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Original article

The spatial structure of habitat selection: A caribou's-eye-view

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ARTICLE INFO

Article history:

Received 16 August 2008

Accepted 12 November 2008

Published online ■

Keywords:

Continuum

Hierarchy

Organism-centred

Rangifer tarandus

Resource selection

Spatial scale

ABSTRACT

Greater understanding of habitat selection requires investigation at the scales at which organisms perceive and respond to their environment. Such knowledge could reveal the relative importance of factors limiting populations and the extent of response to habitat changes, and so guide conservation initiatives. We conducted a novel, spatially explicit analysis of winter habitat selection by caribou (*Rangifer tarandus*) in Newfoundland, Canada, to elucidate the spatial scales of habitat selection. We combined conventional hierarchical habitat analysis with a newly developed geospatial approach that quantifies selection across scales as the difference in variance between available and used sites. We used both ordination and univariate analyses of lichen and plant cover, snow hardness and depth. This represents the first use of ordination with geostatistics for the assessment of habitat selection. Caribou habitat selection was driven by shallow, soft snow and high cover of *Cladina* lichens and was strongest at feeding microsites (craters) and broader feeding areas. Habitat selection was most evident at distance lags of up to 15 km, perhaps an indication of the perceptual abilities of caribou.

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1. Introduction

Increasingly, ecologists acknowledge one feature as critical to understanding habitat selection: scale. The costs and benefits among habitats may depend on scale (Morris, 1987) because the pertinence of limiting factors (Rettie and Messier, 2000) and the densities of resources and conspecifics (Mayor and Schaefer, 2005) also may depend on scale. Proximately, selection is a behavioural response to environmental cues (Hildén, 1965; Hutto, 1985) which also hinges on the scales at

which individuals can perceive and respond to the environment.

Associations with habitat depend on scale (Schneider et al., 1987) and consequently studies of habitat selection conducted at only one scale risk missing associations with habitat occurring at other scales. To decrease this risk, habitat selection is now commonly assessed at multiple levels simultaneously. For example, resource selection functions are used frequently to characterise distribution and abundance of resources at several spatial scales (Boyce and McDonald, 1999;

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doi:10.1016/j.actao.2008.11.004

Boyce, 2006). Investigators typically view selection as a hierarchical process (Johnson, 1980; Senft et al., 1987), based on the idea that selection at broad levels constrains selection at finer levels (O'Neill et al., 1989).

Such levels, however, are sometimes chosen arbitrarily by the researcher and so may fail to represent selection from the perspective of the organisms (Wiens, 1976; Schaefer and Messier, 1995; Thompson and McGarigal, 2002). Human-centred approaches, while informative, are less readily extrapolated to other study areas and species (Jenkins et al., 2007); synthesis is impeded. To provide a more generalizable approach, we allow the response of animals along a spatial continuum to define these scales. By explicitly identifying the range of spatial scales at which animals respond to habitat, we present an animal's-eye-view of habitat selection.

Geostatistics represent a powerful tool to understand scale-dependent phenomena. Variograms, for instance, display semivariance as a function of the distance between sampling points (Meisel and Turner, 1998; Dale et al., 2002). Recently, we showed that the spatial scales of habitat selection can be revealed using variograms by identifying the point of maximum difference in variance of some resource between available and used sites (Mayor et al., 2007; Schaefer and Mayor, 2007). This technique is especially useful for studying habitat selection of wide-ranging species where the long-standing conundrum of what constitutes "availability" (Bowyer and Kie, 2006) has been especially pronounced. Caribou (*Rangifer tarandus*), for instance, exhibit reductions in occupancy following habitat alterations often discernable for kilometres (Mahoney and Schaefer, 2002; Vors et al., 2007), presenting a challenge to conventional notions of edge effects (Laurance, 2000) as local phenomena. Recognising the scales of response to habitat is pivotal to understanding and conserving highly mobile vertebrates.

In a previous study, we used univariate techniques to investigate winter habitat selection by caribou (*R. t. caribou*) of the Middle Ridge herd in Newfoundland, Canada. We showed that spatial statistics, in combination with a conventional hierarchical approach, were capable of uncovering the major patterns and spatial extent of selection for snow depth and lichen abundance. In the present study we extend this analysis to a broader array of habitat attributes associated with caribou foraging during winter. Because habitat can be regarded as a suite of inter-related resources and conditions (Caughley and Gunn, 1995), it is inherently multi-dimensional (James and McCulloch, 1990). Multivariate techniques like ordination, capable of summarizing complex habitat data with fewer variables, might be particularly suited to identifying scales of selection. Indeed, spatial patterns of multiple environmental variables can be uncovered by combining ordination with spatial statistics (Galiano, 1983).

First, we performed an ordination of habitat variables at four hierarchical levels, from feeding craters (microsites to access subnivean food) to the population's winter range (Fig. 1). We inferred selection where use exceeded availability at a coarser level in this hierarchy. To aid interpretation, we conducted univariate analyses following the same hierarchical approach. We expected that at fine scales caribou would select for greater relative abundance of forage (Pruitt, 1959; Bergerud, 1974; Schaefer and Pruitt, 1991). Second, we

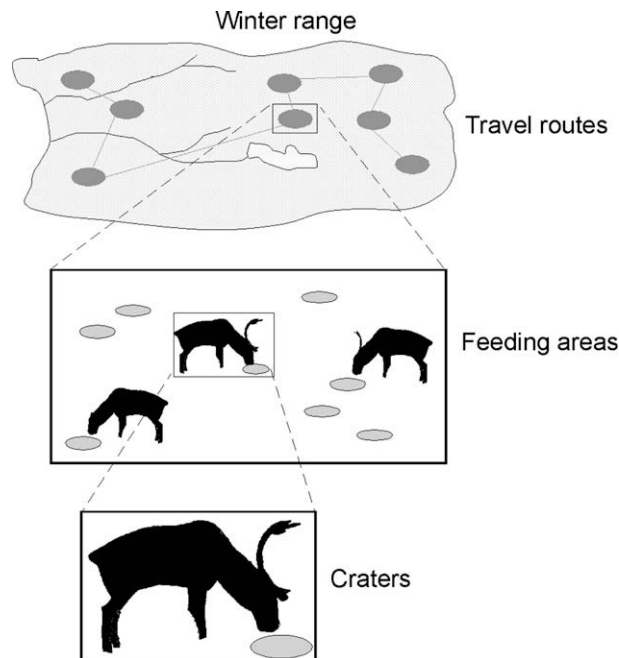


Fig. 1 – Schematic representation of the hierarchical levels of winter habitat selection by caribou.

quantified the spatial scale of selection using variograms applied to each hierarchical level. Following Mayor et al. (2007), we predicted that selection would be manifest as a reduction in semivariance from broader to finer levels in one or more resources.

2. Methods

2.1. Data collection

We sampled the winter habitat of the Middle Ridge caribou herd (47° 55'N, 54° 40'W) in the maritime barrens of east-central Newfoundland, Canada, as defined by the herd's winter distribution (Mahoney, 2000). The study area covered ca. 600 km² and was characterized by low snow cover (average depth during study = 26.6 cm), poor soils, and frequent ponds, bogs, low hills, and occasional rocky ridges.

During winter, caribou dig craters (areas of continuously disturbed snow cover) to access subnivean food. These were generally aggregated into feeding areas that were in turn connected by paths, together forming travel routes dispersed throughout the herd's winter range. Following Schaefer and Messier (1995), we assessed the structural habitat elements at these four hierarchical levels (Fig. 1): the population winter range (approximate extent of distribution), travel routes (courses used by multiple caribou), feeding areas (aggregations of feeding craters), and craters (feeding microsites).

We conducted field research within the winter range from 3 February to 18 March 2005, located caribou or their sign by searching on foot or by snowmobile. To reduce the likelihood of repeated observations of the same animals, our search pattern covered different areas daily and reasonably evenly.

For each hierarchical level, we measured nival conditions including snow depth and snow hardness using a ram penetrometer, and marked the sites. We revisited the sites following snowmelt (25 May–22 June) to assess the vegetation and soil characteristics. We recorded percent cover (in classes of 0, 0–1, 1–5, 5–10, 10–25, 25–50, and 50–100%, and used the midpoint of each class in statistical analyses) of herbs, lichens, mosses, shrubs, and graminoids within a 0.5×0.5 m quadrat, except at the crater level, for which we used the area of the crater (mean = 0.41 m^2 , SD = 0.48 m^2 , $n = 548$).

We sampled the winter range systematically by establishing six transects, each 870 m in length, oriented to the north, each separated by at least 5 km. A variable sampling step (with adjacent steps separated by a repeated sequence of 10, 20, 40, 130 m) was employed (Fortin et al., 1989) and, at each step, stakes were planted and measurements recorded at four sites (step centre, plus 5 m west, south, and east of centre) for a total of 80 measurement sites along each transect. For each site, nival conditions were measured 2–3 times throughout the winter and averaged. For non-nival variables, we established four additional east-oriented transects (with sites at step centre, plus 5 m north, west, and south) using the same design. Distances between sample sites within this and other nested levels ranged from 5 m to nearly 30 km.

We defined travel routes as courses of disturbed snow used by multiple caribou. Individual animal trails led to or from feeding areas and tended to converge. Measurements at travel route sites were taken at the nearest major point of convergence from a feeding area.

We defined a feeding area as an aggregation of craters separated by at least 50 m from the neighbouring aggregation. Generally, craters were clearly clustered into feeding areas. In each feeding area, we established a transect connecting the two most distant craters, which typically bisected the primary feeding part of the area. We sampled undisturbed sites along the transect with a variable sampling step (with adjacent steps separated a repeated sequence of 50, 20, 5 m). The mean area of feeding areas was approximated from half the squared length of each transect.

We defined craters as continuous areas of disturbed snow within which caribou had fed, usually with scattered lichen or plant debris. We sampled snow where it was undisturbed, at the crater margin. Along the transect of greatest diameter of each feeding area, we sampled the nearest clearly defined craters separated by a systematically variable sampling step (with adjacent steps separated by a repeated sequence of 30, 15, 5 m) beginning and ending with the first and last crater of the feeding area, respectively. We marked the perimeter of each crater with 3–10 nails for subsequent observations.

2.2. Data analysis

To compare the major habitat characteristics at each hierarchical level, we performed Principal Components Analysis (PCA), which reduces the multivariate data to a smaller number of components that account for a large percentage of the variation. Our PCA employed a correlation matrix using SPSS (ver 14.0; SPSS Inc., 2005), which tends to be sensitive to variables that occur infrequently, so we excluded variables not present in at least 10% of sample locations. We employed

a scree test (Cattell, 1966) to select the number of Principal Components (PCs) for analysis. We plotted PC scores (from sample sites) and eigenvectors (from habitat variables) on the first two axes. Standard deviations of PC scores for sites on each axis were calculated at each hierarchical level.

We performed a hierarchical analysis of variance (ANOVA) to compare the mean values of habitat elements (i.e. environmental variables) among the four hierarchical levels (winter range to craters; Fig. 1). We treated each level independently (PROC GLM, SAS ver 9.1; SAS Institute, 2003) and assessed the significance among the means of each level with a Bonferroni–Sidak-corrected α of 0.0085 to achieve a family-wise error rate of 5%.

Following Mayor et al. (2007), we determined the scales of habitat selection using geostatistics. When habitat selection occurs, variability in available sites should exceed that in used habitat, because organisms should select habitat similarly among sites (Schaefer and Mayor, 2007). We constructed variograms (Matheron, 1960) to assess the variability (spatial dependence) of each habitat element and Principal Component scores in relation to separation distance at each hierarchical level. We measured habitat selection as the difference in semivariance among hierarchical levels. For example, a difference in semivariance among (used) craters relative to (available) feeding areas showed selection at the level of the crater; changes in this difference across lags showed differences in selection across spatial scales. We measured the range in scales of habitat selection as the spatial scope of lags in which used differed from availability. The empirical semivariance (γ) represents half the sum of the squared difference between pairs and was calculated using Surfer 8.0 (Golden Software, 2002) as $\hat{\gamma}(h) = 1/2n(h) \sum_{i=1}^n [z(x_i) - z(x_i + h)]^2$ where z is the value of the variable x at the sampling location x_i , and $n(h)$ is the number of pairs of sampling locations located at distance h from one another. We excluded lags with less than 30 pairs and grouped similar lags for graphical representation.

3. Results

3.1. Habitat selection

Caribou selected habitat at each hierarchical level. At increasingly finer levels in the hierarchy, from winter range to craters, sites were more similar and appeared as nested subsets of broader levels (Fig. 2). On a gradient from dry *Cladina*-rich barrens to moist areas and bogs (Fig. 3, PC 1), sites selected by caribou were drier and richer in *Cladina* at each progressively finer level (Fig. 2). Similarly, along a gradient from deep snow and ericaceous shrubs to exposed *Empetrum* (Fig. 3, PC 2) caribou generally selected shallower snow and less shrub cover at each level (Fig. 2). PC 1 scores were significantly higher (Table 1) and showed lower variance (Table 2) at the craters and feeding areas than at the broader levels of travel routes and the winter range. PC 2 scores, too, were generally less variable among sites sampled at finer levels (Table 2), but comparison of mean values did not reveal evidence of hierarchical selection.

Evidence of habitat selection varied on the hierarchical level. At finer levels an increasing number of habitat variables were significantly different in means relative to the winter

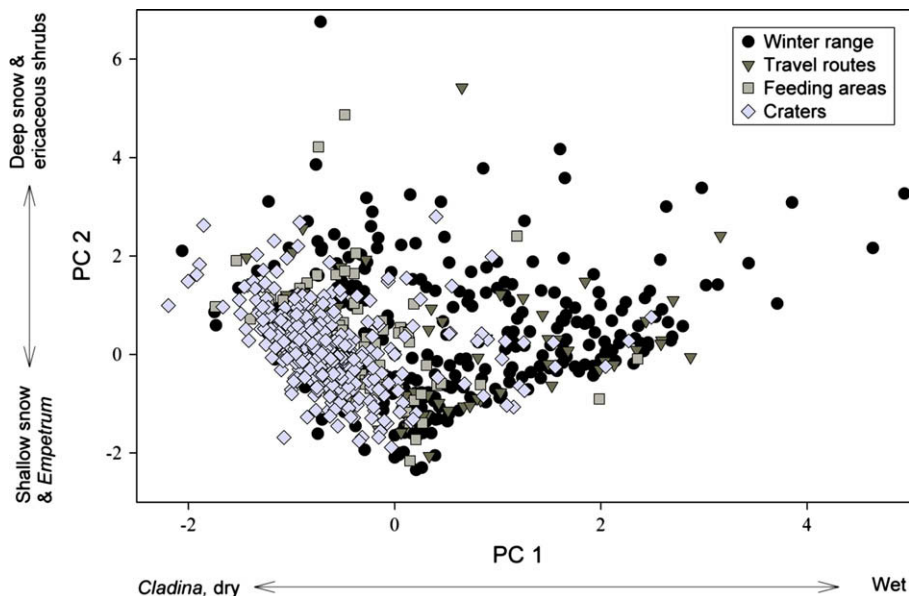


Fig. 2 – Distribution of sampled locations by Principal Component scores at four hierarchical levels of behaviour. The environmental gradients were interpreted from Fig. 3.

range (Table 1). Cover of *Cladina* spp., an important contributor to PC 1, was significantly greater (Table 1) at craters and feeding areas than at travel routes and the winter range. Snow conditions contributed to PC 2 and were significantly softer and shallower in craters than in feeding areas, and in feeding areas than on travel routes or the winter range (Table 1).

3.2. Spatial patterns of habitat selection

Variograms revealed the spatial dependence of PC scores (Fig. 4). Craters and feeding areas were less variable in PC 1 than the winter range at most distances, and at lags greater than 15 km craters were less variable in PC 1 than were feeding areas (Fig. 4a), demonstrating selection at these scales. At feeding areas and travel routes, variability of PC 2 also depended on lag distance (Fig. 4b).

These patterns were generally reiterated with univariate analyses. For snow hardness, semivariance was consistently

lower at craters than throughout the winter range, but at feeding areas was lower than the winter range only at lags above 14 km (Fig. 4c); variability in snow hardness along travel routes was greater than at the winter range level. For *Kalmia*, there was greater cover in all levels relative to the winter range (Table 1), but the higher variability of *Kalmia* at all hierarchical levels relative to the winter range was unanticipated (Fig. 4d). This discrepancy increased at pairwise distances above 18 km for each of the three sampling levels. Finally, graminoids were correlated with hard snow conditions (Fig. 3) and were neither selected at feeding areas nor craters, regardless of spatial scale (Table 1). The variability in graminoids was lower in selected sites than those available across all lags (Fig. 4e). The difference in semivariance between used and available sites increased fourfold from shortest to longest lags (Fig. 4e). The variability in graminoid cover was lower in feeding areas at lag distances below 14 km and between that of crater and winter range levels at longer

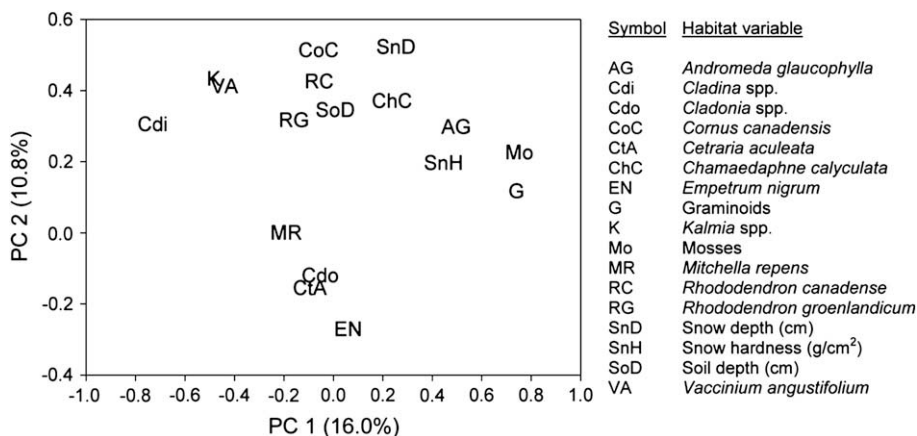


Fig. 3 – Eigenvectors from the first two axes of Principal Components analysis of habitat variables.

Table 1 – Mean habitat conditions across hierarchical levels of selection for caribou in Newfoundland.

	Mean				p-Value					
	Crater	Feeding area	Travel routes	Winter range	Cr – FA	Cr – TR	Cr – WR	FA – TR	FA – WR	TR – WR
Principal Component 1	-0.50	-0.28	0.83	0.76	0.013	<0.001	<0.001	<0.001	<0.001	0.520
Principal Component 2	-0.12	0.66	0.34	-0.08	<0.001	<0.001	0.581	0.047	<0.001	0.003
Soil depth (cm)	42.8	31.7	32.0	33.0	<0.001	<0.001	<0.001	0.920	0.555	0.739
Snow depth (cm)	14.3	20.7	32.3	26.6	<0.001	<0.001	<0.001	<0.001	0.002	0.012
Snow hardness (g/cm ²)	7.5	19.6	37.2	26.6	<0.001	<0.001	<0.001	<0.001	0.004	<0.001
<i>Andromeda glaucophylla</i>	0.2	0.4	1.3	1.4	0.479	0.004	<0.001	0.055	0.001	0.743
<i>Cetraria aculeata</i>	1.3	1.1	0.9	0.7	0.653	0.486	0.005	0.779	0.287	0.612
<i>Chamaedaphne calyculata</i>	1.7	2.5	4.0	1.9	0.164	0.002	0.590	0.091	0.263	0.003
<i>Cladina</i> spp.	63.7	58.1	22.4	25.6	0.072	<0.001	<0.001	<0.001	<0.001	0.405
<i>Cladonia</i> spp.	2.2	1.1	1.4	1.7	0.097	0.339	0.168	0.757	0.346	0.708
<i>Cornus canadensis</i>	1.0	1.5	2.2	2.7	0.428	0.124	<0.001	0.451	0.040	0.473
<i>Empetrum nigrum</i>	2.3	3.5	6.3	3.8	0.369	0.020	0.035	0.182	0.824	0.150
Graminoids	2.5	1.9	19.8	13.0	0.807	<0.001	<0.001	<0.001	<0.001	0.009
<i>Kalmia</i> spp.	19.1	23.4	11.0	8.4	0.051	0.003	<0.001	<0.001	<0.001	0.340
<i>Mitchella repens</i>	1.1	0.3	0.2	0.7	0.032	0.039	0.025	0.774	0.333	0.263
Mosses	4.0	5.0	28.0	19.2	0.705	<0.001	<0.001	<0.001	<0.001	0.006
<i>Rhododendron canadense</i>	1.0	2.1	0.8	1.4	0.084	0.825	0.228	0.182	0.269	0.460
<i>Rhododendron groenlandicum</i>	3.8	5.2	2.2	2.8	0.113	0.150	0.041	0.024	0.007	0.562
<i>Vaccinium angustifolium</i>	10.8	10.8	5.0	6.1	0.911	<0.001	<0.001	<0.001	0.003	0.172

Significant differences between hierarchical levels (Cr = Crater, FA = Feeding Area, TR = Travel Route, WR = Winter Range) are indicated in bolditalics ($p < 0.0085$). Units are in percent cover unless otherwise stated. (PCs are unitless.)

lags. Each of these differences in semivariance between used and available sites represents habitat selection at these scales.

4. Discussion

Caribou habitat selection was driven by *Cladina* lichens not covered by deep or hard snow, a finding that supports studies (Pruitt, 1959; Adamczewski et al., 1988; Schaefer and Pruitt, 1991) showing that lichens and snow conditions can be limiting factors for caribou. As anticipated, caribou selected habitat such that the Principal Components summarizing most habitat variability were less variable in selected sites (Fig. 4). More importantly, we found intriguing congruity in the scales at which caribou responded to habitat and landscape disturbances in this and other investigations. Here, caribou of the Middle Ridge herd selected habitat at feeding areas such that the variability in Principal Components was lower at lags less than 15 km (PC 1) and 18 km (PC 2) than in the winter range. They selected *Cladina* at lag distances up to 13 km (as evidenced by a reduction in semivariance among selected sites), responded to snow depth at craters more than at the broader feeding area level at lag distances up to 12 km (Mayor et al., 2007), and responded to graminoids at feeding areas more strongly than at craters at lag distances below 14 km.

Table 2 – Standard deviations of principal component scores at four hierarchical levels of behaviour by Newfoundland caribou.

	Craters	Feeding areas	Travel routes	Winter range
PC 1	0.53	0.61	1.11	1.08
PC 2	0.68	1.06	1.27	1.27

These distances are comparable to the extent of reaction by *Rangifer* to habitat alterations. During summer, females of this herd responded to areas disturbed by clearcut logging at distances of about 9 km (Schaefer and Mahoney, 2007); the critical distance for extirpation of woodland caribou in Ontario was 13 km to the nearest cutover (Vors et al., 2007); and maternal wild reindeer (*Rangifer tarandus tarandus*) in Norway avoided a 10 km zone around a tourist resort (Nellemann et al., 2000). We suggest that the correspondence among response distances reflects a perceptual range of *Rangifer* and recommend that conservation initiatives consider such distances beyond anthropogenic habitat disturbances as the potential extent of effective habitat loss.

Such responses, on the order of multiple kilometres, exceed usual expectations of edge effects. Broad-scale impacts may be more common than once thought (Laurance, 2000). We posit that the “human perceptual realm” – the scale at which humans typically engage with their surroundings (Gobster et al., 2007) – fails to encompass such wide extents, especially for highly vagile species like caribou. An organism-centred approach is one means to ensure that the relevant scales of habitat selection are considered. Curiously, red deer (*Cervus elaphus*) in Pyrenees Mountains appear to select habitat at a much smaller scale of about 1 km (Schaefer et al., 2008). The ecological basis for interspecific differences in scales of habitat selection remains unclear.

Habitat selection at the feeding area level accounted for much of the response to the spatial structure of the environment. Caribou acquired their most important winter food resource, *Cladina*, by selecting feeding areas richer and less variable in these lichens. Despite the importance of selection at the feeding area level, the actual dimensions of feeding areas did not correspond to the spatial scales of selection by this herd. Although feeding areas had an average maximum

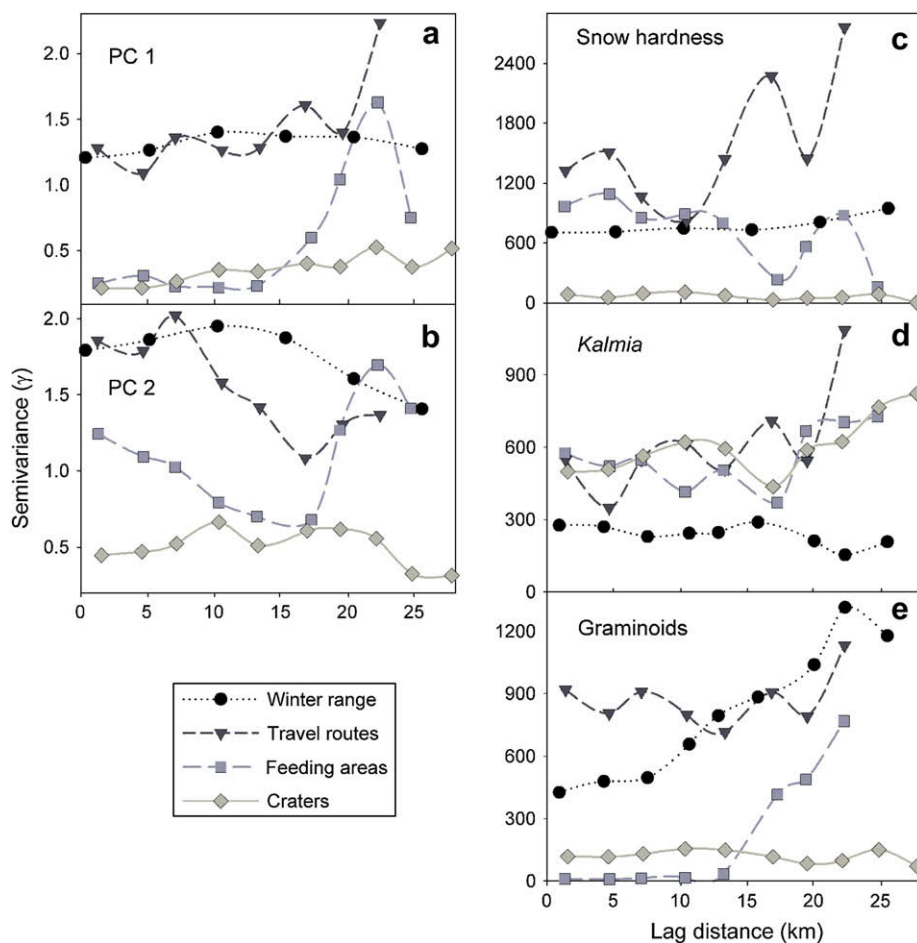


Fig. 4 – Semivariance in (a) Principal Component (PC) 1 and (b) PC 2 (c) snow hardness (g/cm^2), (d) percent cover of *Kalmia* spp., (e) percent cover of graminoids in relation to separation distance between sample pairs. Each panel shows four variograms, each representing a hierarchical level at which habitat use was sampled. Habitat selection is represented by the discrepancy in semivariance at one level relative to the winter range level. The Principal Components summarize variance in habitat elements, as shown in Fig. 3.

diameter of only 134 m, caribou responded to the variability in *Cladina* cover at lags up to 13 km (Mayor et al., 2007). This observation underlines the importance of distinguishing hierarchical levels (like feeding areas and home ranges) – which help explain how selection is accomplished – from explicitly spatial scales, which define the structure of selection as a function of distance or area.

The scale dependence of habitat selection stems in part from the scale dependence of density. When resources are concentrated in patches, their density appears higher when sampled at finer scales and lower when sampled at broader scales (Mayor and Schaefer, 2005). As a result, seemingly arbitrary decisions regarding the scales of measurement of habitat availability and use can therefore have significant impacts on detection and magnitude of habitat selection. Here, we have attempted to minimize this bias by using an organism-centred approach to explore selection on a continuum of spatial scales.

The evaluation of habitat selection as a reduction in variance across scales represents a new approach to understanding how this process occurs on landscapes and we have provided both

theoretical (Schaefer and Mayor, 2007) and empirical (Mayor et al., 2007) support for its use. Here, we extended the approach to multivariate analysis by showing that variance in Principal Components is reduced at finer hierarchical levels. Variograms of Principal Components revealed the scales of selection even when the levels of selection were not clear from conventional hierarchical analysis alone. Univariate variograms were valuable complements to explain these patterns. At small lags (<15 km), the correlated variables represented by PC 1 were selected at feeding areas, but for PC 2 additional crater-level selection occurred.

The results for *Kalmia* were surprising. At finer levels, *Kalmia* cover was greater but also more variable – a pattern contrary to expectation. Bergerud (1974) suggested that *Kalmia* and other shrubs help caribou detect lichen by creating air passages through deep snow. In our study, higher variability in *Kalmia* abundance suggests that it may not be preferred at the finest scales in low snow conditions, probably because its woody stems can physically hinder accessibility and facilitate local snow accumulation. The species is rarely consumed (Bergerud, 1974), although it may be selected at coarser levels.

In such cases, where the variance of a resource is higher owing to greater mean abundance, it might be preferable to apply a Geary's *C*, which represents a standardized semi-variance (Boyce et al., 2003) to uncover spatial patterns. Scale dependence was also apparent for graminoids. While graminoids did form part of the herd's diet, they were associated with low-lying, moist areas with deeper snow and thus were not selected due to low accessibility.

Understanding the scales at which organisms select resources is not merely a question of distance or area; it may also denote the importance of population limiting factors. As proposed by Rettie and Messier (2000), animals are anticipated to select habitat to overcome factors limiting their fitness and should seek to do so in the order of importance of those limiting factors. The scale of selection to escape a limiting factor should indicate the relative importance of that factor.

Dussault et al. (2005) elaborated on this idea; they proposed that animals should make tradeoffs among multiple factors when their effects occur at the same scales. We observed that caribou made a tradeoff between forage abundance and accessibility, consistent with Johnson et al. (2001), balancing the need for food and the energy expenditure required to get it. Selection for shallow, soft snow occurred at all scales, a finding that – particularly in a year of relatively shallow snow (a mean of 26.6 cm across the winter range) – emphasizes the importance of nival conditions. Selection of *Cladina* intensified at finer scales, suggesting that those scales are more important in meeting food requirements than larger scales. Scale-dependent tradeoffs have also been documented in other ungulates (Mysterud et al., 1999; Dussault et al., 2005).

We suggest that animals should attempt to reduce the impact of limiting factors at the scales at which their effects are most easily overcome. When coarse-scale selection constrains selection at finer scales, animals should also attempt to overcome more important limiting factors at the coarser scales, as Rettie and Messier (2000) suggested. However, when coarse-scale constraint is weak (such as restriction of local *Cladina* selection to broad low snow areas), other considerations may determine the optimal scales of selection. For example, animals may instead respond to characteristic scales of patchiness of risks or resources (Turner et al., 1997). This underlines the importance of the heterogeneous distribution of risks and resources to habitat selection and highlights the value of measuring habitat selection as a change in variance.

Multi-scaled habitat selection studies are uniquely positioned to facilitate comprehensive management and conservation recommendations. Hall and Mannan (1999) prescribed a conservation plan that spanned individual trees used as nests by the neotropical migrant bird *Trogon elegans* along with a whole watershed scale in order to maintain the necessary diversity of habitats. Nams et al. (2005) used multi-scale habitat selection analysis to recommend optimum scales for grizzly bear (*Ursus arctos*) conservation planning by linking dominant scales of habitat selection to scales of resource and bear patchiness. Whittingham et al. (2005) showed that selection by Yellowhammers (*Emberiza citrinella*) depended on scale and recommended farm management practices accordingly, such as digging ditches and conserving hedgerows. Johnson et al. (2004) used multi-scale models of habitat

selection to map predicted distribution of mountain caribou and so guide forest harvesting and management of human access. Habitat selection studies spanning multiple scales often require little additional effort beyond those conducted at single spatial scales, but can provide more complete pictures of animal choice, and so guide conservation efforts.

Acknowledgements

We thank R. Curran, S. Hann, E. Loder, F. Norman, and J. Zigouris for field assistance. Thanks to the Natural Sciences and Engineering Research Council of Canada and the Government of Newfoundland and Labrador for financial support.

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