

SPECTRUM OF SELECTION: NEW APPROACHES TO DETECTING THE SCALE-DEPENDENT RESPONSE TO HABITAT

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Abstract. Detecting habitat selection depends on the spatial scale of analysis, but multi-scale studies have been limited by the use of a few, spatially variable, hierarchical levels. We developed spatially explicit approaches to quantify selection along a continuum of scales using spatial (coarse-graining) and geostatistical (variogram) pattern analyses at multiple levels of habitat use (seasonal range, travel routes, feeding areas, and microsites). We illustrate these continuum-based approaches by applying them to winter habitat selection by woodland caribou (*Rangifer tarandus caribou*) using two key habitat components, *Cladina* lichens and snow depth. We quantified selection as the reduction in variance in used relative to available sites, thus avoiding reliance on correlations between organism and habitat, for which interpretation can be impeded by cross-scale correlations. By consistently selecting favorable habitat features, caribou experienced reduced variance in these features. The degree to which selection was accounted for by the travel route, feeding area, or microsite levels varied across the scale continuum. Caribou selected for *Cladina* within a 13-km scale domain and selected shallower snow at all scales. Caribou responded most strongly at the dominant scales of patchiness, implicating habitat heterogeneity as an underlying cause of multi-scale habitat selection. These novel approaches enable a spatial understanding of resource selection behavior.

Key words: animal behavior; blocked quadrat variance; continuum; habitat selection; hierarchy; landscape ecology; *Rangifer tarandus*; scale; semivariance; spatial heterogeneity; spatial pattern analysis.

INTRODUCTION

Habitat selection has emerged as an umbrella concept under which ecology could be unified (Morris 2003). Empowered by the concept of scale, habitat selection has the potential to bond the diverse phenomena of predator avoidance, migration, distributions, gregariousness, movements, dispersion, energetics, and foraging (Orians 1991, Travis and Dytham 1999, Brown 2000). To facilitate this synthesis, in this paper we bring together two large but separate lines of ecological inquiry: first, spatial and geostatistical analyses, which make use of spatial continua to represent patterns of heterogeneity across scales; and second, habitat selection, the disproportionate use of available resources by animals. We unite these by noting that when animals consistently select good (or avoid bad) habitat, the

variance of preferred habitat components should be reduced at used sites relative to available sites. By comparing the spatial structure of habitat components in used and available sites (at several levels of behavior), we go beyond describing patterns of spatial variability in the environment to evaluating the behavioral processes resulting from those patterns. We move from quantifying the spatial structure of habitat to quantifying the spatial structure of habitat selection.

Following Johnson (1980), habitat selection studies are routinely conducted at multiple scales. These studies typically employ arbitrary hierarchical levels (such as nest sites, forage patches, core areas, or home ranges) that tend to be taxon specific and spatially variable, in place of explicitly spatial scales. As a result, this conventional approach has hindered comparison among studies and has failed to facilitate unification. Here, we quantify habitat selection by coupling behavioral levels, which help elucidate how selection is accomplished, to spatial scales, the common comparable feature among studies. By employing a continuum of spatial scales we

Manuscript received 7 November 2006; revised 1 February 2007; accepted 13 February 2007. Corresponding Editor: R. W. Ruess.

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avoid false negatives (erroneous conclusions of no selection) that attend incorrect assumptions of the scales at which animals interact with the environment.

Habitat selection is a response to the spatial heterogeneity of preferred environmental features (MacArthur and Levins 1964). This patchiness results in positive spatial autocorrelation of habitat variables, such that they are more similar when closer (Dale 1999). Although often treated as a statistical nuisance (Legendre 1993), we use spatial autocorrelation to our advantage by quantifying it across behavioral levels of habitat use. The ubiquity of spatial autocorrelation, however, often results in correlations among habitat variables across scales (Battin and Lawler 2006, Kristan 2006). Because multi-scaled studies often rely on correlations between animals and habitat variables, cross-scale correlations can confound interpretations of the presence or strength of selection at any scale and confuse interpretations of selection between scales (Battin and Lawler 2006). To avoid the problem, we investigate habitat selection as a reduction in variance (Lawler and Edwards 2006), quantifying it as a response to heterogeneity. We expect sites selected by animals to be more similar to each other than available sites.

In this study, we develop two new approaches to detailing the selective response of organisms to their environment as a function of scale, using winter habitat selection by woodland caribou (*Rangifer tarandus caribou*; see Plate 1) as an illustration. We conduct analyses in both the distance domain and the frequency domain, comparing approaches based on lag and grain. In the distance domain, we use variogram analysis (Matheron 1960), a geostatistical tool that compares variability between pairs of samples at given separation distances (lags). Blocked quadrat variance (BQV; Greig-Smith 1952) operates in the frequency domain, comparing variability among contiguous blocks in different sized grids, in relation to the size of those blocks. It is the foundational pattern analysis technique of plant ecology and helps identify patch structure. While a wealth of analyses have described the spatial structure of the environment to which animals respond (Greig-Smith 1979, Bell et al. 1993, Dale 1999), neither of these methods have been applied to the response itself. We extend these continuous descriptors of heterogeneity to habitat selection by caribou of the Middle Ridge herd of Newfoundland. We compare the variability in two key habitat components (lichens and snow) measured at four levels of habitat use (from feeding microsites to population winter range) across a spectrum of spatial scales (from 1 to 28 000 m).

METHODS

Data collection

We collected field data on two primary habitat characteristics of the Middle Ridge herd's winter range (47°55' N, 54°40' W, ~600 km²; Mahoney 2000) in the maritime barrens ecoregion of east-central Newfound-

land, Canada. Following Schaefer and Messier (1995) we sampled at four hierarchical behavioral levels of habitat use by caribou: the population winter range, travel routes (paths connecting feeding areas), feeding areas (aggregations of feeding craters), and craters (continuous microsites of disturbed snow to access subnivean food). We located caribou or their sign by searching on foot or by snowmobile from 3 February to 18 March 2005. Rather than characterize the full array of habitat selection in this herd, we restricted our analyses to two key variables (snow depth and lichen cover) to illustrate our analytical methods. At each sampling site we recorded snow depth, an indicator of the energetic costs of foraging and moving (Fancy and White 1985). We then marked the sites, recorded their coordinates with a handheld global positioning system (GPS), and revisited them following snowmelt (25 May 2005–22 June 2005) to record cover of caribou lichens (*Cladina* spp.), the herd's primary winter food (Bergerud 1974, Mahoney 2000). We recorded percent cover (in classes of 0, 0.1–1, 1.1–5, 5.1–10, 10.1–25, 25.1–50, and 50.1–100%, using the midpoint of each class in statistical analyses) of *Cladina* in a 0.5 × 0.5 m quadrat, except at the crater level, for which we used the area of the crater (mean = 0.41 m², SD = 0.48, *n* = 548), which reasonably matched the quadrat area.

Winter range.—Within the winter range, we established six transects, each 870 m in length with a northerly orientation and separated by 6 km. A variable sampling step (with adjacent steps separated by repeated sequence of 10, 20, 40, 130 m) was employed and, at each step, stakes were planted and measurements taken at four sites (step center, plus 5 m west, south, and east of center) for a total of 80 measurement sites along each transect. Thus, the distance between sampled sites ranged from 5 m to 30 km. For each site, snow depth was recorded two to three times throughout the winter and averaged. We measured *Cladina* at these and four additional east-oriented transects (and sites at step center, plus 5 m north, west, and south).

Travel routes.—Travel routes were defined as paths of disturbed snow used by multiple caribou leading to or from one or more feeding areas. Individual animal paths tended to converge at points away from the feeding areas, and measurements at travel route sites were taken at the nearest major point of convergence.

Feeding areas.—Across the landscape, craters were clearly clustered into feeding areas. We defined a feeding area as an aggregation of craters separated by at least 50 m from the nearest neighboring aggregation. 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 variable sampling step (with adjacent steps separated by repeated sequence of 50, 20, 5 m). The mean area of feeding areas was approximated from half the squared lengths of each transect.

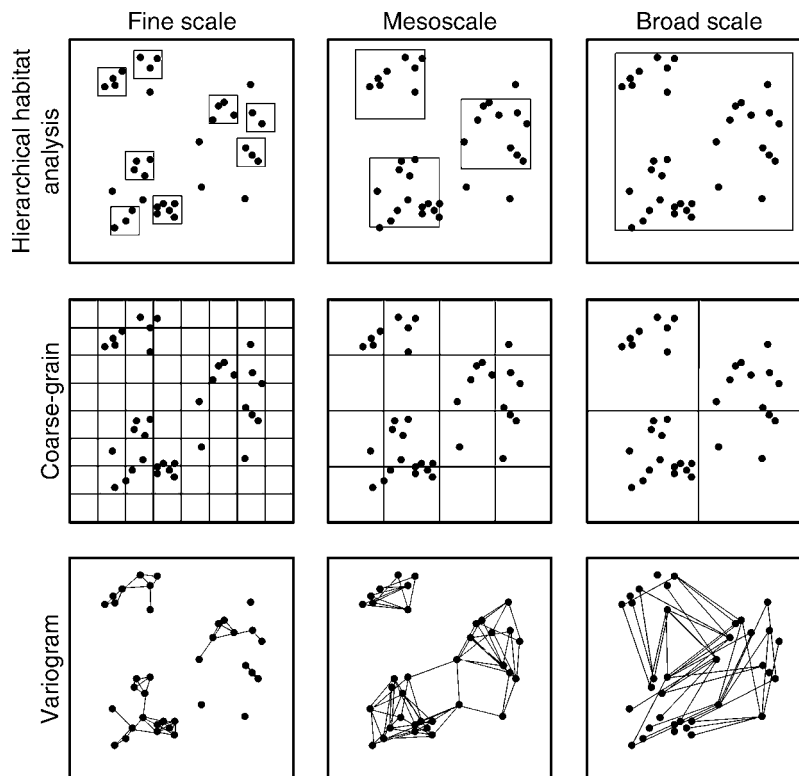


FIG. 1. Analytical approaches for investigating habitat selection at multiple scales. Hierarchical habitat analyses assess habitat use at several nested levels of behavior. In coarse-graining methods, measurements are grouped into progressively larger block sizes, and variance is compared among blocks. Variograms assess variability relative to the separation distance (lag) between points. Coarse-graining and variogram methods employ a continuum of spatial scales, rather than only the three represented. Points represent sampling locations.

Craters.—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 repeated sequence of 30, 15, 5 m) beginning and ending with the first and last crater of the feeding area, respectively. We marked the crater's perimeter with three to ten nails to enable its identification upon revisitation.

Data analysis

We utilized three analytical approaches to investigate habitat selection at multiple scales: conventional hierarchical habitat analysis, plus coarse-graining and variogram analysis. We compare these in Fig. 1, showing that progressively broader scales are measured by larger extent, larger grain, or greater lag, for each method respectively. For hierarchical habitat analysis, spatial scales are implied by behavioral levels. For both variograms and coarse-graining, we quantified habitat

use at all four behavioral levels and considered use at one level relative to the level above.

Hierarchical habitat analysis.—To compare general differences in snow depth and *Cladina* among the four behavioral levels of winter range, travel route, feeding area, and crater, we performed a hierarchical analysis of variance (ANOVA) to determine the mean values across samples at each level independently (PROC GLM, SAS version 9.1; SAS Institute 2003). The significance among the means of each level was assessed at $\alpha = 0.05$.

Variograms.—We constructed variograms to assess variability in each of *Cladina* and snow depth in relation to separation distance within each behavioral level. Variograms are widely used to assess environmental pattern (Webster and Oliver 2001), but we apply them here to habitat selection by comparing variability at each of four levels of habitat use. Treating each level (winter range, travel routes, feeding areas, craters) separately, we plotted the empirical semivariance (γ) of sample sites against the separation distance lag (h) between every possible pair of samples to examine the contribution to total sample variance between pairs separated by a given lag. The semivariance represents

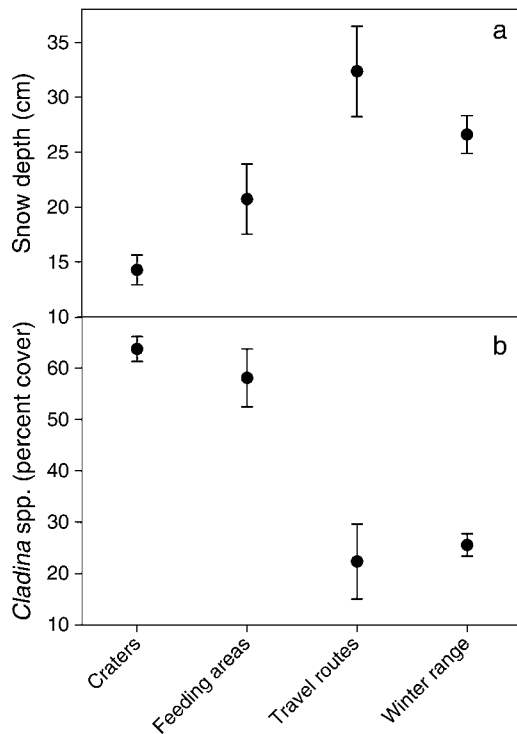


FIG. 2. Hierarchical habitat analysis of (a) snow depth (cm) and (b) *Cladina* spp. showing the mean and 95% confidence intervals (bars) at each behavioral level.

half the sum of the squared difference between pairs (Matheron 1960) and was calculated as

$$\hat{\gamma}(h) = \frac{1}{2n(h)} \sum_{i=1}^n [z(x_i) - z(x_i + h)]^2$$

where z is the value of the variable at the sampling location x_i , and $n(h)$ is the number of pairs of sampling locations located at distance h from one another. The value is divided by 2 (hence the name semivariance) because the summation from 1 to n sampling locations considers each pair twice in the calculation. We excluded lags with less than 30 pairs present.

A rich literature exists on modeling variograms for the identification of the dominant scale of variability (Rossi et al. 1992, Atkinson and Tate 2000). Here, we were instead interested in comparing trends of variability between behavioral levels, and not interpreting our results in terms of expected spatial models, which are unlikely to fit well with field data (Meisel and Turner 1998).

Coarse-graining.—To quantify the spatial patchiness or pattern intensity of the observed habitat components, we analyzed variability as a function of spatial frequency, where high frequency corresponds to high detail (small grain). We calculated BQV by delineating the study area into a grid of contiguous units (Greig-Smith 1952). We then hierarchically grouped adjacent quadrats into blocks. With each progressively coarser

delineation, blocks were twice as large and had half the number of units. We then applied a separate hierarchical analysis of variance (ANOVA; PROC GLM; SAS Institute 2003) with each block size as a nested level. We repeated this analysis at each behavioral level, and assessed habitat selection as the reduction in variance from coarser to finer levels. Peaks in BQV were interpreted as rough estimates of dominant patch size.

RESULTS

Hierarchical habitat analysis.—Feeding areas (112 sites) and the craters ($n = 548$) within them had more than twice the mean cover of *Cladina* than sampled at broader levels (Fig. 2a), but the difference in cover between feeding areas and craters was not significant ($P = 0.072$). Percent cover of these lichens along travel routes (71 sites) did not differ significantly from that of transects throughout the winter range (666 sites; $P = 0.405$, Fig. 2a). Snow was significantly shallower at each progressively finer behavioral level ($P < 0.01$ in each case) except for travel routes (often found between hills), which displayed deeper snow than other levels (Fig. 2b).

Variograms.—Craters were less variable in snow depth at all separation distances than sites available in the winter range, a discrepancy that decreased at greater lag distances (Fig. 3a). The semivariance of snow depth at the feeding area level was intermediate between that of the crater and winter range levels, except at lags above 13 km, where it matched that at the crater level. The semivariance in snow depth of travel routes, though erratic due to fewer data, was similar to that of the winter range across lags.

Although the semivariance of percent cover of *Cladina* in winter range sites remained relatively constant across scales, the variability in sites selected by caribou was scale-dependent (Fig. 3b). As lag increased, *Cladina* cover in craters became more variable, rising to the level in the winter range at about 13 km. In feeding areas, variability in *Cladina* cover increased with lag distance from semivariances similar to those among craters to those more comparable to the broader levels of behavior. Thus, despite consistent selection of craters and feeding areas with greater cover of *Cladina* (Fig. 2), strength of selection was inconsistent across spatial scales. At travel route sites further than 13 km apart, *Cladina* cover along travel routes was more variable than in winter range sites.

Coarse-graining.—Snow depth in the winter range exhibited a characteristic patch size of about 33.0 ha, a pattern not seen in sites selected at the travel route, feeding area, and crater levels (Fig. 4a). Instead variance at these levels gradually increased with coarseness of delineation such that the discrepancy in variance between these scales and winter range was greatest at the patch size of snow depth in the winter range. The variance tended to decrease with each successively finer behavioral level such that selection was strongest at the feeding area and crater levels.

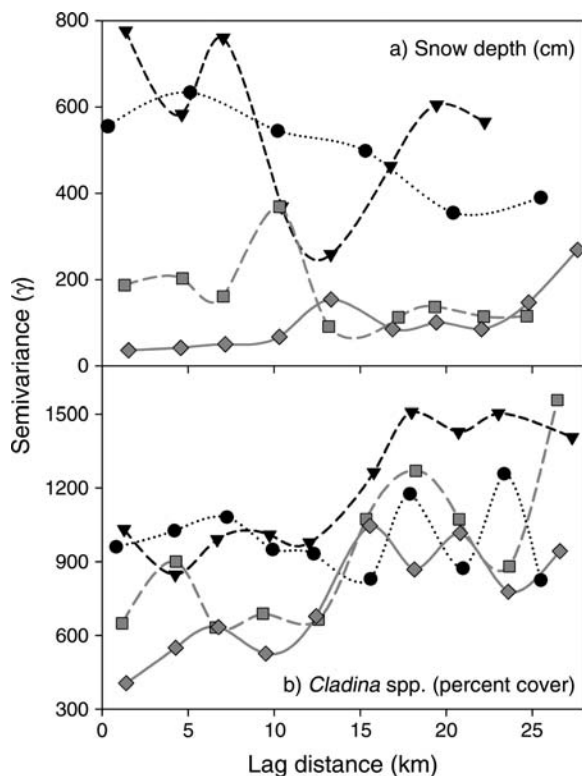


FIG. 3. Variograms of (a) snow depth (cm) and (b) percent cover of *Cladina* spp. showing variability across separation distance between paired sample locations. Habitat selection is represented by the discrepancy between semivariance at crater (gray diamonds), feeding area (gray squares), and travel route (black inverted triangles) levels relative to the winter range (black circles).

The variance in *Cladina* cover increased with coarseness of analysis and the patchiness was greatest at grains larger than 1 ha (Fig. 4b). Variance in craters and feeding areas increased together with scale, and the greatest discrepancy between craters and winter range sites was at intermediate grains between 1 ha and just over 1 km². The average estimated size of feeding areas was 0.90 ha.

DISCUSSION

The concept of scale has two important implications for habitat selection research. First, when habitat selection is viewed on a spectrum of scales, it can unite local feeding decisions and patch choice to long-distance movements and distribution patterns. To facilitate unification, we must explicitly incorporate spatial scale, the commonality among studies. Second, evidence of habitat selection depends on the scale of analysis. To understand scale dependence, investigations must encompass a spatial scope sufficiently wide to uncover scale domains of selection and the thresholds or transitions between them. In both cases, spatial scale is the empowering principle, and scaling continua are the means of application.

Caribou selected shallower snow at all scales (Fig. 3a), highlighting the multi-scaled nature of habitat selection. This broad response range underlies the consistency amongst the multitude of single-scale studies documenting selection for shallower snow cover (Pruitt 1959, Henshaw 1968, Stardom 1975, Brown and Theberge 1990). Although the persistent avoidance of deep snow across scales encourages comparison among studies of the effects of snow cover on energetics and movements, it does not imply that the process can be studied without consideration of scale. The degree of selection for snow and the degree to which behavioral levels accounted for selection, for example, both varied with spatial scale. For snow depth and *Cladina* lichens, selection was strongest at the finest scales. Selection for *Cladina* was scale-dependent, limited to lags under 13 km (Fig. 3b). We recommend this distance, which may result from the actual or perceived availability of resources, as a useful spatial extent for analyses of the feeding ecology of this population.

Organisms respond to the spatial heterogeneity of their environments (Wiens 1976, Turner 1989, Kie et al. 2002). There would be no habitat selection if habitat were uniform. Despite this, our approaches are among

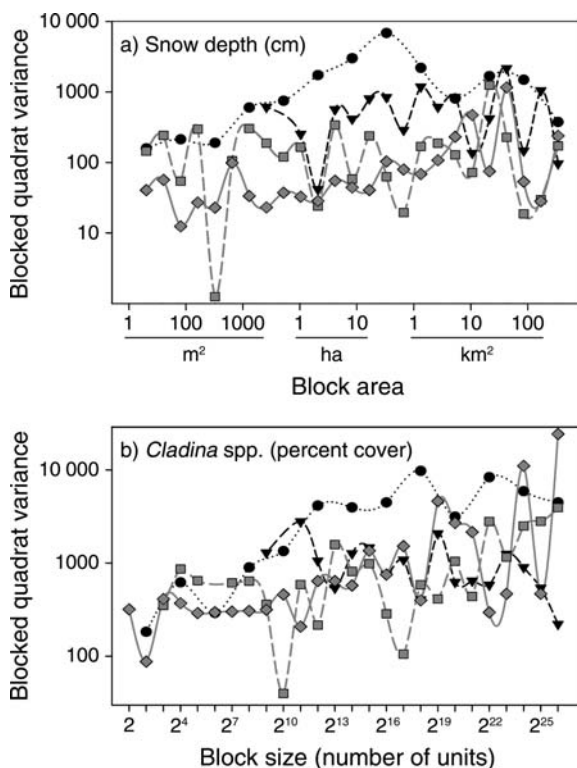


FIG. 4. Blocked quadrat variance of (a) snow depth (cm) and (b) percent cover of *Cladina* spp. in relation to the number of units in each block and block area. Habitat selection is represented by the discrepancy between crater (gray diamonds), feeding area (gray squares), and travel route (black inverted triangles) levels relative to the winter range (black circles). Note log scales.



PLATE 1. Caribou select habitat according to its patchy distribution in the barren landscapes of Newfoundland and Labrador, Canada. The photo shows caribou in August 2006, at Shuldham Island, Saglek Bay, which is now part of the Torngat National Park Reserve, about 200 km north of Nain, Labrador. Photo credit: Geoff Goodyear.

the first to quantify habitat selection explicitly as a response to habitat heterogeneity. Habitat selection can be construed not merely as differences in mean values of conditions or resources (Fig. 2), but also as a reduction in variance of those resources (Fig. 3). By concentrating activity in good habitat, caribou selected sites that were more similar to each other than those available in the winter range. Caribou responded to the heterogeneity of snow depth at all scales, but the greatest response was at the grain of highest patchiness (Fig. 4a). *Cladina* was selected most strongly at the smallest scales of substantial patchiness (Fig. 4b). Because the spatial structure of habitat affects its availability, populations may be limited not only by the abundance of preferred habitat components but also by their patchiness and variability in space. Animals must respond to these spatial patterns, and we suggest that the scale-dependence of habitat selection can result from scale-dependent habitat heterogeneity.

On its own, hierarchical analysis of caribou habitat selection revealed the behavioral levels accounting for

selection (Fig. 2) but not the spatial scales at which selection occurred, nor the influence of habitat structure. Here, we retained Johnson's (1980) widely adopted hierarchical framework, but not his specific levels (from species range to dietary item), whose standardized use and interpretation has been impeded by difficulties in measuring them and the diversity of behaviors among species. We found that the behavioral levels at which caribou accomplished selection varied with scale. Selection occurred primarily at the level of the feeding area, with additional selection at the crater level limited to lags under 13 km for snow depth, and 6 km for *Cladina*. By marrying behavioral levels to spatial scale, and using a scale continuum (instead of the levels) as the consistent standard, we allow the hierarchical levels (here, winter range to craters) to be customized to the specific ecology and behaviors of the taxon (e.g., nest site, migration route, defended territory, breeding ground) and the research questions under investigation. By explicitly quantifying scale domains of selection we free behavioral levels from assumptions of their extents and thereby enable a spatial understanding of habitat selection.

These methods (Fig. 1), a lag-based approach in the distance domain (the variogram) and a grain-based approach in the frequency domain (BQV), are familiar examples representative of broader families of pattern analyses that we suggest are equally applicable to multi-scale habitat selection investigations. Lagging methods such as covariance and correlogram functions (Rossi et al. 1992) and paired-quadrat variance techniques (Ludwig and Goodall 1978) can be applied at several levels to the identification of scale domains of selection. Coarse-graining methods such as refined blocked-quadrat variance techniques and spectral analysis (Platt and Denman 1975) can be employed at multiple behavioral levels to evaluate the response to pattern intensity. Applying these analytical approaches to habitat selection research can provide a broader understanding of the spatial dynamics of habitat selection.

ACKNOWLEDGMENTS

We thank R. Curran, S. Hann, E. Loder, F. Norman, and J. Zigouris for field assistance, and two anonymous reviewers for helpful comments. 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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