Comparative Space Use and Habitat Selection of Moose Around Feeding Stations

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ABSTRACT The practice of feeding cervids in winter, either as a supplement to enhance nutritional status or to divert animals away from roads, railways, or vulnerable habitats, is rising noticeably. Moose (Alces alces) densities in Scandinavia are currently at historically high levels, resulting in amplified damage to economically important young Scots pine (Pinus sylvestris) forest stands. Nevertheless, there is limited information as to how diversionary feeding affects herbivore space use and habitat selection. We followed 32 female moose marked with Global Positioning System collars to evaluate 1) if feeding stations serve as attraction points to the extent that habitat-selection patterns resemble those of central-place foragers (i.e., high usage and more uniform selection close to the attraction point), and 2) if moose using feeding sites select young pine stands less than those not using feeding sites. Moose that used diversionary forage concentrated their space use around feeding stations and selected habitats as predicted for a central-place forager with a decreasing probability of using areas away from feeding sites and a low degree of habitat selectivity close to feeding sites. However, moose that used feeding sites continued to select young pine stands to the same extent as moose that did not use feeding sites. Feeding sites were, therefore, not successful in diverting moose away from valuable natural browse, so we recommend wildlife managers establish feeding sites in sacrifice areas where moose browsing is permissible and, if possible, >1 km from young pine plantations.

KEY WORDS Alces alces, central-place foraging, deer, diversionary winter feeding, habitat use, mixed-effect logistic regression, resource selection function, southern Norway.

The supplementary winter feeding of large herbivores is a widespread, yet controversial, wildlife management practice (Boyce 1989, Smith 2001, Putman and Staines 2004). During the past decade, this practice has increased noticeably throughout Europe and North America. Although there are many reasons for diversionary feeding (reviewed by Putman and Staines 2004), an important goal is the prevention of environmental damage, particularly to agriculture and forests of commercial or conservation value (Smith 2001, Peek et al. 2002, Gundersen et al. 2004, Putman and Staines 2004). The rationale behind such feeding is either to reduce the amount of natural forage required by wintering herbivores via the provision of alternative forage or to redirect animals toward less-vulnerable habitats. However, ungulates will still consume natural forage, and evidence of the effectiveness of winter feeding as a diversionary tactic is equivocal (Schmitz 1990, Doenier et al. 1997, Gundersen et al. 2004, Putman and Staines 2004).

Central-place foraging theory predicts space use and foraging decisions as a function of the distance from a focal point (Orians and Pearson 1979). In the classical case, the focal point is typically a nest or a den, but any key resource that acts as an attraction point may give rise to a space-use pattern resembling central-place foraging (Rosenberg and McKelvey 1999). The central-place foraging theory, a special case of the wider optimal-foraging theory, is, therefore, likely to be useful for predicting ungulates’ habitat-selection patterns if artificial feeding sites can be assumed to serve as attraction points. A typical feature of central-place foraging is a declining probability of use of locations with increasing distance from the focal point (Rosenberg and McKelvey 1999). Also, central-place foragers are expected to show both lower selection for preferred resources and a lower overall variation in selection of resources close to the focal point (Schoener 1979). There is limited information as to whether feeding stations restrict space use of individual ungulates and how that, in turn, affects habitat-selection patterns. For ungulates that use feeding stations, habitat selection may vary with distance to feeding site because of locally high densities and amplified competition for assumed high-quality habitat types close to feeding sites. Studies on smaller cervids have shown that providing artificial winter feed can change migratory movement for white-tailed deer (Odocoileus virginianus; Lewis and Rongstad 1998) and restrict natural space-use patterns to the vicinity of feeding stations for roe deer (Capreolus capreolus; Guillet et al. 1996) and white-tailed deer (Kilpatrick and Stober 2002). For managers, it is important to know the spatial scale at which winter feeding affects space use and habitat selection so that effective winter feeding programs can be designed for various goals.

Moose (Alces alces) populations in Norway, as in the rest of Fennoscandia, have grown considerably during the past...
decades, and densities in local wintering areas can be extreme (e.g., 5–6 moose/km²; Lavsund et al. 2003). A concurrent problem with high moose densities is the excessive winter browsing in regenerating, young Scots pine (Pinus sylvestris) stands, resulting in substantial economic losses to forestry (Andren and Angelstam 1993, Ball and Dahlgren 2002). Gundersen et al. (2004) demonstrated how winter feeding of moose in Norway may reduce browsing damage to forestry interests at a local scale (up to 5 km) but may lead to serious habitat damage at a forest-stand scale (e.g., severe browsing and bark-stripping ≤ 200 m).

Our objectives were to quantify how the provisioning of winter forage affects space-use and habitat-selection patterns of moose. When additional feed at least partly compensates for intake of natural preferred browse, we predicted that (P₁) artificial forage would reduce the selection for commercially valuable young pine stands among moose that used feeding stations, because time spent in pine stands would likely decrease. If moose experience feeding sites as attraction points in their seasonal home range, we predicted (P₂) that space use would be concentrated in the vicinity of feeding stations and (P₃) low habitat selectivity in the vicinity of feeding stations with selectivity increasing with distance.

STUDY AREA

The study area (1,733 km²) was located in southern Norway within parts of Telemark, Buskerud, and Vestfold counties in the boreonemoral zone (Fig. 1). The area was mostly covered by commercially managed, coniferous forest (82%), dominated by Norway spruce (Picea abies, 72%) and, in the drier and poorer locations, by Scots pine (17%). In addition, a few mixed deciduous stands (6%) of birch (Betula spp.), mountain ash (Sorbus aucuparia), willow (Salix spp.), and aspen (Populus tremula) occurred throughout the area. The topography was rugged with steep slopes, and the altitude ranged from sea level to 800 m. Monthly normal temperatures during January and April were −5° C and 4.3° C, respectively (Norwegian Meteorological Institute 2008). Average (±SE) snow depths in the center of the study area during January–April 2007 and 2008 were 49 ± 2.4 cm and 72 ± 1.5 cm, respectively, with deeper accumulation at higher elevations (Norwegian Meteorological Institute 2008). Large predator species were absent, and hunting was the most important cause of moose mortality in this area.

Local landowners have been feeding moose and red deer (Cervus elaphus) ad libitum with ensilaged bales of mixed graminoids for ≤ 6 winters. There were 94 permanent feeding stations, and during the 4-month winter, moose consumed 182 tonnes of forage in 2006–2007 and 244 tonnes in 2007–2008.

METHODS

Moose Telemetry Data and Habitat Maps

We fitted 32 adult female moose with Global Positioning System (GPS) collars, programmed with a 1-hour relocation schedule during 2 winters. We tranquilized moose by dart gun from a helicopter, using established techniques (Arnemo et al. 2003). We used annual snow conditions to define winter length (>30-cm snow depth), which corresponded with the period that artificial forage was supplied. In 2007, winter was from 21 January to 8 April, and in 2008, it was from 4 January to 30 April. We excluded all GPS locations collected within 24 hours of marking a moose.

We used forest-stand indices from 6-year-old Geographic Information System (GIS) maps. Dussault et al. (2001) recommend evaluating the accuracy of important habitat characteristics represented on forest maps via field observations, which is especially important for fine-scale habitat-selection studies. To assess the forest-stand classification accuracy of our GIS maps, we randomly sampled 180 forest stands throughout the study area and determined whether the forest stands were correctly classified with regard to cutting class and dominant tree species. We partitioned cutting classes (cc) by tree height: cc.1 = stands with trees <1 m; cc.2 = stands with trees of 1–7 m tall; cc.3 = 8–14 m tall; cc.4 = 15–20 m tall, and cc.5 = trees ≥ 20 m in height.

Correcting for GPS Bias

A recurring problem in studies reliant on data obtained with GPS technology is variable fix rates in location accuracy (D’Eon and Delparte 2005, Graves and Waller 2006). Because the average GPS-collar fix rate during our study was 91.9% (range among collars: 72–99%), we investigated whether fix rates were biased across habitat types and corrected for it in the habitat-selection analysis. We placed collars 1.5 m above the ground for 24 hours with the antenna pointed directly upwards, during early winter (Nov 2007). We made positioning attempts each hour. We
repeated trials 4 times for each combination of habitat variables (see below), a total of 120 trial sites. We selected trial sites by stratified random sampling across 3 habitat characteristics that we suspected could affect the GPS fix rate: 1) dominant tree species (Scots pine vs. Norway spruce; we did not include mixed deciduous stands because they comprise a minor habitat type [6% of all stands]); 2) slope (flat, <4°; moderate, 4–8°; steep, >8°); and 3) cutting class. Furthermore, we determined sky visibility, defined as the percentage of sky obstructed by terrain features for each trial location. We calculated sky visibility in ArcView GIS 3.2 (script developed by D. O. Wallin, Department of Environmental Science, Western Washington University, Bellingham, WA), and we derived slope from a Triangulated Irregular Network grid (50-m cell size) in ArcMAP 9.2.

We defined and calculated location accuracy as the linear distance between the recorded GPS location and the assumed true location (i.e., the average of 24 GPS positions). The median location error at trial sites was 16 m with 95% of the locations within <75 m. These results are considered acceptable (Hebblewhite and Merrill 2008) and similar to the spatial resolution of our GIS habitat variables.

To test and account for habitat-specific bias in GPS fix rate, we did the following: at each trial site, we knew the number of successes and failures of GPS positioning attempts (average fix success, 96.9%; range, 87.8–100%) and the combination of habitat characteristics. From these data, we built a mixed-effect logistic regression model with success (1) or failure (0) for each location attempt as the response variable, with habitat characteristics as fixed-effect predictor variables, and collar identity as a random intercept (to account for systematic differences in collar quality). Our results indicated that the odds ratio of acquiring a GPS fix were lowest in the spruce-dominated forest of cc.3, compared with the open pine stands of cc.1. The odds of a GPS collar successfully acquiring a location were positive for increased sky visibility and negative for increased slope and cutting class. From this model, we predicted the probability of attaining a fix for all combinations of habitat characteristics. Habitat variables were available as layers in GIS maps, and we could, therefore, use the model to predict the probability of obtaining a GPS fix at every location in the study area (i.e., a probability value for every pixel of a GIS raster map). Pixels of mixed deciduous stands received the same probability as pine-dominated stands (i.e., the reference category). To correct for GPS bias, we used an iterative simulation method (Frair et al. 2004). For each missing location in the moose GPS data set, we randomly selected a location and a randomly drawn probability value of a uniform distribution within a rectangle defined by the previous and next known locations. We compared the predicted value of acquiring a fix for that location (found on the GIS probability map) to the randomly drawn probability value. If the random value was greater than the predicted value, we retained the random location; otherwise we selected a new random location and probability value. Therefore, we retained locations with the lowest predicted probability of obtaining a fix, and thus the higher probability of being a missed location, more often. In this manner, we filled in 2,483 missed locations with 60.5% assigned to spruce-dominated forest (26.4% within cc.3). Pine and mixed deciduous forest received 37.5% and 2% of the filled in locations, respectively.

Feeding Site Use
To categorize individual moose as feeding-site users or nonusers, we used the Euclidean distances analysis (EDA) proposed by Conner and Plowman (2001): \( d_i = u_i/r_i \). Here, \( u_i \) represents a vector of distances from feeding stations to used positions within the wintering home range, and \( r_i \) is a vector of distances from the feeding stations to randomly selected points within the winter home range. When the ratio is \( d_i < 1.0 \), the animal is associated with the feeding stations more than is expected by chance (Conner and Plowman 2001). We used 95% minimum convex polygons (MCPs) to delineate moose wintering home ranges (Mohr 1947). For moose with a range overlapping \( \geq 1 \) feeding station, we randomly selected 2,000 points with replacement from the MCP (i.e., Design III sampling; Boyce et al. 2002, Manly et al. 2002, Thomas and Taylor 2006). The number of random points we chose was comparable with the average number of used locations per individual moose. We excluded individuals without feeding stations in their seasonal home range from the EDA. We calculated distances to the closest feeding station for \( u_i \) and \( r_i \) using Spatial Analyst in ArcMAP 9.2. We used a bootstrap procedure to calculate \( d_i \) 10,000 times and classified an individual as a feeding-site user when the upper limit of the 95% confidence interval did not overlap with 1, where 1 = no selection of feeding sites. We subsequently included feeding status (i.e., feeding-site user vs. nonuser) as a covariate in the habitat-selection analysis.

Dussault et al. (2005) demonstrate that results from distance-based analyses do not disclose habitat preference and, moreover, do not necessarily quantify actual habitat use. We, therefore, determined the proportion of time spent within 100 m of feeding stations to quantify feeding site use for each individual separately and to confirm our EDA results with an alternative classification method. We considered that moose located within a 100 m buffer from feeding sites had visited the station because feeding stations were small (<20 m²) and because the location in between the hourly fixes is not known. As such, we calculated the number of hours spent within a 100-m buffer around feeding stations for each moose separately (each unique location represented a visit of 1 hr because we used a 1-hr GPS relocation schedule) and divided that by the number of GPS locations obtained during winter for that individual.

We used independent sample \( t \)-tests to estimate differences in forest road density, proximity to human settlement, proximity to cc.2 of Scots pine stands, and proximity to tractor roads between used and unused feeding stations. We also used independent sample \( t \)-tests to test for differences in home range size (95% MCPs) between feeding-site users
and nonusers. All variables fulfilled the assumptions of normality and homogeneity of variance between groups. Moreover, we evaluated whether feeding stations within Norway spruce–dominated forests were used to the same extent as feeding stations within Scots pine–dominated forests with Fisher’s Exact Test.

Habitat Selection
We assessed habitat selection by modeling resource selection functions (RSF), defined as any function proportional to the probability of use of a habitat by an animal (Manly et al. 2002). We employed mixed-effect logistic regression models and adopted the extension of the fixed-effect, exponential RSF by Manly et al. (2002), as proposed by Gillies et al. (2006): \( w(x) = \exp(\beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \ldots + \beta_n x_{in} + \gamma_0) \). Here \( x_n \) are covariates with fixed regression coefficients \( \beta_n \), the \( \beta_0 \) is the mean intercept, and \( \gamma_0 \) is the random intercept, which is the difference between the mean intercept \( \beta_0 \) for all groups and the intercept for group \( j \) (Skrodel and Rabe-Hesketh 2004, Gillies et al. 2006). Incorporation of a random intercept into RSFs is especially beneficial with unbalanced sampling designs because it adjusts the overall average probability of use, which depends on an arbitrary number of randomly sampled points (both used and available) for each individual (Gillies et al. 2006, Godvik et al. 2009). Based on parsimony, the final mixed-effect RSF models contained only a random intercept for moose identification (because the inclusion of a second random intercept for year did not improve model fit (Alog-likelihood, <3.84; Hilborn and Mangel 1997, Gillies et al. 2006).

We estimated habitat availability by drawing a random sample of points from within each individual’s wintering home range (i.e., the third-order scale of selection; Johnson 1980). The number of available points selected equaled the number of points used by each individual. Thus the response (dependent) variable in our RSF models consisted of used (1) and available (0) locations. We selected the independent variables included in the RSF models a priori to answer our predictions. Variables were 1) dominant tree species (a 3-level factor: Norway spruce, Scots pine, and mixed deciduous), 2) cutting class (as described above), and 3) feeding-status (feeding-site user vs. nonuser). To quantify differences in selection between feeding-site users and nonusers for the various habitat types (\( P_q \)), we included them as second-order interactions. We did not include the interaction between dominant tree species and cutting class because of some missing category combinations within the study area.

To analyze selection patterns of feeding-site users (\( P_2 \) and \( P_3 \)), we excluded all nonusers from the analysis. Moreover, because we used distance from feeding stations as an explanatory variable, we excluded all simulated positions associated with unsuccessful fixes to ensure that no bias toward distance from feeding stations entered the analysis. We categorized distance from feeding stations for all used and available locations into 4 classes of 500-m intervals.

We developed mixed-effect RSF models using R version 2.7.0 (R Foundation for Statistical Computing, Vienna, Austria). The outcome of all these models is the log odds of using a pixel in the map; therefore, we could not derive absolute probabilities of selection. However, calculation of log-odds ratios relative to a reference category consisting of a chosen combination of levels of the categorical independent variables is informative and reliable (Godvik et al. 2009). We set the reference category in our mixed-effect RSF models to pine-dominated stands of cc.2 because differences in selection for this habitat type were our primary interest. To evaluate the properties of the individual coefficients in the mixed-effect models, we used 10,000 Markov Chain Monte Carlo samples and 95% Highest Posterior Density (HPD) intervals. The use of Bayesian HPD confidence intervals is preferred when analyzing large, unbalanced data sets with mixed-effect models because the resulting inferences are more conservative compared with standard 95% confidence intervals (Baayen et al. 2008). For example, the 95% HPD interval for parameter \( \tau \) is the shortest interval where the posterior probability that \( \tau \) lies within the interval is 0.95. We used HPD intervals to evaluate whether selection estimates were significantly different from zero and plotted parameter estimates to assess biological importance (Baayen et al. 2008).

RESULTS
Feeding Site Use
No moose or collars were lost during the study period, but the malfunction of one collar resulted in fewer data points for one individual during winter 2007. After we corrected for GPS bias, the average (±SE) number of GPS locations used per moose (\( n = 32 \)) and year (\( n = 2 \)) were 2,022 ± 93 and 32,354 ± 1,984, respectively.

Of the 32 collared adult female moose, we classified 15 individuals (47%) as feeding-site users, and 17 animals as nonusers, including 8 individuals (25%) that did not have feeding stations within their wintering range (Fig. 2). All feeding-site users spent ≥35 hours each at feeding stations within the 3-month study, whereas all nonusers were far below that threshold (max. 12 hr). The mean proportion of time (±SE) spent within 100 m of feeding stations for feeding-site users was 4.85 ± 0.98% (i.e., 92 ± 17.3 hr), and for nonusers with feeding stations in their wintering range, it was 0.19 ± 0.06% (i.e., 3.8 ± 1.29 hr). Of the 61 feeding stations located in wintering home ranges of the feeding-site users, we recorded that 31 (51%) were never used by the collared moose (i.e., no locations within 100-m circular buffer). Feeding site users had a mean of 12 feeding stations available within the winter home range (min. = 1, max. = 24), with a mean of 3 feeding stations used per individual (min. = 1, max. = 6). Feeding stations used by the GPS-collared moose were located in areas with higher forest road density (1.37 ± 0.08 km\(^2\)) than feeding stations not used by collared moose (1.14 ± 0.07 km\(^2\), \( t_{SM} = 2.019, P = 0.042 \)). We found no difference between used and unused feeding stations in relation to proximity to human settlement (\( t_{SM} = 1.579, P = 0.119 \)), proximity to cc.2 of Scots pine stands (\( t_{SM} = 0.432, P = 0.667 \)), or proximity to tractor roads (\( t_{SM} = 0.828, P = 0.411 \)). Furthermore, we
found no difference in home-range size between feeding-site users (mean ± SE; 34.5 ± 5.4 km²; \( t_{50} = -1.227, P = 0.229 \)) and nonusers (27.8 ± 4.2 km²). The odds of using a feeding station in Norway spruce–dominated habitat were 2.8 times higher than in Scots pine, but this was not significantly different (Fisher’s Exact Test, \( P = 0.142 \)).

**Habitat Selection**

In our assessment of forest-stand classification accuracy, we found that 94.8% of the forest stands were correctly classified with regard to cutting class and dominant tree species. A substantial part of the misclassification (2.7%) was attributed to recent clear-cut felling of cc.5 in Norway spruce–dominated forest stands. We considered the accuracy of the GIS layers adequate for our purposes.

Among moose that did not use feeding stations, selection was highest for young Scots pine stands (cc.2), indicated by HPD intervals of other cutting classes below zero and not overlapping with the reference category for this group (Fig. 3). Among moose using feeding sites, selection was higher for older pine-dominated stands (cc.2–cc.5) than it was for nonusers (\( P_1 \)) and lower for spruce and deciduous stands (Table 1; Fig. 3). However, estimates of selection for the critical habitat type cc.2 within pine stands was not statistically different between feeding-site users and non-users, with HPD intervals between groups overlapping (Fig. 3).

For feeding-site users, the likelihood of using a location was highest close to feeding stations and decreased markedly with distance from feeding station, as expected from central-place foraging theory (\( P_2 \); Table 2; Fig. 4). This pattern was not a result of confounding spatial elements (such as other types of attraction points systematically located close to feeding stations) because overall space use by nonusers with feeding stations available in their home range (\( n = 10 \)) was unrelated to distance from feeding sites (Table 2; Fig. 4). Also as predicted (\( P_3 \)), variation in selection for the different pine cutting classes (with the exception of recently felled areas of cc.1) was relatively small in the vicinity of feeding stations (HPD intervals overlap the most \( \leq 1.5 \) km), but increased at locations greater than 1.5 km from feeding stations (Table 3; Fig. 5). Moreover, as distance from feeding stations increased, the use of mixed deciduous forest and Norway spruce stands by feeding-site users increased (Table 3).
Figure 3. Selection estimates (log odds ratio ± 95% Highest Posterior Density [HPD] intervals) for cutting class within Scots pine-dominated forest stands by moose using feeding stations (feeding-site users, n = 15) and those not using feeding stations (nonusers, n = 17) in southern Norway during the winters of 2007 and 2008. All estimates are in comparison with the reference category: cutting class 2 for nonusers; HPD intervals >0 indicate selection and <0 indicate avoidance of habitat compared with the reference category. Habitat categories with HPD intervals overlapping with the reference category are used at a similar rate.

DISCUSSION

Although feeding was initiated with the aim of reducing browsing damage to the commercially important young Scots pine, we found that moose using feeding sites selected these stands to the same extent as moose not using feeding sites (rejecting $P_1$). Unfortunately, we had no control over the spatial positioning of the feeding stations, so, as with any correlational study, there is the potential for confounding factors. However, the observed patterns emerged despite most feeding sites used by the collared moose being located within spruce-dominated, rather than pine-dominated, habitat. This could be attributed to the availability of shelter habitat and abundant forage within close range of the feeding stations.

In the classical case of central-place foraging theory, an animal’s foraging trip starts at a central place (e.g., a nest or den) and continues until the animal captures a prey, after which, the animal returns to the central place (Orians and Pearson 1979). The application of distance-based models is preferred when analyzing habitat selection for animals for which a central place can be identified (but see Dussault et al. 2005) because they incorporate potential spatial clustering of habitats surrounding the central place and, thus, account for potential bias in selection estimates (Rosenberg and McKelvey 1999). An artificial feeding site can be regarded as an additional component in the habitat selection of ungulates using such sites, and we argue that a feeding site resembles a central-place attraction point. How to analyze this specific case has not been addressed before.

Table 1. Selection estimates (log odds ratio ± 95% Highest Posterior Density [HPD] intervals) of mixed-effects, logistic-regression model predicting selection for habitat (i.e., cutting class, dominant tree species) by moose using feeding stations (feeding-site users, n = 15) and those not using feeding stations (nonusers, n = 17) in southern Norway during the winters of 2007 and 2008 (Fig. 3). All estimates are in comparison with the reference category. The model includes a random intercept for each individual (moose identification; SD = 0.275 [HPD interval 0.221–0.380]).

<table>
<thead>
<tr>
<th>Variable</th>
<th>$\beta$</th>
<th>SE</th>
<th>Lower</th>
<th>Upper</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
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<td>0.071</td>
<td>0.546</td>
<td>0.844</td>
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<td>Dominant tree species$^a$</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mixed deciduous</td>
<td>-0.492</td>
<td>0.070</td>
<td>-0.626</td>
<td>-0.354</td>
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<tr>
<td>Norway spruce</td>
<td>-0.956</td>
<td>0.022</td>
<td>-1.000</td>
<td>-0.913</td>
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<tr>
<td>Cutting class (cc.)$^b$</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>cc.1</td>
<td>-0.693</td>
<td>0.074</td>
<td>-0.836</td>
<td>-0.551</td>
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<tr>
<td>cc.3</td>
<td>-0.204</td>
<td>0.023</td>
<td>-0.249</td>
<td>-0.159</td>
</tr>
<tr>
<td>cc.4</td>
<td>-0.288</td>
<td>0.037</td>
<td>-0.361</td>
<td>-0.216</td>
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<tr>
<td>cc.5</td>
<td>-0.331</td>
<td>0.029</td>
<td>-0.390</td>
<td>-0.277</td>
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<tr>
<td>Feeding status$^c$</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Feeding-site user</td>
<td>0.151</td>
<td>0.103</td>
<td>-0.064</td>
<td>0.370</td>
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<tr>
<td>Dominant tree species × feeding status</td>
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<tr>
<td>Mixed deciduous × feeding-site user</td>
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<td>-0.781</td>
<td>-0.389</td>
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<td>Norway spruce × feeding-site user</td>
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<td>-0.175</td>
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<tr>
<td>Cutting class × feeding status</td>
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<tr>
<td>cc.1 × feeding-site user</td>
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<td>cc.3 × feeding-site user</td>
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<td>0.053</td>
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<td>cc.4 × feeding-site user</td>
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<td>cc.5 × feeding-site user</td>
<td>0.151</td>
<td>0.040</td>
<td>0.073</td>
<td>0.229</td>
</tr>
</tbody>
</table>

$^a$ Reference category = Scots pine.

$^b$ Reference category = cc.2.

$^c$ Reference category = nonuser.

Consistent with our predictions, the relative probability of a location being used decreased significantly as distance from feeding sites increased (supporting $P_2$). In addition, the variation in selection for pine-dominated habitat increased with distance from feeding stations (as expected by $P_3$). Several observational studies report that herbivores developed an increased reliance on artificial feed and reduced natural forage intake to near zero (Putman and Staines 2004). Nonetheless, persistent use of natural forage has been observed in white-tailed deer (Schmitz 1990, Doenier et al. 1997) and moose (Gundersen et al. 2004) while being offered supplementary forage. This behavior may be related to a shortage of essential nutrients or fiber in the supplied forage (e.g., hay is not considered high-quality forage for moose; Schwartz and Hundertmark 1993).

Feeding sites attracted approximately half of the individual moose marked in our study area: 25% did not have feeding sites within their home range, and 28% had feeding stations available in their winter home range but did not use them. This may be due to several factors, such as individual variation in vigilance (White et al. 2001), migration status (Luccarini et al. 2006), or social rank (Schmidt and Hoi 1999). Also, severity of winter conditions (e.g., increasing snow depth) is an important factor influencing the use of...
supplementary feed by cervids (Doenier et al. 1997). Snow conditions may have been sufficiently mild for moose not to need the feeding stations during the winters studied. Moreover, feeding history in this area is relatively short (6 yr). It is, therefore, possible that some individuals with feeding stations in their wintering range have not discovered them simply because they have not visited all parts of the area we define as their winter range (95% MCP area) or have not yet learned to feed on the supplied forage. Although the proportion of time spent on feeding stations during winter was, on average, only 5% per individual, diversionary winter feeding as a management intervention has nonetheless altered space-use and habitat-selection patterns of moose, even throughout this relatively short period. Changes in behavior patterns can be expected to be even stronger in situations where animals use feeding stations more intensively.

Local densities around feeding stations can become exceedingly high (≤80% of a local population; Peek et al. 2002 and references therein). In agreement, we found that the likelihood that habitat selected by a feeding-site user within 500 m from feeding sites was almost 5 times higher

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than selecting locations beyond 1.5 km from the feeding sites. However, we did not observe an increase in selection of assumed high-quality habitat types with increasing distance from feeding sites, which is inconsistent with predictions from central-place foraging theory. Instead, selection for assumed high-quality winter foraging habitat (i.e., pine stands of cc.2) by moose was highest closer to feeding stations (<1 km) and decreased as distance from feeding stations increased. This suggests that intraspecific resource competition, potentially leading to resource depletion near feeding stations, was not a major factor influencing habitat selection of feeding-site users. Moreover, our results indicate that selection for older pine stands and spruce-dominated forest increased with distance from feeding stations. These habitat types are generally characterized by reduced snow cover, which facilitates traveling, provides shelter (Dussault et al. 2006), and holds important forage resources, such as dwarf shrubs (Heikkila et al. 1996).

**MANAGEMENT IMPLICATIONS**

Diversionary winter feeding as a management intervention can greatly alter space-use and habitat-selection patterns. However, it may not be effective in protecting valuable stands if the valued species (in our case, Scots pine) remains an important part of the diet of individuals using feeding stations. Because feeding-site users concentrated their movements around feeding stations, we recommend establishing feeding sites in sacrifice areas where browsing is permissible and, if possible, >1 km from valuable stands. Future assessment of the effectiveness of diversionary feeding as a tool to reduce browsing damage would benefit from a detailed analysis of the cost of supplying additional feed and the benefits it may generate in reduced forestry losses. Additional evidence from regions with longer feeding traditions is needed to assess how space-use and habitat-selection patterns evolve over time and change with winter severity and intensity of feed use.

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**LITERATURE CITED**


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