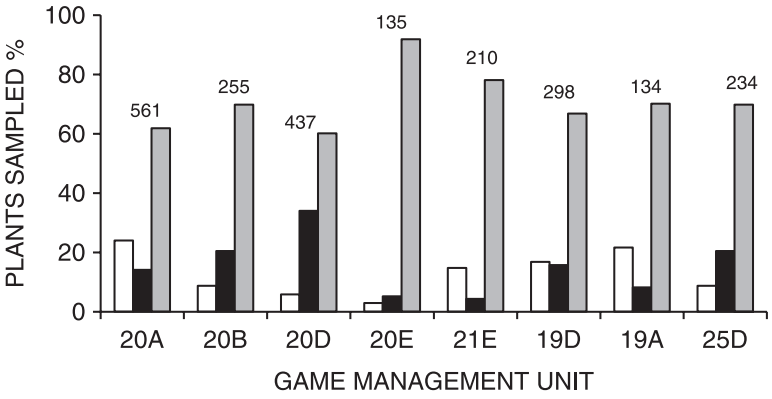


Figure 2. Genera composition (*Betula* spp. □, *Populus* spp. ■, *Salix* spp. ■) of browse plants sampled to estimate biomass removed by moose browsing in eight areas of Interior Alaska, USA, 2000-2007. Sample size by study area is listed above the bars. *Cornus stolonifera* was also sampled in Game Management Units 19D (N = 2) and 21E (N = 6).

(see Fig. 3B), although the confidence limit was substantially larger at 46% of the mean, and the bootstrap confidence interval was three-fold larger than the deterministic calculation at the actual sample size. Coefficient of variation in the proportion of browse removed did not increase significantly as the proportion removed decreased (Spearman's rho = -0.381, $P > 0.1$), and the relationship did not appear to be strongly influenced by number of plots sampled among study areas (Fig. 4). Browse biomass removed by moose varied from 9 to 43% of CAG among our eight study areas and was inversely correlated with moose twinning rate, which ranged within 7-64% (Spearman's rho = -0.863, $P < 0.005$; Fig. 5). The proportion of CAG browse removal on riparian willow bars in GMU 19D was 0.205 (bootstrap 95% confidence interval: 0.169-0.273, N = 23 plots) compared with off-river removal of 0.122 (bootstrap 95% confidence interval: 0.095-0.181, N = 16). The overall proportion of browse removal in GMU 19D was 0.170 (bootstrap 95% confidence interval: 0.144-0.222, N = 39). We judged that browsing at diameters larger than CAG occurred in all study areas (no data was available from GMU 20A). Estimates ranged from 1% of twigs sampled in GMU 25D (N = 201 twigs) to 21% in GMU 20D (N = 721 twigs).

Discussion

Proportional browse biomass removal appeared to be an adequate index of the nutritional

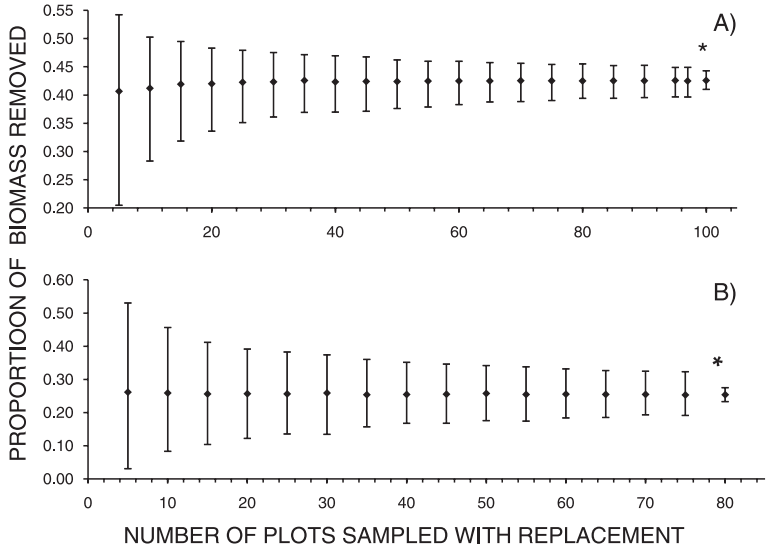


Figure 3. Simulated effect of number of plots sampled on mean and 95% confidence limit for proportion of browse biomass removed by moose in A) Game Management Unit 20A (N = 97 plots) and B) Game Management Unit 20D (N = 76 plots) in Interior Alaska, USA. Estimates at each sample size were derived by bootstrapping with 1,000 iterations except for the last in each series (*), which was the deterministic estimate and confidence interval at the actual sample size.

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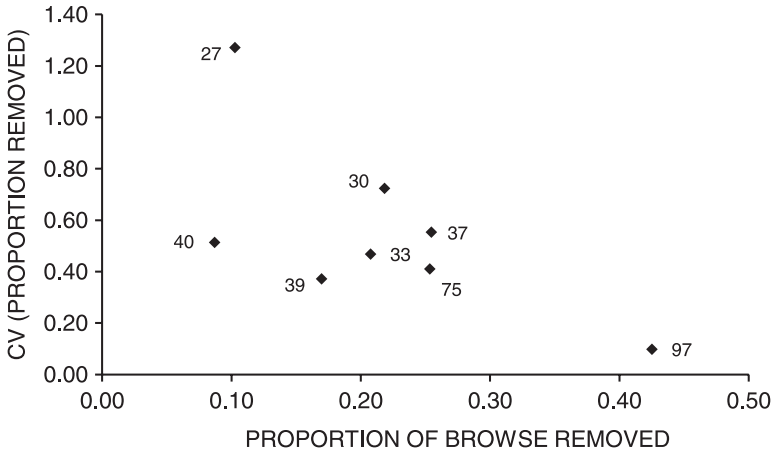


Figure 4. Relationship between the proportion of browse removed and its coefficient of variation for eight browse study areas in Interior Alaska, USA, 2000-2007. Number of plots sampled is shown for each study area.

condition of moose. We observed an inverse relationship between proportional browse removal and twinning rate (see Fig. 5) despite some variation in sampling design and differences in sampling intensity among our eight study areas across the large region (see Fig. 1). Our comparison among study areas represented the gradient of nutritional status from nearly the highest to lowest extremes observed for twinning rates (Boer 1992, Gasaway et al. 1992, Boertje et al. 2007:Table 1) and density (Boertje et al. 2007:Table 1) among Alaskan moose. Based on local differences in winter moose distribution in GMU 19D, the biomass removal technique also appeared sensitive enough to detect differences in proportional browse removal on a relatively small geographic scale.

We believe the technique functioned appropriately because it is a simple measure of the relationship between the biomass of moose and the biomass of woody browse in a given landscape. When the ratio of moose to browse is high, moose remove higher quantities of browse than when that ratio is low. This technique was based on forage from the winter season. However, twinning rates should be strongly influenced by forage acquired during summer months by female moose. This simple relationship between the biomass of moose and the biomass of one season's forage (winter) may parallel the relationships with forages from other seasons. Plants consumed by moose in both winter and summer grew side by side during summer while being influenced by the same growing conditions (light intensity, temperature and water availability). Summer forages in these study areas were so diverse, ephemeral and remote that they were logistically and financially prohibitive to measure.

We recognize that our sampling intensity represented a small fraction of the browse twigs in the large areas we sampled. When habitat selection is

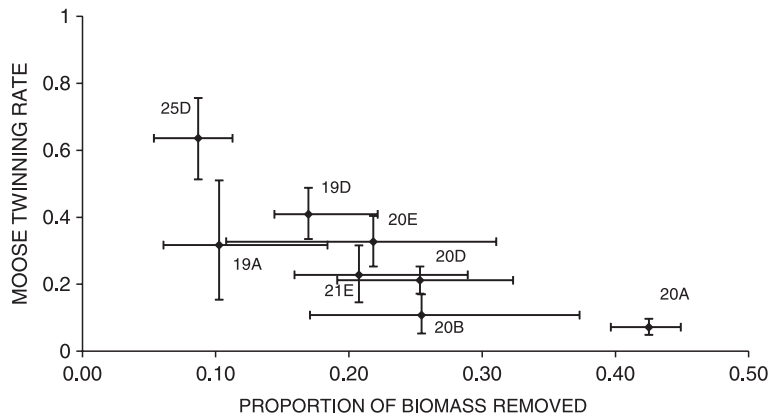


Figure 5. Relationship between proportional removal of browse biomass by moose and moose twinning rate for eight study areas in Interior Alaska, USA, 2000-2007. Estimates were derived by bootstrapping, and error bars indicate bootstrap 95% confidence limits.

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not constrained by resource competition or the environment (e.g. deep snow), we expect moose to consume twigs at a diameter optimal for nutrient and energy intake (Kielland & Osborne 1998). However, twig morphology or other factors sometimes allowed moose to browse beyond CAG, so our estimate of annual browse production is a measurable surrogate, not the immeasurable true production in a given year. Nonetheless, we believe that proportional browse biomass removal objectively characterizes the extent to which moose are utilizing their forage resources on the range. The biomass technique also permitted estimation of browse production and removal by area per species, bite diameter, bite mass, size of CAG twigs and other parameters useful in modeling moose foraging ecology (Seaton 2002, Lord 2008). Also, we could extrapolate production by the type of class for landscape estimates in a geographic information system (Paragi et al. 2008). Additional information on the nutritional quality of the browse and the effect of snow depth on energy expenditure would permit further inference on the potential carrying capacity of the winter range of moose.

We desired cost-effective techniques to assess browse use at a sufficiently large scale to be germane to moose population management. Estimating browse removal is labour intensive and must occur just before the start of new growth in spring when travel conditions on snow begin to deteriorate. Cost of access by snowmobile, riverboat or ATV was about 10% that of helicopter access per plot. We believe the helicopter heading procedure presently represents a practical means to objectively sample browse in large remote areas. For comparison between indices, the total cost of a browse survey by helicopter in a remote area (ca $12,000 excluding biologist salary) typically exceeds the cost of two years of twinning surveys unless several flights of fixed-wing aircraft are needed to collect adequate twinning data. When the public proposed a moose population increase, both they and the critics of population manipulation often demanded a direct measure of the status of the range. Browse biomass removal was the only direct range assessment available that was authenticated by a correlation with other measures of moose herd nutritional plane. Thus, the higher cost was justified based on the technique's ability to provide added information and support for other indices of moose herd nutrition.

Future evaluation of the proportional browse biomass removal technique should include estimating proportional browse removal over successive years in the same areas. Moose populations in these areas should be relatively stable in abundance. The objective is to understand whether the index is robust to temporal variation induced by sampling or annual environmental variables, such as growing season length or snow depth. Incorporating diverse habitats at the level of study area produces removal estimates of comparatively high variance (see Fig. 5). Consequently, sampling diverse habitats could hinder statistical inference on trends in proportion of CAG browse removal caused by a change in moose density or habitat (e.g. burns). We recognize a potential for spatial bias in the browse removal index if moose movements were restricted in a particular year because of deep snow, a phenomenon that complicates inference on carrying capacity from range assessment alone (Edwards 1956). Stratified sampling by habitat attributes, other than simply vegetation type (or by moose density during time-specific aerial surveys), might help reduce year-specific spatial bias. Climate data defining which portions of a range that frequently experience deep snow may ensure adequate sampling in areas where moose are known or expected to concentrate based on access to remaining available forage (Van Beest et al. 2010).

Management implications

Along with nutritional indices measured directly from moose or moose populations (Boertje et al. 2007), we propose that proportional browse biomass removal be considered as a nutritional index for use by wildlife managers. This browse assessment has proved useful when making decisions on moose harvest strategies, predator management and habitat manipulation in the boreal forest of Alaska. Thus, measuring proportional browse removal had utility for assessing resource limitation in moose populations inhabiting boreal forest.

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Sutherland wrote bootstrapping code and B. Taras calculated twinning rates.

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Appendix I

Regression coefficients to predict dry matter (g) from twig diameter (mm) of moose browse species by game management unit (GMU) in Interior Alaska, USA, 2000-2007. Samples sizes in GMU 20A were larger because of research design to contrast Tanana Flats from Alaska Range foothills (Seaton 2002). For a species with < 100 mass-diameter pairs collected in a GMU, we pooled data from the nearest GMU for calculations. Using log transformed data for the regression equation, dry mass = $e^{a} * e^{mse/2} *$ diameter^{b} where a is intercept and b is slope. The term $e^{a} * e^{mse/2}$ is listed as parameter 'a' in Seaton (2002:Table 3).

Species	GMU	Intercept	Slope	MSE	N	r^2
Betula neoalaskana	19A	-4.352	3.344	0.134	59	0.928
Betula neoalaskana	19D	-3.273	2.967	0.107	55	0.972
Betula neoalaskana	20A	-3.914	3.338	0.124	259	0.974
Betula neoalaskana	21E	-3.519	2.829	0.097	25	0.763
Betula neoalaskana	25D	-3.721	3.204	0.146	50	0.972
Cornus stolonifera	21E	-5.427	4.023	0.180	61	0.896
Populus balsamifera	19D	-3.335	2.705	0.080	111	0.968
Populus balsamifera	20A	-3.392	2.792	0.100	217	0.947
Populus balsamifera	25D	-5.082	3.660	0.074	10	0.990
P. tremuloides	20A	-3.087	2.694	0.105	259	0.970
P. tremuloides	25D	-4.160	3.139	0.132	100	0.973
Salix alaxensis	19A	-5.645	3.763	0.259	209	0.925
Salix alaxensis	19D	-4.439	3.264	0.192	129	0.953
Salix alaxensis	20A	-4.558	3.304	0.275	751	0.903
Salix alaxensis	21E	-6.154	3.882	0.117	95	0.974
Salix alaxensis	25D	-4.326	3.318	0.161	104	0.963
S. arbusculoides	19A	-3.860	3.076	0.105	58	0.969
S. arbusculoides	20A	-3.575	3.284	0.158	123	0.963
S. arbusculoides	20E	-3.712	3.276	0.223	89	0.947
S. arbusculoides	21E	-3.780	3.294	0.211	37	0.940
S. arbusculoides	25D	-3.604	3.135	0.095	109	0.980
S. bebbiana	20A	-3.880	3.225	0.128	345	0.966
S. bebbiana	25D	-3.286	2.987	0.091	100	0.980
S. glauca	20D	-3.517	2.473	0.201	123	0.909
S. glauca	20E	-5.250	3.585	0.326	127	0.866
S. interior	19D	-3.578	3.014	0.125	96	0.969
S. pulchra	19A	-3.907	2.894	0.389	40	0.824
S. pulchra	19D	-3.203	2.844	0.166	69	0.963
S. pulchra	20A	-3.449	3.010	0.225	637	0.936
S. pulchra	20E	-4.816	3.581	0.277	148	0.926
S. pulchra	21E	-4.428	3.527	0.183	100	0.954
S. Richardsonii	20D	-4.751	3.074	0.242	32	0.903

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