DISTRIBUTION OF WINTER BROWSING BY MOOSE: EVIDENCE OF LONG-TERM STABILITY IN NORTHERN SWEDEN

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ABSTRACT: Predicting spatial distribution of large herbivore foraging is important for successful management, but accurate predictions remain elusive against a background of multiple causes modified by environmental stochasticity. Moose (*Alces alces*) might prefer to browse areas with high plant density, but if snow depth co-varies with plant density, this could restrict access to these sites and force use of sites with lower plant density and snow depth. Moose browsing was measured in 72 plots distributed within the subarctic birch (*Betula* spp.) forest landscape at Abisko in northern Sweden in 1996. In 2010, the same plots were revisited and the measurements repeated. A generalized linear model predicted moose browsing on birch in 2010 from the browsing pattern on birch measured in 1996. The model suggested that neither total density of willow and birch stems nor snow depth were influential of foraging distribution of birch at multiple spatial scales. The spatial scale at which clustering of browsing on birch occurred, coincided with the scale of clustering of birch and willow (*Salix* spp.) stems at distances of 1000–2500 m; at lesser distance browsing was distributed randomly. We concluded that moose demonstrate stability in spatial browsing patterns after 14 years which corresponds to 3–4 generations of moose, and that plant density represents a cue for moose only at certain scales. Predictability of feeding sites is valuable for long-term moose and forest management, and conservation planning.

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Key words: *Alces alces*, foraging distribution, moose, mountain birch, predictability, spatial scale, willow.

INTRODUCTION

A key objective in the field of foraging ecology is to detect, quantify, and explain the patterns of spatial heterogeneity by feeding herbivores (Bailey et al. 1996). Moose (*Alces alces*) browsing has high potential impact on the structure, dynamics, and composition of both natural and managed forests (Pastor and Naiman 1992, Heikkilä and Tuominen 2009). At the stand level in boreal forests, moose herbivory causes increased heterogeneity of vegetation due to patchy distribution of their browsing over the landscape (Shipley and Spalinger 1995, Edenius et al. 2002).

There are several possible underlying reasons for this spatial variation in foraging patterns. Moose might seek the best available habitats (i.e., areas with comparatively high density and high quality of food) or they may avoid certain areas because of high intra- or interspecific competition, high predation risk, or because landscape barriers prevent access (Creel et al. 2005, Van Beest et al. 2011) resulting in a mosaic of browsing distribution.

Browsing density is an important predictor of home range size and browsing distribution by moose (Van Beest et al. 2011). Although their large body size (400–600 kg) requires a large quantity of food (Shipley 2010), moose tolerate a low quality diet, on a relative scale, because of the nutritional influence of allometric scaling (i.e., the Bell-Jarman-Principle) (Geist 1974, Müller

et al. 2013). According to the Snow-Shrub Interaction Hypothesis, snow depth is positively related to leaf area index, stem diameter, and canopy height (Sturm et al. 2001). Deep snow may hinder moose from utilizing the best sites and force animals to feed in areas with less snow depth and poorer sites such as ridges and wind exposed areas (Kelsall 1969).

Scale-dependency is evident in the geographical distribution of foraging sites, but also in terms of the hierarchical arrangements of plant tissues, individuals, populations, and communities upon which herbivores feed (Palo et al. 1992, Hodar and Palo 1997). This scale-dependent heterogeneity is one fundamental factor that can restrict diet quality in a particular environment (Bailey et al. 1996). Both spatial and temporal variation in environmental characteristics, including food availability, influence patterns of herbivory (Wiens 1989, Horne and Schneider 1995, Kie et al. 2002, Van Beest et al. 2011). Thus, a multi-scale perspective is useful to understand patterns of foraging distribution that underlie herbivore-plant interactions (Owen-Smith 2002, Owen-Smith et al. 2010).

One approach is to determine the distribution of food resources, specifically their extent (geographical boundary), resolution (sites, plants, tissues), and complexity (diversity, interactions) across a landscape. Distribution of "good patches" (i.e., areas with relatively high density of plants available to herbivores) often show spatial autocorrelation, meaning that nearby locations are more likely to have similar features than by chance alone (Wagner and Fortin 2005). It is expected that browsing will be clustered at the landscape scale since foraging is concentrated on certain valuable sites (Shipley and Spalinger 1995). The spatial scale at which foraging is clustered shows at what scale animals make foraging decisions, and it should coincide with the scale of clustering of forage that is tracked by the animal (Saracco et al. 2004). Since spatial distribution of high-value patches are predetermined by landscape structures such as soil nutrients, moisture, slope, and elevation, temporal consistency in foraging distribution would be expected (Bjørneraas et al. 2012). Further, previous observations of repeated browsing by moose on the same individual plant suggest that browsing patterns are consistent even at a landscape perspective since the same trees are visited repeatedly (Danell et al. 1985).

We tested this prediction by mapping the spatiotemporal distribution of winter browsing by moose in a subarctic landscape within unmanaged mountain forest in northern Sweden during 2 winters, 14 years apart. We hypothesized that the same locations are used by moose repeatedly over time, and tested 2 possible explanations for spatial structuring of moose foraging: that browsing intensity at a particular site is 1) positively related to high tree species density and 2) negatively related to low snow depth. We also investigated how tree density covaries with snow depth which may hinder use of sites with relatively high tree density.

STUDY AREA

This study was conducted in the Abisko Valley (68° 21′ N, 18° 49′ E) in northern Sweden (Fig. 1) where the low diversity of plant species (i.e., mostly birch and willow were prevalent in this Scandinavian mountain ecosystem) provides herbivores with limited food choice, and consequently, study of feeding behaviour in a fairly simple system. Moose occur year-round in the Abisko Valley but in higher numbers in winter, possibly because of its relatively low snow cover that may attract seasonally migratory moose (Lundmark and Ball 2008). The Abisko Valley receives less precipitation than the surrounding mountain region, with annual precipitation of 300 mm (Abisko

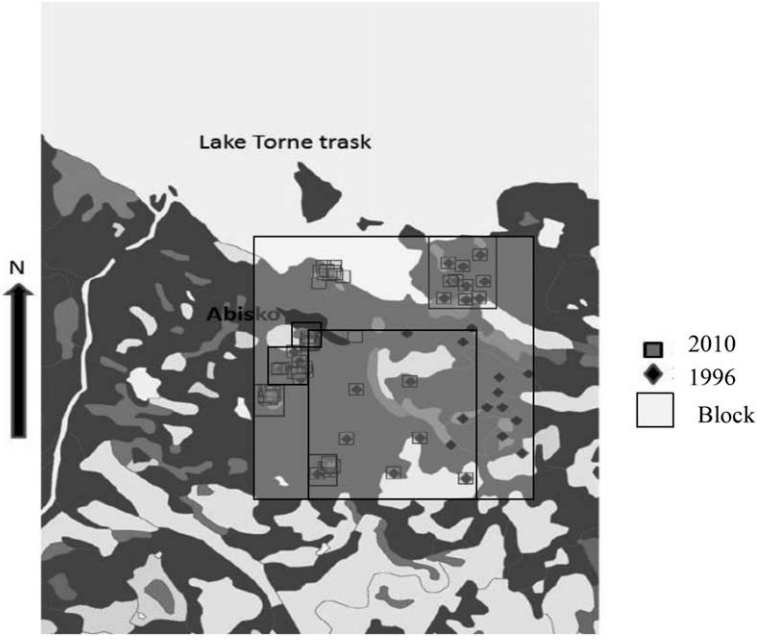

Fig. 1. Location of the study sites at Abisko with approximate position of blocks with sample plots in 1996 and 2010. Dark grey areas are birch forest, light grey are mires, and white areas are bare ground or lakes; black is the village of Abisko Östra, Sweden. The side of the largest block is 3 km.

Research Facility). Snow depth is about 50 cm at its peak in March (Kohler et al. 2006), but varies spatially across the landscape.

The study area is a mountain birch forest extending from Lake Torne träsk at 340 m to tree line at 670 m. Mountain birch (*Betula pubescens* sp. *czerepanovii*) is the dominant tree in the forest in mountainous areas of northern Fennoscandia. It is limited in the south by boreal coniferous forest and in the north by tundra. Shrubby willows (*Salix* spp.) are also common in the region and some aspen (*Populus tremula*) and scattered Scots pine (*Pinus sylvestris*) occur. Moose have a notable impact on the vegetation as birch, young pines and willow in the Abisko Valley reflect continuous winter browsing (Stöcklin and Körner 1999). Environmental conditions in the study area, as in similar subarctic environments, change abruptly within short distances, resulting in sharp contrasts in density of plants, levels of nutrients, and concentrations of plant secondary metabolites (Karlsson 1991, Hodar and Palo 1997). Mountain birch forests are typically not harvested, but infrastructural development has impacted nearby forest vegetation in the past century and natural disturbances such as insect outbreaks and prolonged frost drive vegetation change in the area (Callaghan et al. 2013). Tree and shrub cover have increased in the Abisko Valley from 1970 to 2010, mostly for mountain and dwarf birch (*Betula nana*); willow response has been inconsistent (Rundqvist et al. 2011).

METHODS

Study design

Seven blocks ranging from 3–740 ha were placed within the 3000 ha study area in 1996. Within each block, we established 10 randomly distributed 25 × 25 m sample

plots, with the exception of a single block with 12 plots. In this design the distance between plots increases systematically as block size increases, while the grain (i.e., the smallest pixel size is the plot: 25 × 25 m) and number of observations per block remain constant. All mountain birch and willow stems were counted in all sample plots in 1996; these measurements were repeated in 61 of 72 plots in 2010. We counted birches with accumulated bites by moose from last leaf fall to the time of investigation in February-March, hereafter denoted as "current season". Snow depth (cm) and all stem diameters at the snow surface (cm) were measured in each plot. Annual snow depth in January-March was provided by the Abisko Research Station from permanent plots in the area. We used only birch stems with diameter >1 cm for comparison between 1996 and 2010 to prevent bias in stem density due to variable annual snow depth; many of the thinnest stems are not visible in deep snow. Relative moose density was estimated along 9, 1-km transects located systematically within the study area. Moose tracks that intersected these transect were counted (# of tracks/km, Table 1) within a 1-week period in February 1996 and 2010.

Table 1. Densities of birch and willow, snow depth, and moose tracks/km measured in the study area near Abisko, Sweden, January–March 1996 and 2010.

Year	1996	2010	
Variable	Mean (SD)	Mean (±SD)	*P*-value
Birch density (stems/m^2)	0.13 (0.12)	0.43 (0.25)	<0.001
Willow density (stems/m^2)	0.06 (0.06)	0.19 (0.3)	<0.009
Snow depth (cm)	66.9 (9.3)*	28.6 (9.6)*	<0.0001
Moose tracks (#/km)	16.4 (16.9)	2.2 (2.3)	<0.05

*Data provided by the Abisko Scientific Research Station.

Statistical analyses

In both sample periods (1996 and 2010) the distance matrix was used to calculate autocorrelation variograms (correlograms) at different spatial intervals (distance lags) using local Moran's I. This measurement is used to detect significant autocorrelation among factors varying over time or space (Anselin 1995). Values of local Moran's I were produced using the software SAM (Rangel et al. 2010). Correlograms were drawn using R version 3.1.2 (R Development Core Team 2014). Distance lags were calculated using pairs of plots within distances of 0–5000 m with breakpoints every 500 m. Distance lags beyond 5000 m contained a declining number of plot pairs and were excluded from analyses. The number of plot pairs included in each distance lag in the Moran's I analyses ranged from 290–294 for birch and 50–70 for willow.

A Generalized Linear Model (GLM) was used to test for factors affecting moose browsing in the year 2010. We assumed that moose browsing in 2010 would reflect previous browsing history and current distribution of willows, because willow is preferred forage. We also assumed that variation in snow depth within the study area in 1996 reflected the conditions in 2010. We accounted for spatial dependence between sample plots with a set of 23 mean distances constructed from a distance matrix between pairs of plots within and between blocks. Each data point for factors in the model is the mean at each of the 23 distances. Mean distances between plots ranged within lags from 87–5133 m and the number of plot pairs within lags was 36–90. We used a backward stepwise procedure with variables removed from the model at $P > 0.05$. The best model was judged from Akaike's Information Criteria with correction for finite sample size (AICc). Analyses were performed in SYSTAT 2013.

RESULTS

Basic forest characteristics differed between the 2 study periods as the density of birch and willow increased from 1996 to 2010 (Table 1). The proportion of plots containing willow increased from 44 to 62%. There was considerable variation in stem density for both species over the landscape. Birch density varied from 3–325 stems per plot in 1996 to 3–685 in 2010; similarly, willow ranged from 2–867 stems per plot. This reflected a heterogeneous landscape and a varied mosaic of forage distribution.

Mean snow depth and the estimated moose density (track counts) declined between 1996 and 2010 (Table 1). No correlation was found between snow depth and birch and/or willow density. However, birch density in 1996 was positively correlated with birch density in 2010 (Spearman's rho = 0.39, $P = 0.002$); a similar correlation was not found for willow. Temporal browsing on birch trees showed considerable variation ranging from 0.6–77% of birches in the sample plots in 1996 to 0.2–19% in 2010. Browsing on birch was observed in 53% (SD = 17.4) of plots in 1996 and 35% (SD = 2.0) in 2010; corresponding browsing on willows was 84% and 70%, respectively. Only 4% of available birch stems were browsed in 1996, declining to 0.5% in 2010. The most parsimonious model retained only browsing on birch in 1996 as a significant factor to predict browsing on birch in 2010 (Table 2). The best model rendered the following equation:

$$Y = 1.18 \times X - 6.18,\ \text{F-ratio} = 109.8,\ P < 0.0001,\ R^2 = 0.84 \quad (1)$$

where Y = browsing on birch in 2010, and X = browsing on birch in 1996.

The proportion of browsed birch stems was not correlated with birch density in 1996 or 2010. Similarly, the proportion of browsed willows was not correlated ($P > 0.05$) with the density of willows, but almost all willows were browsed independent of their density. In general, for either year, browsing on willow stems did not depend on density of adult birch stems.

Table 2. Stepwise selection of the best model with AICc for each proposed browsing model, Northern Sweden. Variables are: A) moose browsing on birch in 2010, B) birches browsed in 1996, C) willows browsed in 2010, D) willow density in 2010, E) birch density in 1996, and F) snow depth in 1996.

Model	AIC (corr.)
A= 1.2×B-C + D + 0.007×E-0.04×F	164.6
A= 1.2×B + 0.015×D + 0.196×E-0.04×F	160.4
A= 1.2×B + 0.196×E-0.04×F	156.7
A= 1.2×B + 0.196×E	153.3
A= 1.2×B	150.5

According to Moran's I, the spatial variation of birch and willow densities, as well as of browsed birches, showed significant autocorrelation at distances between 1000–2500 m (Fig. 2). At greater distance, the number of browsed birch varied between plots more than expected by chance. Spatial consistency between years was shown by Moran's I for birch densities which was consistent with the distribution of moose browsing, which was clearer in 1996 than in 2010. Moran's I for browsing on willow was inconsistent and randomly distributed at most distances (Fig. 2).

DISCUSSION

There was a profound change in density of birch and willows in the Abisko Valley from 1996 to 2010 despite the absence of forest management. Rundqvist et al. (2011) also found an increase in shrub and tree density in the area in recent decades. An increase in snow depth in the Abisko region has occurred recently with higher precipitation

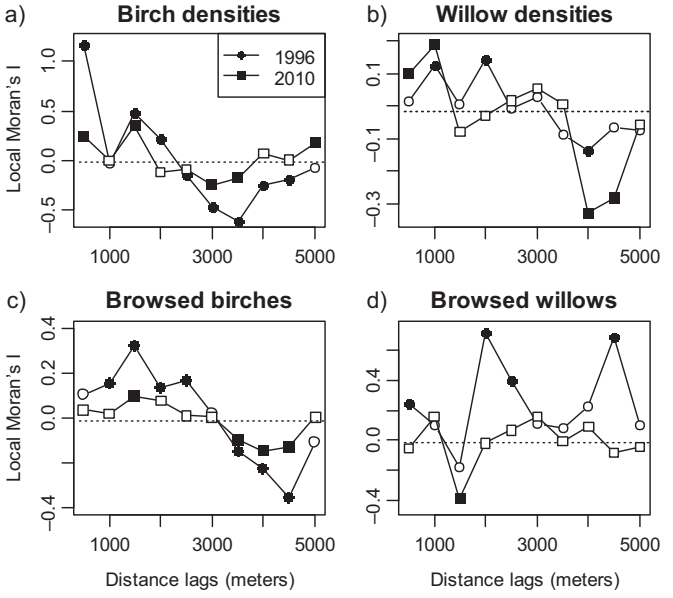

Fig. 2. Local Moran's I for density of birches and willows (A, B) and number of browsed birches and willows (C, D) within 625 m^2 sample plots in Abisko, 1996 and 2010. Black symbols indicate significant positive and negative autocorrelations at $P < 0.05$. Dotted lines denote the expected value of Moran's I if observations were distributed randomly.

in the mountainous region (Callaghan et al. 2010). Contrary to this trend, snow depth was much lower in 2010 than 1996, but this did not attract more moose to the area. Snow depth was not a significant parameter in the statistical model predicting browsing in 1996 or 2010. Further, we did not find support for the hypothesis that birch and willow density were related to snow depth. Although the average snow depth was less than the critical threshold that inhibits moose movement in both years (Kelsall 1969, Lundmark and Ball 2008), the large variation across the landscape may result in certain sites having deep snow that hinders movement in any given year.

Our and the Rundqvist et al. (2011) study suggest that more moose forage existed in the Abisko Valley in 2010 than in 1996. This difference may reflect several underlying causes including a decline in moose density that allowed increase in willow abundance and survival of young pine trees. Other possible long-term factors include recovery of birch trees from insect outbreaks, change in human activities, or climate warming (Emanuelsson 1987, Tenow 1996, Callaghan et al. 2010). An outbreak of the autumnal moth (*Epirrita autumnata*) in the mid-1950s defoliated and killed a large proportion of the birch forest, and it is possible that birch biomass is still recovering to levels prior to the outbreak (Tenow 1996). We were not able to distinguish the specific effect of moose on vegetation dynamics in the long-term, and despite large scale changes and varied snow depth in the landscape and between years, browsing distribution was unaffected and relatively unchanged in the study area. Although profound changes

occurred in vegetation cover, birch density was correlated between 1996 and 2010, without concurrent correlation for willow density. Moose had high fidelity to feeding sites across the 14 years of the study, representing 3–4 generations of northern Swedish moose (G. Ericsson, Swedish University of Agricultural Sciences, pers. comm.).

Our results correspond with that of Månsson (2009) who also found that distribution of moose browsing was independent of the density of birch. Although willow was browsed wherever it occurred in Abisko, the presence of this preferred browse species did not result in higher browsing of birch at sites with high willow density. As expected from the theory of spatial autocorrelation, birch and willow density and moose browsing intensity had a trend of declining autocorrelation with increasing distance between plots (Legendre and Legendre 1998). At the smallest scale of observation, up to 500 m as indicated by Moran's I, browsing distribution is randomly dispersed. We observed a clustering of both density of birch and browsing of birch at lag distances of 1000–2500 m, indicating the spatial scale at which moose foraging choice occurs. At this lag distance, birch and willow density are cues that interact to facilitate spatial clustering, which is most visible in the 1996 data. Wallgren et al. (2013) also found spatial autocorrelation for moose browsing on pine similar to birch and willow in this study.

Accurate prediction of animal distribution increases the probability of realizing management goals (Månsson 2009). A prerequisite for making such predictions is to identify patterns of behaviour among animals that are stable over time, and to identify environmental factors that govern animal behaviour. Although forage density did not explain moose browsing across all spatial scales considered in the model, the correlograms indicate that this is an important cue for moose at certain scales. The spatial distribution of preferred forage, and the animal's perception and utilisation of it, were consistent and remained stable over a time period that spanned several generations of moose. Our results indicate that spatial patterns of moose browsing across multiple scales can persist over a long time period despite changes in vegetation density and snow depth, specifically in unmanaged habitat like our study area. The ability to predict population distribution and utilization of resources relative to management strategies may be better is such situations because resource distribution remains stable for long periods of time.

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