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Source: Arctic, Antarctic, and Alpine Research, 38(3) : 413-420

Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado

URL: [https://doi.org/10.1657/1523-0430\(2006\)38\[413:SHAHFH\]2.0.CO;2](https://doi.org/10.1657/1523-0430(2006)38[413:SHAHFH]2.0.CO;2)

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Spatial Heterogeneity and Hierarchical Feeding Habitat Selection by Reindeer

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Abstract

Reindeer, *Rangifer tarandus*, live in subarctic and alpine environments with spatially and temporally heterogeneous resource distribution. In this study, we used a hierarchical approach to test whether reindeer responded to spatial heterogeneity during the plant growing season (divided into three distinct periods) in a mountainous subarctic environment in northern Sweden. A reindeer herd in northern Sweden was surveyed using radio-telemetry (8 female reindeer) and the selection of feeding habitats by observing individuals/groups (135 observations) using laser range-finding binoculars. Reindeer selected feeding areas (evaluated at 5-km grid size), as well as feeding habitats (evaluated at 0.5- and 1-km grid size) during spring, in response to high terrain ruggedness and habitat heterogeneity. Reindeer switched during summer to select against terrain ruggedness and habitat heterogeneity at the level of feeding habitats, while preferring southward facing habitats. During autumn, a broader spectrum of feeding habitats was used. We conclude that reindeer seem to adopt a hierarchical strategy in agreement with general foraging theory, and are capable of responding to seasonal changes in resource distribution occurring across spatial scales. Furthermore, our results support the idea that spatial heterogeneity is an important factor to large-sized herbivores at high and intermediate levels of habitat selection. Conservation of large continuous and undeveloped landscapes is an important management goal, as they provide a wide range of habitats necessary for animals such as reindeer that use large territories.

Introduction

Reindeer (*Rangifer tarandus* L.) are part of the native large-sized herbivore community in northern Fennoscandia (Oksanen et al., 1995). Though in modern times it is semi-domesticated in Sweden and most parts of Finland and Norway (Dahle et al., 1999), it plays an important role ecologically, economically, as well as culturally (Sandström et al., 2003). Winter conditions are harsh and may affect reindeer populations severely (Gunn and Skogland, 1997; Klein, 1999), but recent studies have demonstrated the importance of summer forage conditions to population dynamics of reindeer (Post and Klein, 1999; Tveraa et al., 2003). The Scandinavian mountain range contains important summer ranges for reindeer where the extent of different vegetation associations and their nutritive value vary in relation to, for example, relief, aspect, and edaphic conditions (Edenius et al., 2003; Mårell et al., 2006). Consequently, resource distribution patterns at the summer ranges in northern Sweden are spatially and temporally heterogeneous. However, recent rapid environmental and social changes in the north exert a pressure on these large diverse landscapes (Chapin et al., 2004), and subsequent land-use changes might dramatically affect reindeer and other animals that depend on large continuous territories.

Spatial and temporal heterogeneity of environmental resources have long been recognized as governing the distribution of animals and their movements as well as affecting population dynamics (Levin, 1976; Wiens, 1976; Pastor et al., 1997). Animals respond to the environment either in a fine-grained (i.e., no selection at a given scale) or coarse-grained (i.e., selection) fashion (Kotliar and Wiens, 1990). By providing refuges, prey can reduce the risk of predation in heterogeneous environments (Wiens, 1976), as observed, for example, among reindeer at calving grounds (Bergerud et al., 1984). Furthermore, arctic, subarctic, and alpine ecosystems are heterogeneous environments wherein snowmelt and altitudinal gradients affect plant nutrient dynamics (Körner, 1989; Kudo et al., 1999; Mårell et al.,

2006) and forage availability (Nellemann and Thomsen, 1994) in such a way that the period of high quality forage across small and large spatial scales is prolonged (Skogland, 1980; Albon and Langvatn, 1992). Feedback mechanisms within soil-plant-animal interactions have also proven to cause spatial heterogeneity (Pastor et al., 1997), where reindeer summer grazing has been observed to increase plant species diversity (review by Suominen and Olofsson, 2000) and alter ecosystem productivity (Olofsson et al., 2001).

Animal decision making, for example that of herbivore foraging, can be considered as a hierarchical process where selection occurs at (i) high levels such as that of region, landscape, or home range/territory, (ii) intermediate levels such as that of feeding area, patch, or plant community, and (iii) low levels such as that of feeding site/station, micropatch, plant species, or plant part (Roughgarden, 1974; Johnson, 1980). Environmental factors affect this hierarchical process differently depending on spatial as well as temporal scales (Senft et al., 1987; Wiens, 1989; Levin, 1992). Furthermore, decisions made at a given level, such as feeding habitat selection, are often trade-offs between different evolutionary constraints such as forage quality and quantity (Stephens and Krebs, 1986; Johnson et al., 2001) or predation and energy gain (Festa-Bianchet, 1988; Skogland, 1989; Lima and Dill 1990). Reindeer are well-studied, large-sized herbivores in the boreal to the arctic region for which it has been shown that forage quality and quantity affect decision making at the levels of plant parts (Cooper and Wookey, 2003), plant species (Danell et al., 1994), feeding patch (Ball et al., 2000; van der Wal et al., 2000; Mårell et al., 2002), plant community (Skogland, 1984), as well as feeding area (Post and Klein, 1996). Furthermore, insect harassment/high temperature (Ion and Kershaw, 1989; Walsh et al., 1992; Folstad et al., 1991; Andersen and Nilsen, 1998), snow (Skogland, 1978; Johnson et al., 2001), predation risk (Bergerud et al., 1990; Fancy and Whitten, 1991; Johnson et al., 2002), and human activities (Chubbs, et al., 1993; Helle and Särkelä, 1993) are other important

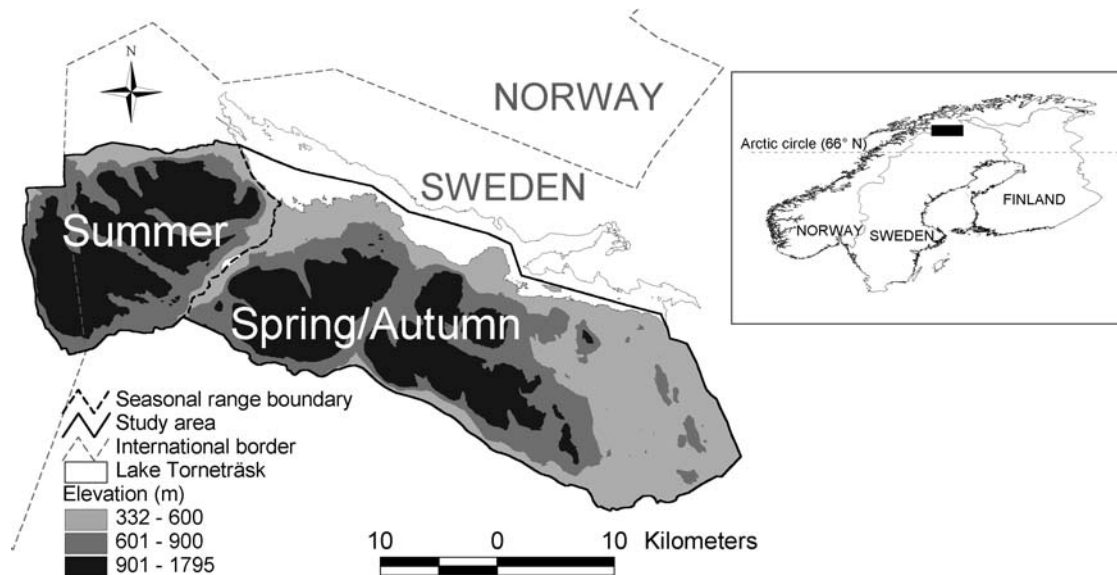


FIGURE 1. The study area (habitat use analyses were only performed on the Swedish side of the border) comprising the entire summer (600 km²), and spring and autumn (1500 km²) ranges for the reindeer herd belonging to Gabna Saami community, northern Sweden.

environmental factors affecting reindeer foraging, distribution, and movement patterns at different spatial and temporal scales. Most such studies have looked at specific levels one at a time. Few attempts have tried to elucidate the dominating factors at different levels simultaneously (year-round: Skogland, 1984; Rettie and Messier, 2000; winter: LaPerriere and Lent, 1977; Nellemann, 1996; Johnson et al., 2001; Johnson et al., 2002; summer: White and Trudell, 1980).

In the present study we focus on the high and intermediate levels of selection by reindeer applying a hierarchical approach. Specifically, we evaluate the importance of spatial heterogeneity, terrain features, and land cover on feeding habitat selection by reindeer at three different spatial scales. Additionally, we address the seasonal dynamics corresponding to three distinct ecological periods (late spring, summer, and early autumn) during the plant growing season in a mountainous subarctic environment in northern Sweden.

Study Area

The study was done in a mountainous landscape of subarctic northern Sweden including the Abisko National Park (68°19'N, 18°40'E). The study area (2100 km²) was defined by the spring, summer, and autumn ranges (the Norwegian part excluded) used by the semi-domesticated reindeer herd belonging to Gabna Saami community (Fig. 1). The area is characterized by a strong climatic gradient over short distances with prevailing oceanic influences in the west and continental influences in the east (Andersson et al., 1996). The long-term average of annual mean temperature (1961–1990) at Abisko Meteorological Station (68°21'N, 18°49'E, 388 m a.s.l.) is –0.8°C, and mean temperature of the warmest month, July, is 11.0°C (Alexandersson et al., 1991). The elevation in the area ranges from 332 to 1803 m (25% of the study area is >1000 m), with the highest mountains in the western parts. The tree line runs at approximately 550–600 m in the west and 700–800 m in the east. Valleys below tree line have mountain birch forests, *Betula pubescens* ssp. *czerepanovii* (Orlova) Hämet-Ahti, mixed with open fens and sub-alpine heaths (Berglund et al., 1996). The low alpine belt above the tree line has heaths dominated by dwarf shrubs such as *B. nana* L., *Vaccinium myrtillus* L., and *Empetrum nigrum* L. (Sjörs, 1999), and patches of willow (*Salix* spp.). The middle alpine belt is characterized by graminoid and herb-dominated communities; the prevalent species are *Carex bigelowii* Torr., *Calamagrostis lapponica* (Wahlenb.) Hartm., *Juncus trifidus* L., *Ranunculus acris* L., *Viola*

biflora L., and *Rumex acetosa* L. The high alpine belt above approximately 1100 m has discontinuous plant cover (Sjörs, 1999).

Methods

REINDEER HABITAT USE AND ANALYSES

Reindeer herding is traditionally divided into eight seasons in Scandinavia (Sandström et al., 2003). Observations of reindeer habitat use were made from end of May to beginning of September, thus covering three of these eight seasons: (1) end of May to beginning of July (hereinafter “spring”), (2) July (“summer”), and (3) August to beginning of September (“autumn”). In the study area, passing from one season to another was marked by herding interventions moving the reindeer herd westward from the spring to the summer range across Abisko river, and eastward from the summer to the autumn range, respectively (Fig. 1). Within seasons, reindeer were left to graze freely. Analyses of habitat selection followed this division and considered between-seasonal movements as mainly man-induced and thus excluded, while within-seasonal movements were considered as independent of herding activities and thus reflected inherent habitat selection behavior by reindeer.

Eight female reindeer were tagged with radio collars (TXE-3 Televilt International AB, Lindsberg, Sweden) in July 1998 and were only used to determine the area in which to search systematically for and observe reindeer habitat selection. Groups and individuals of reindeer were approached by using available cover and features of the terrain and were observed from a position distant enough that the animals were not disturbed. No reindeer was observed more than once during the same day, and groups of reindeer were considered as single observation units, to ensure statistical independence. Only observations of groups and individuals of reindeer displaying feeding behavior as dominant behavior were used in order to reflect feeding habitat selection. Animals were observed and geographically positioned with the help of laser range-finding binoculars (Leica Vector 1000, Leica Geosystems AG, Heerbrugg, Switzerland). Field observations were carried out during three consecutive plant growing seasons: 1998, 1999, and 2000. Feeding reindeer were observed on 135 occasions (mean group size = 17, min = 1, max = 159, SD = 24).

Logistic regression (PROC LOGISTIC, SAS Institute Inc., Ver. 8.2) was used to study feeding habitat selection (Manly et al., 1993).

TABLE 1

Descriptive statistics (Zar, 1999) for topographical features (derived from a Digital Elevation Model, Lantmäteriet GSD, 1997) summarized over the summer (600 km²), and spring and autumn (1500 km²) ranges for the reindeer herd of Gabna Saami community (see Fig. 1).

| Abbr. | Variable | Summer | | Spring/Autumn | |
|--------|-----------------------------------|--------|-----|---------------|-----|
| | | Mean | SD | Mean | SD |
| ELEV | Elevation (m) | 930 | 247 | 719 | 301 |
| EA, NO | Exposure (degrees) | 84 | 135 | 16 | 99 |
| SLOPE | Slope (degrees) | 12.1 | 8.8 | 8 | 8.2 |
| H' | Index of land cover heterogeneity | 3.34 | — | 3.43 | — |

Selection was evaluated in a two-step hierarchical process. First, habitat selection was analyzed at a coarse scale (5-km grid size) using the whole study area as defining available habitat. Second, habitat selection at finer scales (0.5- and 1-km grid size) was evaluated assuming that reindeer had selected feeding area at a higher spatial scale, i.e., using the 5-km grid cells where reindeer were observed to limit the amount of hypothetically available habitats (number of grid cells). The response variable (presence/absence) is binomial, so a logit link function was used (Crawley, 1993). Akaike's Information Criterion (AIC) was used to select the best model (Burnham and Anderson, 1998).

HABITAT CHARACTERIZATION

The study area was divided into a grid with cell sizes 0.5, 1, and 5 km, respectively (Porter and Church, 1987). Topographical characteristics (Table 1) for each grid cell were derived from a digital elevation model (DEM) with 50-m resolution (Lantmäteriet GSD, 1997) using standard procedures (ESRI ArcView, Ver. 3.2). Mean, standard deviation (SD), and coefficient of variation (CV) of topographical variables were used in further statistical analysis. Surface area and heterogeneity of land cover types (Table 1) were derived from the digital "Swedish Vegetation Map" at 1:100,000 scale produced by

the Swedish National Land Survey from color infrared photography and field visits (Lantmäteriet GSD, 1997). The Shannon-Wiener diversity index (H') was used as a measure of land cover heterogeneity and was calculated using the logarithms to base 2 (Zar, 1999).

Principal Component Analysis (PROC FACTOR, SAS Institute Inc., Ver. 8.2) was used to derive major uncorrelated environmental factors influencing the spatial pattern of topographical and land cover characteristics (Manly et al., 1993). Topographical and land cover characteristics (in total 35 variables) were standardized to unit variance and a scree plot of eigenvalues (>1) of extracted principal components after varimax rotation was used to select the minimum number of components explaining the observed pattern (Tabachnik and Fidell, 2001).

Topographical characteristics, and total number and percentage of land cover types were similar between the summer and spring/autumn ranges, although the former had slightly higher coverage (in percentages) of alpine environments such as blocky areas and bedrock outcrops, grass heaths, meadows with low herbs, and snow beds (Fig. 2). Correspondingly, the spring/autumn range had relatively higher coverage of low altitude environments such as birch and coniferous forest types (Fig. 2).

At 5-km grid size, PCA identified four components explaining 43.2% (SSL = 15.13) of the total variance (Appendix 1). Six components were identified at 1-km grid size, and eight components at 0.5-km grid size, explaining 37.1% (SSL = 12.98) and 39.8% (SSL = 13.95) of the total variance, respectively. The components were interpreted as major environmental factors (alpine environment, habitat heterogeneity, light exposure, lowland plains, moisture, plant community structure, productivity, steepness, terrain ruggedness, and valley bottoms) determining the observed spatial pattern within the study area (Appendix 1). These factors were used in the above analyses on reindeer habitat selection.

Results

REINDEER HABITAT SELECTION

In our study, habitat heterogeneity and terrain ruggedness were the two most important factors explaining reindeer feeding habitat selection. The heterogeneity of land cover types were higher at all

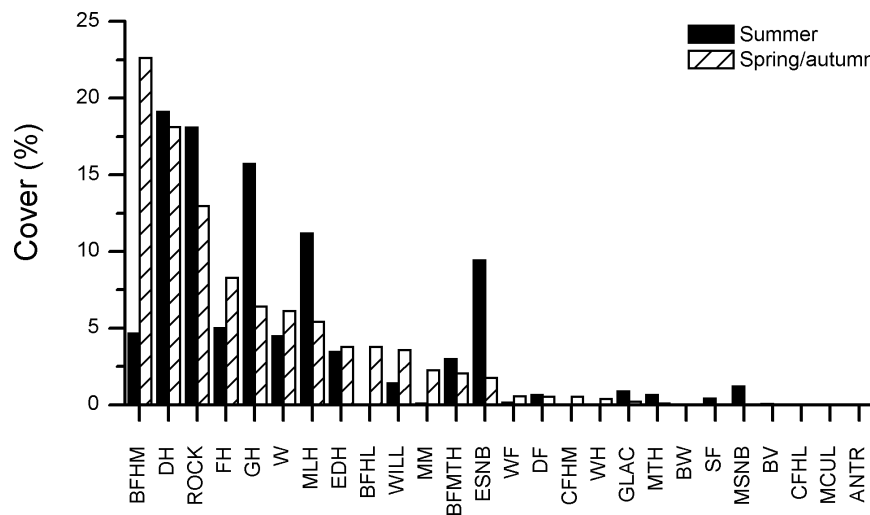


FIGURE 2. Percent cover of land cover types (Swedish Vegetation Map, Lantmäteriet GSD, 1997) summarized over the summer (600 km²), and spring and autumn (1500 km²) ranges for the reindeer herd of Gabna Saami community (see Fig. 1). BFHM = birch forest (heath type, mosses); DH = dry heath; ROCK = blocky areas and bedrock outcrops; FH = fresh heath; GH = grass heath; W = water; MLH = meadow with low herbs; EDH = extremely dry heath; BFHL = birch forest (heath type, lichens); WILL = willow; MM = mosaic mire; BFMTH = birch forest (meadow type, tall herbs); ESNB = extreme snowbed; WF = wet fen; DF = dry fen; CFHM = coniferous forest (heath type, mosses); WH = wet heath; GLAC = glacier; MTH = meadow with tall herb; BW = bog with mud-bottoms, water-filled pools; SF = sloping fen; MSNB = moderate snowbed; BV = bog and fen hummock vegetation; CFHL = coniferous forest (heath type, lichens); MCUL = cultivated meadow; ANTR = built-up area.

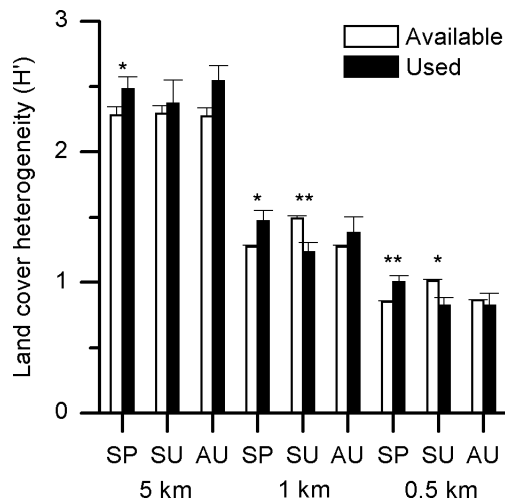


FIGURE 3. Heterogeneity of land cover types (Shannon-Wiener diversity index, H') within grids at different scales (grid size 0.5 km, 1 km, and 5 km, respectively) where reindeer were observed to feed (used) compared to non-used grids (available) during the plant growing season, which was divided into three seasons (spring, summer, and autumn).

scales in areas where reindeer were observed than elsewhere (Fig. 3). During summer, reindeer selected to feed in areas with lower heterogeneity of land cover types (Fig. 3). Selection of feeding habitats also differed among seasons (Fig. 4).

At a coarse scale (i.e., 5-km grid size), reindeer selected for feeding areas with high habitat heterogeneity and terrain ruggedness while avoiding lowland plain environments throughout the study period (Table 2).

At finer scales (i.e., 0.5- and 1-km grid size), combined analyses distinguishing between the different seasons by two dummy variables indicated that reindeer habitat selection was different between seasons (Table 2). Separate analyses confirmed contrasting patterns between seasons (Table 3). During spring, reindeer habitat selection was positively correlated to terrain ruggedness and habitat heterogeneity and negatively correlated to alpine environment. To the contrary,

reindeer summer feeding habitat selection was negatively correlated to terrain ruggedness and habitat heterogeneity and positively correlated to southward exposed habitats (and alpine environment for 1-km grid size). The selection of feeding habitats was less pronounced during autumn and differed markedly from that during spring and summer (Table 3). The patterns at the scale of 0.5- compared to 1-km grid size were the same for all three seasons.

Discussion

Reindeer selected to feed in areas at middle to high elevation with high spatial heterogeneity in agreement with findings from other similar tundra and alpine environments (White et al., 1981; Skogland, 1989; Nellemann and Cameron, 1996). Early in the season (spring), such feeding area selection based on elevation and environmental heterogeneity may result from predator avoiding behavior during the early post-calving period (Bergerud et al., 1984; Skogland, 1989), which also has been observed among other ungulates in alpine environments (Festa-Bianchet, 1988). It might equally be due to the fact that reindeer track the new emerging plant growth (Klein, 1970; Skogland, 1980, 1984), which is high in nutritive quality (Chapin et al., 1975; Chapin et al., 1980; Klein, 1990) and which has been found to be at higher abundance in rugged terrain (Nellemann and Thomsen, 1994). Such migratory movements along resource gradients have also been observed for ungulates in the tropics as well as the temperate zones (McNaughton, 1990; Albon and Langvatn, 1992). Later in the season (summer and early autumn), reindeer find themselves in a trade-off situation—on the one hand selecting refuge habitats (low in forage) due to insect harassment/high temperature (Ion and Kershaw, 1989; Walsh et al., 1992; Folstad et al., 1991; Andersen and Nilsen, 1998), but on the other hand selecting alpine snowbeds, meadows, and heath communities (Skogland, 1980, 1984; Edenius et al., 2003) for their higher forage quality and quantity while increasing exposure to parasites. Thus, by selecting feeding areas that are heterogeneous in the sense that they are rich in both refuge and feeding habitats, reindeer could reduce their energetic costs through decreased movements between these two opposing but preferred habitat categories (White et al., 1981). Such behavior has been observed for central-place foragers, being most apparent among birds that reduce the distance between their nest and feeding habitats (Orians and Wittenberger, 1991). However, it

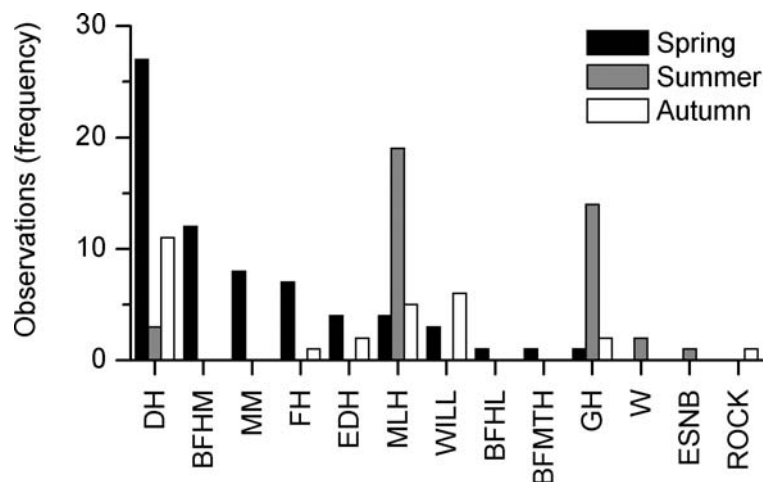


FIGURE 4. Number of reindeer observations (center position of groups of reindeer) in different land cover types during spring, summer, and autumn (see Fig. 2 for relative frequency of land cover types for the different seasonal ranges). DH = dry heath; BFHM = birch forest (heath type, mosses); MM = mosaic mire; FH = fresh heath; EDH = extremely dry heath; MLH = meadow with low herbs; WILL = willow; BFHL = birch forest (heath type, lichens); BFMTH = birch forest (meadow type, tall herbs); GH = grass heath; W = water; ESNB = extreme snowbed; ROCK = blocky areas and bedrock outcrops.

TABLE 2

Parameter estimates and statistics for the three best groups of logistic-regression models, as well as the full model, on reindeer habitat selection at grid sizes 0.5, 1, and 5 km and ranked according to Akaike's Information Criterion (AIC) from left to right; default: spring; model statistics in bold italics; * = $\alpha < 0.1$, ** = $\alpha < 0.05$, *** = $\alpha < 0.01$.

| Variables and statistics | 1. Model | 2. Model | 3. Model | Full model |
|---|-----------------|-----------------|-----------------|-----------------|
| Grid 5 km (Model without selection: Chi-square = 137.02, AIC = 139.02, df = 177) | | | | |
| Intercept | -2.10 (0.27)*** | -2.22 (0.30)*** | -2.69 (0.49)*** | -2.69 (0.50)*** |
| Habitat heterogeneity and | | | | |
| terrain ruggedness | 0.60 (0.35)* | 0.57 (0.35) | 0.57 (0.36) | 0.61 (0.38) |
| Lowland plains | -0.64 (0.32)** | -0.61 (0.33)* | -0.61 (0.33)* | -0.62 (0.34)* |
| Steepness | — | — | — | 0.11 (0.23) |
| Valley bottoms | — | — | — | 0.19 (0.21) |
| Summer | — | 0.52 (0.50) | 0.98 (0.63) | 0.91 (0.66) |
| Autumn | — | — | 0.81 (0.59) | 0.82 (0.59) |
| <i>No. parameters</i> | 2 | 3 | 4 | 6 |
| <i>Chi-square</i> | 125.73 | 124.71 | 122.71 | 121.78 |
| <i>AIC</i> | 131.73 | 132.71 | 132.71 | 135.78 |
| <i>df (model)</i> | 175 | 174 | 173 | 171 |
| Grid 1 km (Model without selection: Chi-square = 448.46, AIC = 450.46, df = 547) | | | | |
| Intercept | -1.50 (0.16)*** | -1.51 (0.16)*** | -1.53 (0.16)*** | -1.47 (0.22)*** |
| Steepness | — | — | — | -0.039 (0.14) |
| Terrain ruggedness | — | — | — | 0.0069 (0.16) |
| Alpine environment | -0.25 (0.14)* | -0.27 (0.14)* | -0.23 (0.15) | -0.21 (0.18) |
| Habitat heterogeneity | 0.19 (0.13) | — | 0.20 (0.13) | 0.18 (0.14) |
| Plant community structure | — | — | -0.13 (0.14) | -0.14 (0.14) |
| Light exposure | 0.39 (0.11)*** | 0.36 (0.11)*** | 0.38 (0.11)*** | 0.39 (0.11)*** |
| Summer | — | — | — | -0.14 (0.37) |
| Autumn | -1.03 (0.29)*** | -0.93 (0.28)*** | -1.08 (0.30)*** | -1.14 (0.34)*** |
| <i>No. parameters</i> | 4 | 3 | 5 | 8 |
| <i>Chi-square</i> | 417.06 | 419.20 | 416.17 | 415.91 |
| <i>AIC</i> | 427.06 | 427.20 | 428.17 | 433.91 |
| <i>df (model)</i> | 543 | 544 | 542 | 539 |
| Grid 0.5 km (Model without selection: Chi-square = 1066.78, AIC = 1068.80, df = 2146) | | | | |
| Intercept | -2.35 (0.12)*** | -2.36 (0.12)*** | -2.35 (0.12)*** | -2.30 (0.16)*** |
| Terrain ruggedness | — | -0.089 (0.12) | — | -0.096 (0.12) |
| Moisture | -0.76 (0.27)*** | -0.70 (0.27)** | -0.67 (0.25)*** | -0.69 (0.27)** |
| Steepness | -0.32 (0.09)*** | -0.33 (0.09)*** | -0.32 (0.09)*** | -0.33 (0.09)*** |
| Alpine environment | -0.27 (0.11)** | -0.26 (0.11)** | -0.25 (0.11)** | -0.23 (0.12)* |
| Light exposure | -0.37 (0.08)*** | -0.36 (0.08)*** | -0.36 (0.08)*** | -0.37 (0.08)*** |
| Habitat heterogeneity | 0.23 (0.09)*** | 0.22 (0.09)** | 0.21 (0.09)** | 0.21 (0.09)** |
| Plant community structure | 0.21 (0.09)** | 0.20 (0.09)** | — | 0.19 (0.09)** |
| Productivity | — | — | — | 0.04 (0.11) |
| Summer | — | — | — | -0.13 (0.25) |
| Autumn | -1.53 (0.22)*** | -1.53 (0.22)*** | -1.56 (0.22)*** | -1.58 (0.25)*** |
| <i>No. parameters</i> | 7 | 8 | 6 | 10 |
| <i>Chi-square</i> | 968.38 | 967.79 | 973.23 | 967.36 |
| <i>AIC</i> | 984.38 | 985.79 | 987.23 | 989.36 |
| <i>df (model)</i> | 2139 | 2138 | 2140 | 2136 |

has also been proposed in general terms by Senft et al. (1987) to apply to landscape-level decision making among large-sized herbivores, a phenomenon for which we here provide some empirical evidence.

Apparent seasonal differences in feeding habitat selection by reindeer were found at intermediate levels of selection (0.5- and 1-km grid size). These results conform with those from behavioral studies where reindeer have been shown to shift their diet (White et al., 1981; Heggerget et al., 2002) and movement patterns (Mårell et al., 2002; Ferguson and Elkie, 2004) in response to seasonal changes in resource distribution. Contrary to the spring situation (see our results and Nellemann and Cameron, 1996), reindeer selected against terrain ruggedness and habitat heterogeneity during summer at intermediate levels (0.5- and 1-km grid size). Rugged terrain determines food availability during early snowmelt as the new emerging plants first appear in patches where the snow cover during winter has been shallow or absent; i.e., habitats abundant in rugged terrain (Nellemann and

Thomsen, 1994). Later in the season, when the most productive alpine plant communities are free from snow, their value as forage (quality and quantity) is determined by other environmental factors such as light exposure and soil conditions (Jonasson et al., 2000). Accordingly, we found that light exposure correlated positively with selection of feeding habitats during summer. Likewise, Skogland (1984) found that reindeer in the southern parts of the Scandinavian mountains discriminated among habitats differing in light exposure.

In agreement with observations of reindeer in southern Norway (Skogland, 1984), our results suggest that reindeer perceived the spring and summer environment in a coarse-grained manner responding to spatially heterogeneous resource distribution. On the contrary, autumn habitat use was poorly explained, indicating a broader spectrum of habitat use, which Skogland (1984) also observed. We conclude that reindeer might have shifted from coarse-grained strategy in spring and summer to fine-grained strategy in the autumn in relation to changes of

TABLE 3

Separate analyses of reindeer habitat selection during spring, summer, and autumn showing parameter estimates and statistics for the best logistic-regression models (selected on the basis of Akaike's Information Criterion, AIC) at grid sizes 0.5 and 1 km; model statistics in bold italics with values for the no-selection model shown within brackets; * = $\alpha < 0.1$, ** = $\alpha < 0.05$, *** = $\alpha < 0.01$.

| Variables and statistics | Spring | Summer | Autumn |
|---------------------------|------------------------|------------------------|------------------------|
| Grid 1 km | | | |
| Intercept | -2.49 (0.43)*** | -2.72 (0.53)*** | -2.98 (0.41)*** |
| Steepness | — | — | — |
| Terrain ruggedness | 0.45 (0.23)* | -1.30 (0.48)*** | -0.56 (0.34) |
| Alpine environment | -1.70 (0.45)*** | 0.73 (0.33)** | — |
| Habitat heterogeneity | 0.45 (0.23)** | -1.09 (0.46)** | — |
| Plant community structure | — | — | -0.54 (0.37) |
| Light exposure | — | 0.40 (0.21)* | 0.34 (0.22) |
| No. parameters | 3 | 4 | 3 |
| Chi-square | 150.28 (176.95) | 95.64 (116.32) | 131.40 (139.39) |
| AIC | 158.28 (178.95) | 105.64 (118.32) | 139.40 (141.39) |
| df (model) | 169 (172) | 120 (124) | 246 (259) |
| Grid 0.5 km | | | |
| Intercept | -2.95 (0.30)*** | -3.21 (0.33)*** | -4.28 (0.36)*** |
| Terrain ruggedness | 0.32 (0.14)** | -1.07 (0.30)*** | -0.68 (0.29)** |
| Moisture | -1.74 (0.62)*** | 0.60 (0.39) | — |
| Steepness | -0.27 (0.18) | — | -0.42 (0.23)* |
| Alpine environment | -0.74 (0.28)*** | — | — |
| Light exposure | -0.30 (0.16)* | -0.46 (0.14)*** | -0.39 (0.16)** |
| Habitat heterogeneity | 0.64 (0.15)*** | -0.80 (0.26)*** | — |
| Plant community structure | 0.26 (0.12)** | 1.04 (0.43)** | -0.58 (0.30)* |
| Productivity | — | — | — |
| No. parameters | 7 | 5 | 4 |
| Chi-square | 403.34 (447.68) | 244.88 (297.89) | 258.13 (276.40) |
| AIC | 419.34 (449.68) | 256.88 (299.89) | 268.13 (278.40) |
| df (model) | 639 (646) | 494 (499) | 995 (999) |

the biophysical environment. A coarse-grained strategy is preferable when differences in habitat quality are predictable in time, while a fine-grained strategy is advantageous when differences are highly unpredictable, as shown theoretically by Bryant (1973). Snow controls the progression of plant growth in alpine environments in a highly predictable way early in the season (van Wijk et al., 2003), thus favoring a coarse-grained strategy. Later in the season, reindeer forage in the Arctic and Subarctic might either be more homogeneously distributed (Klein, 1990), or unpredictable or widely dispersed (such is the case for mushrooms, preferred diet during early autumn by reindeer; Gaare and Skogland, 1975), thus supporting a fine-grained strategy. We do not, however, exclude any possible coarse-grained selection at lower or higher spatial scales by reindeer during autumn. We are also aware that our analyses did not take into consideration all possible environmental factors that could be important to reindeer habitat selection, and thus do not exclude the possibility that reindeer could show coarse-grained selection during autumn at the studied intermediate levels of selection in response to other environmental factors (predation risk, insect harassment, etc.).

Conclusions

Our study supports the general foraging theory that reindeer adopt a hierarchical feeding strategy. In this way, our results imply that reindeer distinguish between general habitat needs at a high level of selection (i.e., a large area or landscape that serves multiple purposes), and more specific habitat needs at lower levels of selection (i.e., habitat

or patch that serves a specific or limited function). The discrepancy in behavior between seasons further indicates that large-sized herbivores such as reindeer are capable of shifting between coarse- and fine-grained perceptions of the environment in response to the spatial scales corresponding to the resources selected for. The results show that spatial heterogeneity is important to reindeer habitat selection at high levels of selection (5-km grid size), and at least during spring and summer (though with opposing effect) at intermediate levels of selection (0.5- and 1-km grid size). Spatial heterogeneity should therefore be taken into consideration and incorporated in models of reindeer habitat use. These results also have potential management implications in terms of modeling reindeer habitat use by using easily available georeferenced information that could be incorporated in participatory management schemes such as that proposed by Sandström et al. (2003). Finally, our results show the importance of large diverse landscapes for animals such as reindeer, and hence, access to a wide range of habitats providing foraging conditions throughout the season. This ought to be considered in future management guidelines for alpine landscapes in the Arctic and Subarctic.

Acknowledgments

Climate Impacts Research Centre (CIRC) within the Environment and Space Research Institute, Kiruna, provided funding for this work through a grant to Annika Hofgaard. We gratefully acknowledge Lilian Ericsson, Majlis Kardefelt, Helena Karlsson, Eva Romell, Anna Sjöstedt, and Thomas Westin for their assistance in the field. We also thank Terry Callaghan, Christer Jonasson, and the staff of Abisko Scientific Research Station for their generous support. Christian Nellemann and David Armstrong provided useful comments on the manuscript.

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Ms accepted October 2005

APPENDIX 1

Environmental factors (determined by PCA) characterizing the study area at grid sizes 0.5, 1, and 5 km; explained variance for each factor is shown within brackets; associated variables (see Table 1 and Fig. 2) with loadings >0.45 are shown where loadings are indicated within brackets (Tabachnik and Fidell, 2001). See text for explanation of abbreviations.

| Grid 0.5 km | Grid 1 km | Grid 5 km |
|--|---|--|
| F1. Terrain ruggedness (6.5%) SD: EA (0.74), NO (0.72) % cover: MM (0.49) CV: ELEV (–0.45) | F1. Steepness (9.8%) % cover: BLOCK (0.64), W (–0.51) mean: SLOPE (0.90), ELEV (0.55) CV: SLOPE (0.85), ELEV (0.77) | F1. Habitat heterogeneity and terrain ruggedness (15.8%) % cover: W (–0.92), MLH (0.50) H' (0.82) CV: SLOPE (–0.80) |
| F2. Moisture (5.7%) % cover: W (0.92) CV: SLOPE (0.88) | F2. Terrain ruggedness (6.3%) SD: EA (0.77), NO (0.74) % cover: MM (0.47) | SD: NO (0.72), EA (0.71) mean: ELEV (0.61), SLOPE (0.52) |
| F3. Steepness (5.6%) % cover: BLOCK (0.74) mean: SLOPE (0.68) CV: ELEV (0.58) | F3. Alpine environment (6.0%) % cover: ESNB (0.68), GH (0.58), BFHM (–0.50) mean: ELEV (0.64) | F2. Lowland plains (10.9%) % cover: MM (0.79), BFHM (0.66), BFHL (0.55), WF (0.49) MLH (–0.48) mean: ELEV (–0.48) |
| F4. Alpine environment (5.5%) % cover: ESNB (0.70) mean: ELEV (0.62) | F4. Habitat heterogeneity (5.2%) H' (0.64) % cover: WILL (0.50), FH (0.46), DH (0.46) | F3. Steepness (9.4%) % cover: BLOCK (0.75), ESNB (0.65), GLAC (0.59) FH (–0.59) mean: SLOPE (0.54), ELEV (0.51) |
| F5. Light exposure (4.6%) % cover: MLH (–0.69) mean: NO (0.69) | F5. Plant community structure (4.9%) % cover: BFTH (0.53), DH (–0.46), BFHM (0.45) | F4. Valley bottoms (7.1%) % cover: BV (0.71), ANTR (0.68) BFMTH (0.65) CV: ELEV (0.56) |
| F6. Habitat heterogeneity (4.2%) H' (0.58) % cover: FH (0.57), WILL (0.50) | F6. Light exposure (4.8%) % cover: MLH (0.65), mean: NO (–0.65) | |
| F7. Plant community structure (4.0%) % cover: BFHM (0.68), DH (–0.56) | | |
| F8. Productivity (3.9%) % cover: BFMTH (0.64) | | |