THE SPATIAL STRUCTURE OF HABITAT SELECTION
BY CARIBOU (RANGIFER TARANDUS CARIBOU)
IN NEWFOUNDLAND:
NEW MULTI-SCALED APPROACHES WITH
APPLICATIONS TO LIMITING FACTORS

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NEW MULTI-SCALED APPROACHES WITH APPLICATIONS TO LIMITING FACTORS

by

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ABSTRACT

Habitat selection is a multi-scaled phenomenon. Selection depends on the scales

perceived by organisms, while our ability to detect selection depends on analytical scale.

Traditional studies of habitat selection have been limited by the use of discrete, arbitrary

scales, because a quantitative basis has not existed for evaluating how animals perceive

the availability of habitat. I developed new approaches based on common geostatistical

and spatial analyses that use continua to represent multi-scaled winter habitat selection by

caribou (*Rangifer tarandus*) from the perspective of the organisms, letting their responses

define the scales of analysis. Caribou responded most strongly at the feeding area level,

at distances up to 13 km, and at scales of patchiness of about 1 ha. Although habitat

selection among levels of behaviour was hierarchical, caribou selected habitat variables

across overlapping scale domains, suggesting that limiting factors were not hierarchically

constrained. My results implicate habitat heterogeneity as an underlying cause of multi-

scaled habitat selection.

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CO-AUTHORSHIP STATEMENT

Both manuscripts in this thesis were co-authored by Stephen J. Mayor, James A. Schaefer, David C. Schneider, and Shane P. Mahoney. Stephen J. Mayor was the principal investigator and author, designed and identified the research proposal, led the collection of field data, performed all data analyses, and prepared the manuscript. Dr. James A. Schaefer contributed to the conception of the research proposal, development of ideas and both field and analytical methods, and interpretation of results. Dr. David C. Schneider contributed to the analysis of data, development of ideas and analytical methods, and quantitative interpretation of results. Shane P. Mahoney contributed to the logistical design of field data collection, biological interpretation of results, and development of ideas. All co-authors contributed to the editing of the manuscript.

Chapters 2 and 3 will be submitted as a separate manuscript for publication. Consequently, there is necessary repetition among the chapters of this thesis.

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CHAPTER 1: INTRODUCTION AND OVERVIEW

Habitat selection is a cornerstone of animal ecology. Studies in the early and mid 1980's (Schneider & Piatt 1986, Schneider et al. 1987), however, showed that habitat use and selection (the disproportionate use of available habitat) depend on the spatial scales at which they are conducted. This finding and those of the several hundred studies that it generated, have revealed that scale is an integral characteristic of habitat selection. For example, different species select habitat at different scales. Also, different habitat components can be selected at different scales. This thesis investigates the role of spatial scale in the study of habitat selection and develops new analytical approaches to multi-scaled habitat selection by caribou (*Rangifer tarandus*) during winter.

Habitat selection, empowered by the concept of scale, has been promoted as a unifier of ecology. The diverse concepts of predation, migration, distribution, gregariousness, movements, dispersion, energetics, foraging, and diet, can all be viewed as components of habitat selection operating at different scales (Orians 1991, Travis & Dytham 1999, Brown 2000). As Orians (1991) stated, "habitat selection goes by different names at different spatial scales." Morris (2003) suggested that habitat selection can be an evolutionary strategy, a source of speciation, and a mechanism of population regulation and community assembly.

Divergent and ambiguous use of the term 'scale' has however hindered potential for unification and comparison among studies. Habitat selection was recognised as a multi-scaled phenomenon as early as 1965, when levels of causation were identified (Hildén 1965). At an ultimate 'scale', or level, habitat selection is a response to fitness costs and benefits provided by various environments, and proximately it is a behavioural

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reaction to environmental stimuli and cues (Hildén 1965, Hutto 1985; see Table 1.1).

The rise of the concepts of scale (Schneider 2001) and hierarchy theory (Allen & Starr 1982) since the early 1980's was accompanied by a large increase in the number of habitat selection studies conducted at multiple scales, often employing a hierarchical framework. These studies often followed Johnson (1980) and designated hierarchical levels of behaviour, geography, or the environment (see Table 1.1). Levels of behaviour have included feeding, nesting, or perching sites, individual home ranges, population ranges, daily ranges, and movement or migration paths, to name a few. Geographic levels have, for example, included tree species, forest patches, and ecoregions. While informative, use and delineation of these levels has often been haphazard and arbitrary. Here, I use 'scale' as a general term to refer to the grain, extent, lag, or size of observation, phenomenon, or analysis. I use 'behavioural level' to indicate the relative scale of a behavioural process or phenomenon. By contrast, 'spatial scale' refers to absolute, spatially explicit, and quantified extent. Behavioural levels are hierarchically organised while spatial scales are expressed on a continuum.

Multi-scaled studies of habitat selection explain more variation than those conducted at single scales (Poizat & Pont 1996), but they are typically conducted at only two to four scales. Thus they may fail to capture the full range of responses to habitat. For caribou, Rettie & Messier (2000) proposed two levels of habitat selection (seasonal range and daily area), and Griffith et al. (2002) defined nine similar levels from species range to use of plant parts. Clearly, any number of levels can be identified, and to understand the full suite of selective behaviours a continuum of scales may be necessary. But behavioural levels are not spatial scales themselves with definite points on a

continuum and the spatial scales associated with different levels of behaviour, for example, are not always clear. Whereas behavioural levels such as feeding areas vary in scale among individuals, populations, species, environmental conditions, and measurement techniques, spatial scales instead offer a consistent standard.

I employ a continuum of explicitly spatial scales allowing habitat selection to be assessed from a full slate of possibilities. With this approach I attempt to represent habitat selection from the perspective of caribou. I let the selective responses by organisms define the scales along spatial continua because different species may perceive the world at vastly different and unexpected scales (Lima & Zollner 1996), potentially unrelated to the perspectives of researchers. What is viewed as habitat by one species may be unusable to another. Scale is an important component of these differences in perspective.

The heterogeneity of habitat components may also be perceived differently by different species, and plays an important role in the ecology of ungulates (Wallace et al. 1995, Kie et al. 2002, Boyce et al. 2003, Frair et al. 2005). Stewart et al. (2000) suggested that "environmental heterogeneity is important for individual organisms only when it occurs at a scale to which the organism itself can respond." Thus, it is of interest to know at what scales organisms can perceive and respond to heterogeneity.

With increasing knowledge of the scales of habitat selection relevant to specific species, the interpretation of these scales is emerging as an important research direction. Rettie & Messier (2000) suggested that the scales of selection, assumed to be hierarchical, should indicate the importance of limiting factors (i.e. environmental factors that limit the fitness of individuals within the population, where fitness is the probability

of survival and reproduction of individuals). I examine this assumption by first testing the degree of hierarchical constraint between scales, and second by investigating the importance of limiting factors based on the strength of selection across scales.

Habitat ecology of caribou

This study investigates the habitat selection of the Middle Ridge caribou herd in east-central Newfoundland, Canada. Caribou have a circumpolar distribution, ranging throughout the tundra and boreal forest biomes. There are four extant subspecies in North America, but only woodland caribou (*R. t. caribou*) exist in insular Newfoundland. Caribou are at risk in many parts of Canada, and the Middle Ridge herd in Newfoundland is currently declining in numbers (S.P. Mahoney, unpublished data).

Potential limiting factors affecting the fitness of individuals in caribou populations include predation (Bergerud 1974, Rettie & Messier 2000), insect harassment (Walsh et al. 1992), disease (Lankester & Fong 1998), snow conditions (LaPerriere & Lent 1977, Adamczewski et al. 1988), and food (Pruitt 1959, Bergerud 1972), notably *Cladina* lichens. In insular Newfoundland, predators include black bears (*Ursus americanus*), and introduced coyotes (*Canis latrans*), lynx (*Lynx canadensis*), and bald eagles (*Haliaeetus leucocephalus*), but (unlike for most populations of caribou) not wolves (*Canis lupus*), which were extirpated around 1920 (Mahoney & Virgl 2003). Among these, black bears are responsible for the greatest proportion of calf mortalities but their role in winter predation is minimal, and coyotes, active in winter, are a growing concern whose effects on caribou are under current investigation (Mahoney 2006, pers. comm.). While it is generally accepted that predation can limit caribou, there is less consensus on whether forage and snow conditions can do so. Terrestrial lichens, high in

carbohydrates, are the main winter food source of this herd (Mahoney 2000). Its winter range is primarily barren of forest (although scattered larch (*Larix laricina*) and black spruce (*Picea marinara*) are present), so arboreal lichens are not a major source of energy. Caribou are well adapted to both snow and lichens, with large hooves to distribute weight on snow and dig craters (Figure 1.1) to access forage, a keen olfactory sense to smell lichens under snow, and an ability to efficiently digest lichens (Miller 2003). Due to the gregarious nature of caribou, craters are typically aggregated (Figure 1.2)

Outline and goals

The primary goals of this study include the following: (1) to develop analytical approaches able to assess the spatial structure of habitat selection (i.e. the response to habitat along a continuum of spatial scales); (2) to determine the spatial scales at which Middle Ridge caribou select winter habitat and the behavioural levels at which this is accomplished; (3) to detail the selection of structural winter microhabitat by Middle Ridge caribou herd; (4) to test the hypothesis that the scales of selection indicate the importance of selection; (5) to investigate the role of heterogeneity of habitat components on multi-scale patterns of habitat selection

In Chapter 2 I develop and illustrate new approaches to habitat selection based on familiar spatial and geostatistical techniques utilizing continua of spatial scale. In Chapter 3 I apply these approaches to the study of caribou winter habitat selection in Newfoundland. I explore the hierarchical nature of habitat selection and interpret the scale domains and degree of selection in terms of the importance of limiting factors. In

Chapter 4 I present a summary and conclusion to the thesis by discussing implications for conservation and management of caribou and recommend future directions of research.

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Table 1.1: Types of scales (and levels) used in multi-scaled habitat selection studies.

Type of scale	Examples	Comments	Key references
Causal levels	a) Ultimate to proximate	Ultimately, selection is the behavioural response to fitness costs/benefits; proximately selection is the response to perceivable environmental stimuli and cues to fitness	Hildén (1965); Hutto (1985) Morris (2003)
Organisational levels	a) Species, subspecies/ecotype, population, group, individual	Habitat selection occurs at the individual level, but its effects can be measured as disproportionate use of habitat at any organisational level.	Bradshaw et al. (1995)
Environmental or geographic levels	a) Biome, ecoregion, forest patch, tree species, tree b) Watershed, stream order, reach, riffle/pool, microsite	Levels are independent of focal species (or the perception of individuals of that species) and represent hierarchical levels of the structural environment.	Danell et al. (1991)
Behavioural levels	a) Species distribution, population distribution, seasonal population range, individual home range, travel route, feeding area, feeding or nesting site	Levels are dependent on focal species and derived from observations of the distribution or movements of individuals.	Johnson (1980); Schaefer & Messier (1995);
Spatial scales	a) 10^7 m to 10^{-2} m b) 10^7 m^2 to 10^{-2} m^2 c) 10^7 m^3 to 10^{-2} m^3	Explicitly spatial scales expressed as spatial grain (resolution) and extent (range) of analysis, pattern, or process. Measured in a) distance, b) area, or c) volume. Patch size, perceptual range, and movement distance are examples of measurable spatial scales.	Schneider & Piatt (1986) Johnson et al. (2001)
Temporal scales or levels	a) Century, decade, year, day, hour, minute, second b) Disturbance cycle (e.g. burn frequency), multi-annual forage cycle (e.g. snowshoe hare population cycle), seasonal cycle, lunar light cycle, daily light cycle, tidal cycle, environmental pulse. c) Population abundance cycle, generation time, annual breeding/birthing cycle, travel time, feeding bout, bite time	Can be explicitly temporal scales as in a), environmental/geographic temporal levels as in b), or behavioural temporal as in c). Causal and organisational levels can also be examined temporally. Temporal scales of selection should correspond in magnitude to spatial scales of selection such that larger scales are less frequent.	Orians & Wittenberger (1991) Mysterud et al. (1999) Revilla et al. (2004)
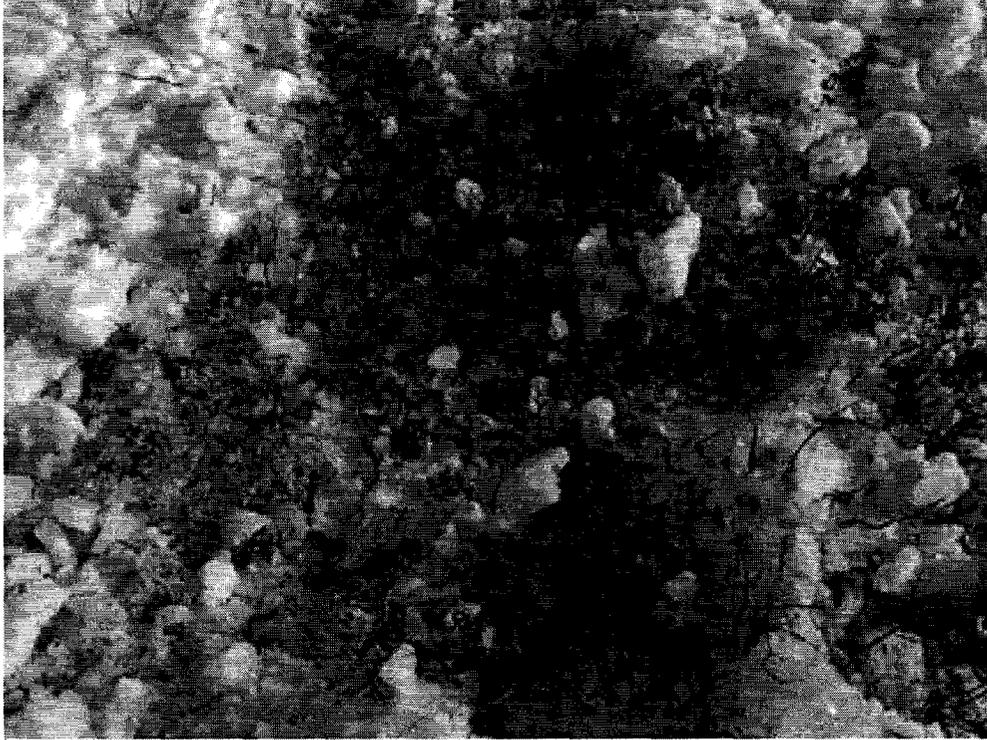
Figure 1.1: A typical feeding crater dug by a caribou, uncovering *Cladina* lichens.
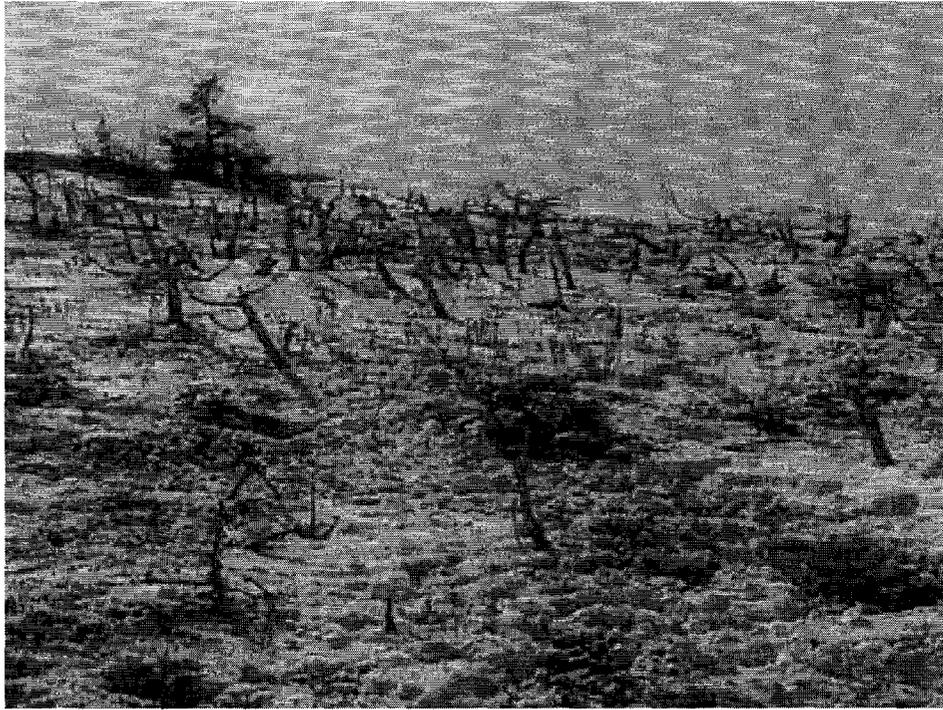
Figure 1.2: A typical feeding area, characterized by an aggregation of craters (dark patches) dug by caribou to access subnivean food.

CHAPTER 2: SPECTRUM OF SELECTION: NEW APPROACHES TO DETECTING THE SCALE-DEPENDENT RESPONSE TO HABITAT

Abstract

Habitat selection depends on scale, but multi-scaled studies of this fundamental phenomenon have been limited by the use of arbitrary hierarchical levels of behaviour in place of explicitly spatial scales. By applying spatial (blocked-quadrat variance) and geostatistical (variogram) tools, I compare variance between used and available sites to evaluate habitat selection along a continuum of spatial scales. When habitat components are correlated across scales interpretations of correlations between organisms and habitat can be impeded, so I instead quantified habitat selection as a reduction in variance. In this methodological study, I illustrate these approaches by applying them to winter habitat selection by Newfoundland caribou (*Rangifer tarandus caribou*) using two key habitat components, *Cladina* lichens and snow depth. I then compare the results across four behavioural levels. Caribou consistently selected favourable sites such that the variance that they experienced in *Cladina* and snow depth was reduced. Comparison of variograms at four behavioural levels showed that selected sites were more similar in snow depth and lichen cover than sites in the available winter range, and that selection for lichens increased at smaller scales. Scale-dependent habitat selection may result from scale-dependent heterogeneity in the environment, so next I used blocked-quadrat variance at various behavioural levels of habitat use to compare patchiness in key habitat variables. I found that habitat variables in selected sites were less patchy than in the

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available environment, but the selective reduction in patchiness varied across spatial scales. Selection for snow depth occurred within a single scale domain, but the degree of selection varied across scale and was accomplished at several behavioural levels. Habitat selection, as measured by a reduction in variance, resulted from a choice of *Cladina*-rich feeding areas corresponding in size to the patch structure of these lichens in the winter range. Diverse analytical approaches produced complementary results that allowed a more comprehensive understanding of habitat selection across scales.

Introduction

Habitat selection, among ecology's most intriguing and heavily researched phenomena, has emerged as an umbrella concept under which ecology might be unified (Morris 2003). Although habitat selection occurs at the level of the individual, it is ultimately an evolutionary strategy to increase fitness, a mechanism of population regulation and community assembly, and even a source of speciation (Morris 2003). Concepts as diverse as predator avoidance, migration, distributions, gregariousness, movements, dispersion, energetics, and foraging can be viewed as components of habitat selection operating at different scales (Orians 1991, Travis & Dytham 1999, Brown 2000). Indeed, the concept of scale is fundamental to our understanding of habitat selection. Habitat selection often depends on the scale of analysis (Schneider & Piatt 1986, Schneider et al. 1987, Becker & Beissinger 2003, Garcia & Oritz-Pulido 2004, Morin et al. 2005) and different habitat components may be selected at different scales (Bergin 1992, VanderWerf 1993, Mosnier et al. 2003, Anderson et al. 2005, Apps et al. 2001, Johnson et al. 2002a). To understand fully the scale-dependent complexities of habitat selection, studies now routinely

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investigate the process at multiple scales simultaneously. Far from united, these studies have generated increasingly disparate results, taxon-dependent tactics, and divergent definitions of scale.

Most multi-scaled studies of habitat selection follow Johnson (1980), who suggested a standard framework of four levels of behaviour: species range, home range, feeding area, and diet. But the uniqueness of different ecological systems and our means to measure them has resulted in nearly as many 'scales' of selection as studies. The scales utilized, such as forage patches, core areas, or home ranges, while convenient, are often subjectively delineated and arbitrarily designated by the observer. Usually they represent levels of behaviour implying or operating at different spatial scales, but are not explicitly spatial scales themselves (Allen & Hoekstra 1992, O'Neill & King 1998, Hobbs 2003). A home range level, for example, is a broader scale relative to a forage patch level, but the grain and extent of home ranges can be ambiguous and are spatially variable between individuals and among populations.

I suggest that explicitly spatial scales may better facilitate comparisons across behavioural levels, individuals, populations, and taxa, within and among studies. Whereas behavioural levels may express how selection is accomplished (e.g. by targeting good foraging patches), explicitly spatial scales quantify behavioural outcomes on the landscape (e.g. a 5 km^2 area).

Describing the spatial structure of habitat selection not only relates the process to the common currency of scale, but helps avoid false negatives due to researchers' assumptions of the scales at which animals interact with the environment. By encompassing a continuum of spatial scales in the analyses, analyses are less likely to

mistakenly conclude a lack of selection. By measuring the response to habitat across a spectrum of spatial scales, I assess selection from the perspective of the organisms. If habitat selection is scale-dependent, then analyses should be conducted at the scales at which animals select habitat. Without knowing these *a priori*, I assess habitat selection objectively from a slate of possibilities, letting the response to habitat define the scales. This approach allows the potential of identifying scale domains (*sensu* Wiens 1989) over which selection is similar, and the transitions or thresholds between them at which selection patterns vary.

Habitat selection is a response to the spatial and temporal heterogeneity of preferred environmental features (MacArthur & Levins 1964). Thus, the scale-dependence of habitat selection may result from scale-dependent habitat heterogeneity (Kotliar & Wiens 1990). How an animal responds to patchiness depends on any dominant scales of that heterogeneity (Kie et al. 2002, Heikkinen et al. 2004) and the organism's ability to perceive and physically take advantage of habitat at those scales. The patchiness of the environment means that habitat variables may be positively autocorrelated, or more similar when closer (Dale 1999). Although often treated as a statistical nuisance (Legendre 1993), I use spatial autocorrelation here to my advantage by quantifying it across behavioural levels of habitat use.

The ubiquitous pattern of spatial autocorrelation, however, often results in correlations among habitat variables across scales (Battin & Lawler 2006, Kristan 2006). Most multi-scaled studies rely on correlations between animals and habitat variables, and cross-scale correlations can confound interpretations of the presence or strength of selection at any scale and confuse selection between scales (Battin & Lawler 2006). But

when animals consistently select good (and avoid poor) habitat components, the variability that they experience in the environment is reduced. Thus, I predict that sites selected by animals should be more similar to each other than other sites on the landscape. By investigating habitat selection as a reduction in variance, I avoid the problematic aspects of correlations across scales (Lawler & Edwards 2006).

In this study, I assess habitat selection as the response to variability in habitat. Habitat components in sites selected by animals should be less variable than in the available environment and I hypothesized that selection would be strongest at scales that facilitate the exploitation of habitat components most efficiently. I develop two new approaches to detailing the selective response of organisms to their environment as a function of scale, then compare them with a traditional multi-scaled analysis by assessing habitat components at four hierarchical scales of behaviour. Winter habitat selection by Newfoundland caribou (*Rangifer tarandus caribou*) is used as an example.

I draw my approaches from half a century of spatial pattern analysis in ecology. Greig-Smith (1952) developed the foundational pattern analysis technique of plant ecology, called blocked-quadrat variance (BQV). BQV compares variability among contiguous blocks in different sized grids, in relation to the size of those blocks. It represents variability across a spectrum of analytical grains and is thus a form of coarse-graining (Dale 1999). It helps identify patch structure, and is a form of spectral analysis in which a square wave window is used without smoothing (Ripley 1978). Although a large family of techniques has been developed from BQV (see Dale 1999, Dale et al. 2002), I adopt it for simplicity and to demonstrate the applicability of the family to habitat multi-scaled studies of habitat selection. Many studies would benefit from using

four-term local quadrat variance (4TLQV) to avoid the sensitivity of BQV to starting location of the grid. Here, this limitation is minimized by the large number of block sizes, which produce the same smoothing effect as a moving window employed in 4TLQV (Dale 1999). Variogram analysis (Matheron 1960), in contrast to BQV, is a geostatistical tool comparing variability between pairs of samples at given separation distances. It represents variability across an range of lags and is similar to paired-quadrat variance techniques (Ludwig & Goodall 1978) and covariance and correlogram functions (Rossi et al. 1992). While a wealth of analyses have described the spatial structure of the environment to which animals respond, the methods have not been applied to the response itself. I apply these descriptors of habitat heterogeneity to the study of habitat selection by comparing the patterns of variability in key habitat components measured at four levels of habitat use (from feeding microsites to population winter range) by caribou of the Middle Ridge herd of Newfoundland across a spectrum of spatial scales (from 1 to 28 000 m).

Methods

Data collection

I collected field data on two primary habitat characteristics of the Middle Ridge herd's core winter range (47°55'N, 54°40'W; Mahoney 2000) in the maritime barrens ecoregion of east-central Newfoundland, Canada (Meades & Moores 1989). The study area covered ca. 600 km² and lacked any obvious spatial gradients or anisotropy. Following Schaefer & Messier (1995) I sampled at four hierarchical behavioural levels of habitat use by caribou: the herd's core winter range, travel routes (paths connecting feeding

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areas), feeding areas (aggregations of craters), and craters (continuous areas of disturbed snow to access subnivean food). I located caribou or their sign by searching on foot or by snowmobile from 3 February to 18 March 2005. At each sampling site I recorded snow depth, an indicator of the energetic costs of foraging and moving (Tucker et al. 1991). I then marked the sites, and revisited them the following spring to record cover of caribou lichens (*Cladina* spp.), the herd's primary winter food (Bergerud 1974, Mahoney 2000). I restricted my analyses to snow depth and *Cladina* cover to illustrate the analytical methods rather than characterize the full array of habitat features selected by this herd.

I recorded percent cover of *Cladina* spp. in a 0.5 x 0.5 m quadrat, except for at the crater level, for which I used the area of the crater (mean = 0.41 m^2, SD = 0.48, n = 548), which reasonably matched the quadrat area. I recorded percent cover in classes of absent, <1%, 1-5%, 5-10%, 10-25%, 25-50%, 50-100%, and used the midpoint of each class in statistical analyses.

Winter range. Within the winter range of the Middle Ridge caribou herd, I established six linear transects, each 870 m in length with a northerly orientation and separated by five km. I employed a variable sampling step (0, 10, 30, 70, 200, 210, 230, 270, 400, 410 ... 870 m) and at each step planted stakes, recorded coordinates with a handheld Global Positioning System (GPS; Garmin GPS III Plus), and took measurements at four sites (step centre, plus 5 m west, south, and east of centre) for a total of 80 measurement sites along each transect. Varying the sampling step allowed me to efficiently obtain data at sites a wide variety of distances apart and over a broad spatial extent. For each site, snow depth was recorded two to three times throughout the winter

and averaged. I measured *Cladina* at these and four additional east-oriented transects (and sites at step center, plus 5 m north, west, and south).

Travel routes. I defined travel routes 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 travel route sites were recorded and measurements taken at the nearest major point of convergence. I used a flagged nail and GPS coordinates to mark the sites for revisiting later.

Feeding areas. Across the landscape, craters were clearly clustered into feeding areas. I defined feeding areas as an aggregation of craters separated from the next nearest crater by 50 m or more. For each feeding area, I established a transect connecting the two most distant craters in the feeding area. As feeding areas were usually elliptical in shape, this diameter typically bisected the primary feeding part of the area. I sampled the centre of the closest clearly undisturbed site to a variable sampling step (0, 50, 70, 75, 125, 145, 150 m …) along the transect from the edge of the feeding area, marked each site with a nail, and recorded the GPS coordinates. I approximated the mean area of feeding areas from half the squared lengths of each transect.

Craters. Craters are areas in which caribou have dug through the snow with their hooves or antlers to access subnivean food such as terrestrial lichens and plants. I defined craters as continuous areas of disturbed snow within which caribou had fed, usually with scattered lichen or plant debris. Because the snow was disturbed, I sampled undisturbed snow at the nearest point to the crater margin where snow depth was equivalent to crater depth. Along the transect of greatest diameter of each feeding area, I sampled the nearest clearly defined craters separated by a systematically variable

sampling step (0, 30, 45, 50, 55, 70, 100, 130, 145 m…) beginning and ending with the

first and last crater of the feeding area, respectively. I marked each crater with 3 to 10

nails and recorded the GPS coordinates.

Data analysis

I utilized three analytical approaches to investigate habitat selection at multiple scales:

hierarchical habitat analysis (consisting of four behavioural levels of winter range to

craters), coarse-graining, and variogram analysis. I compare these in Figure 2.1, showing

that progressively broader scales are measured by larger extent, greater distance, or larger

grain, for each method respectively. For both variograms and coarse-graining, I

considered habitat use at all four behavioural 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 winter range, travel route, feeding area, and crater levels I performed

a hierarchical analysis of variance to determine the mean values across samples at each

level independently (PROC GENMOD, SAS ver 9.1; SAS Institute, 2003). I assessed the

significance among the means of each level at $\alpha = 0.05$.

Variograms. I constructed variograms to assess variability in each of *Cladina* and

snow depth in relation to separation distance within each behavioural level. Variograms

are widely used to assess environmental pattern (Webster & Oliver 2001), but I apply

them here to habitat selection by comparing variability at each of four levels of habitat

use. For each level (winter range, travel routes, feeding areas, craters), I plotted the

empirical semivariance (γ) of sample sites over 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 half the sum of the

squared difference between pairs (Matheron 1960) and I calculated it 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 x at the sampling location 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 *semi*variance) because the summation from 1 to n sampling

locations considers each pair twice in the calculation. I excluded lags where at least 30

pairs were not present.

A rich literature exists on modeling variograms for the identification of the

dominant scale of variability (see Rossi et al. 1992, Atkinson & Tate 2000). Here, I was

instead interested in comparing general trends of variability between behavioural levels,

and not interpreting my results in terms of expected spatial models, which are unlikely to

fit well with field data (Meisel & Turner 1998). Modeling of these would necessarily

entail not only spatial rules but behavioural rules, a feat I did not attempt.

Coarse-graining. To quantify the spatial patchiness, or pattern intensity, of the

observed habitat components I analysed variability as a function of analysis detail (grain).

I calculated the blocked quadrat variance (BQV) by delineating the study area into a grid

of contiguous units (Greig-Smith 1952). I then hierarchically grouped adjacent quadrats

into blocks doubling in size with each increment. Blocks in each progressively coarser

delineation were twice as large, and therefore half as numerous. I then applied a separate

hierarchical analysis of variance (ANOVA; PROC GLM, SAS ver 9.1; SAS Institute, 2003)

with each block size as a nested level. I repeated this analysis at each behavioural level,

and assessed habitat selection as the reduction in variance from coarser to finer levels. I interpreted peaks in BQV as estimates of characteristic patch sizes.

The BQV method is the basis for a multitude of similar coarse-graining methods that attempt to overcome the initial limitations. I use this simplest method to illustrate its applicability to multi-scale habitat selection and facilitate comparison with other methodological approaches. The most sophisticated form of coarse-graining recommended by Ripley (1978) is spectral analysis (Platt & Denman 1975), but the absence of continuous data precluded its use.

Results

Hierarchical habitat analysis. Percent cover of *Cladina* along caribou travel routes (71 sites) did not differ significantly from that of transects throughout the winter range (666 sites; Figure 2.2a). Feeding areas (112 sites) along travel routes and the craters (n = 548) within them had more than twice the cover of these lichens, but were not significantly different from each other. Snow was significantly shallower at each progressively finer behavioural level except for travel routes, which displayed deeper snow than other levels (Figure 2.2b).

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 (Figure 2.3a). 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, 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 (Figure 2.3b). At lags increasingly shorter than 13 km, *Cladina* cover in

craters was increasingly less variable. 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 behaviour. 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 (Figure 2.4a). 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 behavioural level.

Variance in *Cladina* cover increased with coarseness of analysis and the

patchiness was greatest at grains larger than 1 ha (Figure 2.4b). 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 km^2. The

average estimated size of feeding areas was 0.90 ha.

Discussion

Spatial scale as a unifier of habitat selection research

Habitat selection is among the most fundamental behaviours of organisms and links the

evolutionary fitness of organisms to environments in which they live. When viewed on a

spectrum of scale, it unites local feeding decisions and patch choice to long-distance movements and distribution patterns (Orians 1991, Travis & Dytham 1999). Despite its biological significance and high levels of investigative activity, habitat selection is far from fully understood. Recognition of the scale-dependence of habitat selection has led to a multitude of studies at multiple scales (Orians & Wittenberger 1991, VanderWerf 1993, Schaefer & Messier 1995, Thompson & McGarigal 2002, Boyce et al. 2003, Becker & Beissinger 2003), but the promise of unification has not been fulfilled.

Hierarchical analyses of habitat selection rely on discrete levels at which organisms might associate with habitat. Selection is inferred where the mean value of some feature differs between used and available sites. Caribou, for instance, responded to lichens in craters and feeding areas but not along travel routes (Figure 2.2a). These results are not, however, easy to generalize or compare across taxa. For example, even though direct comparisons among ungulates foraging in snow might be conducted (Ihl & Klein 2001), it is more difficult to apply knowledge of selection at the crater level by caribou to feeding habitat selection by other herbivores, let along carnivores, even within the same system. The use and interpretation of four standardized levels proposed by Johnson (1980) – from species range to diet – has been impeded by the diversity of behaviours among species and our varying ability to measure them. Even within a species, selection at the same behavioural level may be manifest at very different spatial scales (Figures 2.3, 2.4). For example, seasonal range selection is associated with vastly different migration distances and extents of range for caribou of woodland versus barren-ground ecotypes (Edwards 1988).

Because behavioural levels vary among species both in scale and kind, and because spatial pattern is a ubiquitous characteristic of all systems (Milne 1991, Bell et al. 1993), spatial scale – as revealed by spatial and geostatistical tools – offers greater potential for unification. Knowing how habitat selection plays out in space may facilitate a better understanding of how the scale-dependent responses of species to heterogeneous landscapes interact to structure communities (August 1983).

The application of the hierarchical approach (Allen & Starr 1982, O'Neill et al. 1989) to habitat selection (Johnson 1980, Senft et al. 1987) assumes that selection at smaller scales is constrained by selection at larger scales (O'Neill et al. 1989, Schaefer & Messier 1995). Alternatively, selection at large scales may be viewed as the outcome of selection at small scales (Wiens 1989). The degree of constraint, if it does exist, may depend on the similarity between hierarchical levels (Kotliar & Wiens 1990) and may affect the degree of trade-offs between coarse- and fine-scaled variables (Kristan 2006). But the degree of constraint, or the order in which variables at different scales are selected, is largely untested, so the utility of a constrained design is unclear. Hierarchy can be a useful framework for understanding habitat selection but varying selection patterns across scales do not necessarily indicate that selection for different habitat components occurs in the ordered linear sequence implied by a hierarchy.

Habitat selection on the continuum

Hierarchical habitat analysis revealed the behavioural levels at which selection was accomplished, but not the spatial scale at which selection occurred, nor the influence of habitat structure. Caribou selected *Cladina* at the feeding area level, but at what spatial scales? Hierarchical studies of selection imply a spatial understanding of

behaviour, because the levels are spatially nested and differ qualitatively in scale. These studies may be limited by arbitrary designations of scales of aggregations, cover types, or levels of organisation and subjective delineations of their borders. A goal of habitat selection studies should be to conduct analyses at the grains and extents as those perceived by the organisms under investigation. Without knowing the scope of response *a priori*, investigators should use a scale-sensitive approach to reveal selection from the perspective of the organism.

Using spatial and geostatistical tools, I objectively identified the range of scales at which caribou responded to habitat along a spatial continuum. Caribou selected shallower snow at all scales (Figure 2.3a), indicating a single, extensive scale domain of selection for snow depth. This single domain underlies the consistency amongst multitudes of single-scale studies documenting caribou selection for softer, shallower snowcover (Pruitt 1959, Henshaw 1968, Stardom 1975, Brown & Theberge 1990). Although the persistent avoidance of deep snow across scales encourages comparison of studies of the effects of snow cover on energetics and movements, it does not mean that the process can be studied without consideration of scale. The degree of selection for snow and the degree to which behavioural levels accounted for selection, for example, both varied across lag distances. Selection for *Cladina* lichens was scale-dependent, limited to lags under 13 km (Figure 2.3b). I therefore recommend analyses of the feeding ecology of this population to be restricted to lags smaller than 13 km, the maximum distance at which caribou responded to *Cladina* lichens. For other populations of *R. t. caribou*, results of foraging studies might be expected to be most pronounced at scales

under 13 km, but scale-sensitive analyses (such as the variogram and BQV) are required to confirm this prediction.

A number of parallel methods representing habitat selection along a continuum have recently been developed. Approaches based on movement paths compare tortuosity, time spent, or movement rates at various scales in various habitat types. Fractal analysis has been used to show that the tortuousity of animal movement paths is non-random (Mårell et al. 2002), depends on scale (Nams & Bourgeois 2004, Nams 2005), and that the variance in tortuosity can indicate response to spatial heterogeneity (Nams 2005). Johnson et al. (2002a, b) applied a non-linear "broken-stick" model to the frequency distribution of movement rates to identify the scales of movement and then related them to habitat use. Similarly, variance in time spent foraging in given areas (measured by first-passage times) revealed the scales at which animals concentrated their movements (Fauchald & Tveraa 2003, Pinaud & Weimerskirch 2005), the behavioural levels of movement associated with these scales (Frair et al. 2005), and when related to heterogeneity of habitat variables, described scale-dependent habitat selection. In each of these movement-based approaches, the scales of habitat selection are determined independently of the habitat variables, and then related back to habitat. In contrast, Thompson & McGarigal (2002) and Anderson et al. (2005) varied the diameter of focal windows around mapped locations of bald eagle (*Haliaeetus leucocephalus*) and elk (*Cervus elaphus*) habitat use, respectively, to show varying scale domains of selection among habitat components. I adopted a similar approach to determine the scales of selection from the observed response to habitat components. Additionally, I employed

behavioural levels to reveal how selection was accomplished and investigated variance

across scales to avoid misinterpretations of selection due to cross-scale correlations.

The importance of heterogeneity to habitat selection

Organisms respond to the spatial heterogeneity of their environments (Turner

1989, Kie et al. 2002). There would be no habitat selection if habitat were uniform. For

this reason I employed analytical approaches explicitly measuring habitat variability. I

found that caribou responded to the heterogeneity of snow depth at all scales, but the

greatest response was at the grain of highest patchiness (Figure 2.4a). For *Cladina*, the

variability among selected sites was decreased at the smallest scales of high patchiness

across the winter range (Figure 2.4b). *Cladina* was patchiest at grains greater than 1 ha,

and within this range caribou responded to these lichens increasingly with smaller grains.

At smaller scales patchiness decreased, as did the response to *Cladina*. The Middle

Ridge herd selected from a winter range of limited heterogeneity, with low relief and few

distinct habitat types. The response to variability may therefore be greater in highly

heterogeneous environments. The relationship between habitat heterogeneity and scale-

dependent habitat selection needs further investigation.

Habitat uniformity is unrealistic, even within a habitat patch (Kotliar & Wiens

1990), but uniformly good habitat is an ideal outcome of consistent choice of good

habitat. By concentrating their space-use in good habitat, animals not only increase the

amount of favourable conditions or resources available, but also reduce the experienced

variability in habitat from that of the general environment. Reduction in the variability of

habitat is thus an important means of foraging optimally (Pyke 1984). Caribou responded

to variability in snow depth at all spatial scales within the winter range (Figure 2.3a), and

to lichen cover at lags up to 13 km, with increasing response at shorter lags (Figure 2.3b). By responding to variability of key habitat components, sites selected by caribou were more similar than in the broader environment. Because the spatial structure of habitat impacts its availability, animals may be limited by patchiness and variability as well as abundance of selected habitat components.

In concert with hierarchical habitat analysis, the variogram and BQV approaches to studying habitat selection revealed complementary results. The heterogeneity of *Cladina* reached a plateau at 1 ha, a grain size at which a major reduction in variance in *Cladina* amongst selected sites was observed (Figure 2.4b). Similarly, the approximate mean area of feeding areas was 0.90 ha. I suggest that by selecting *Cladina*-rich feeding areas (Figure 2.2) corresponding in size to the patch structure of their food source (Figure 2.4b), caribou experienced reduced local variability of *Cladina* in selected sites (Figure 2.3b) and hence increased foraging success.

Despite this correspondence in results among various approaches, the multilevel variogram and BQV analyses can be challenging to interpret due to the inherent noise in variance across space. I therefore recommend that only general trends and discrepancies in levels be interpreted, and minor fluctuations be disregarded. To add inferential power to the study, more intensive investigations such as modelling of selective responses to a simulated landscape are required.

The approaches I develop to characterize habitat selection as a spatial response to habitat variability are adapted from familiar methods of spatial pattern analysis. The spatial structure of the environment has been well characterized by plant ecologists (Greig-Smith 1979, Bell et al. 1993, Dale 1999), but the spatial response of mobile

organisms to this structure has received little attention. A number of analytical approaches exist for describing spatial structure, and many of these characterize variability as a function of either lag or grain. I utilized one lag-based method (the variogram) and one grain-based method (BQV), as representative examples to detail habitat selection at a series of behavioural levels, across a spectrum of spatial scales. The variogram approach shows the response to variability in relation to separation distance, which may represent the domains of selection. The domain of selection may be a function of the perceptual range of individuals (Zollner & Lima 1997) in the population or indicate the constraints on movement. The coarse-graining approach, by contrast, shows the response to variability in relation to grain size, and may indicate how scales of habitat patchiness are selected. By comparing use versus availability, these approaches can be extended to more advanced characterizations of spatial variability such as refined blocked and paired quadrat variances, spectral analysis, and covariance functions to explore the spatial structure of habitat selection. I suggest that these methods are broadly applicable to studies of habitat selection at multiple scales.

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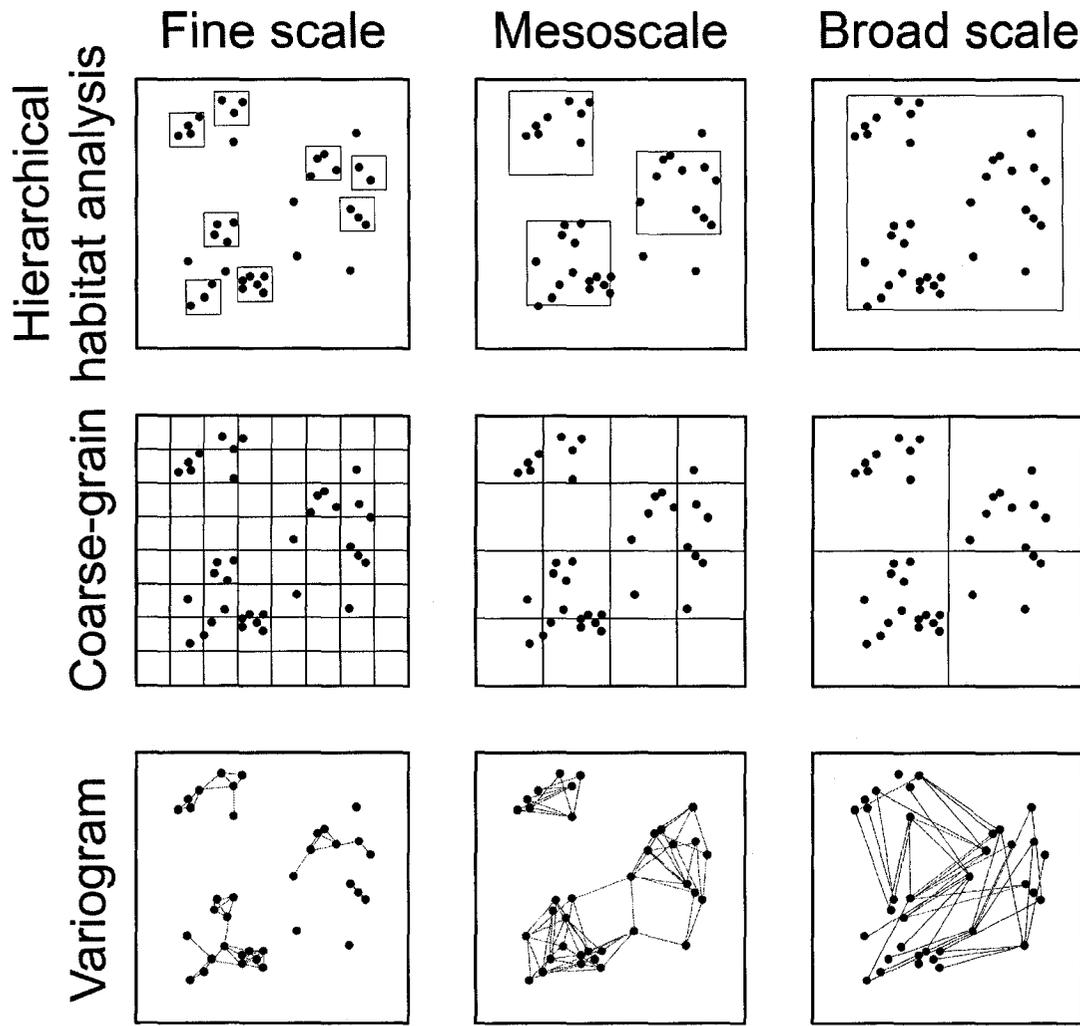
Figure 2.1: Analytical approaches applied to habitat selection at multiple scales. Hierarchical habitat analyses assess habitat use at several nested levels of aggregation or behaviour. In coarse-graining methods, such as blocked quadrat variance, measurements are grouped into progressively larger block 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.
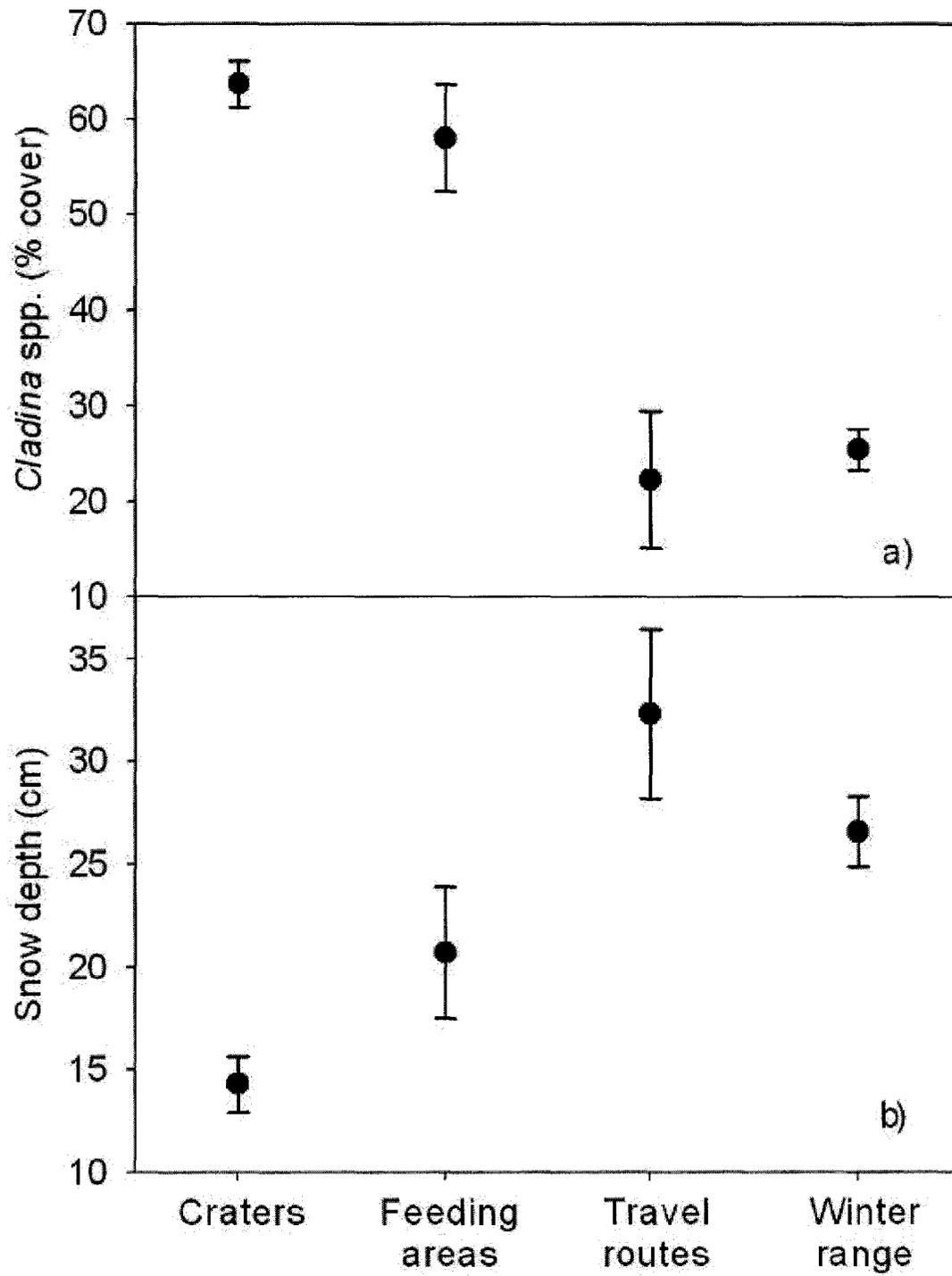
Figure 2.2: Hierarchical habitat analysis of a) snow depth (cm) and b) Cladina spp. showing the mean (dot) and 95% confidence intervals (bars) at each behavioural sampling level.
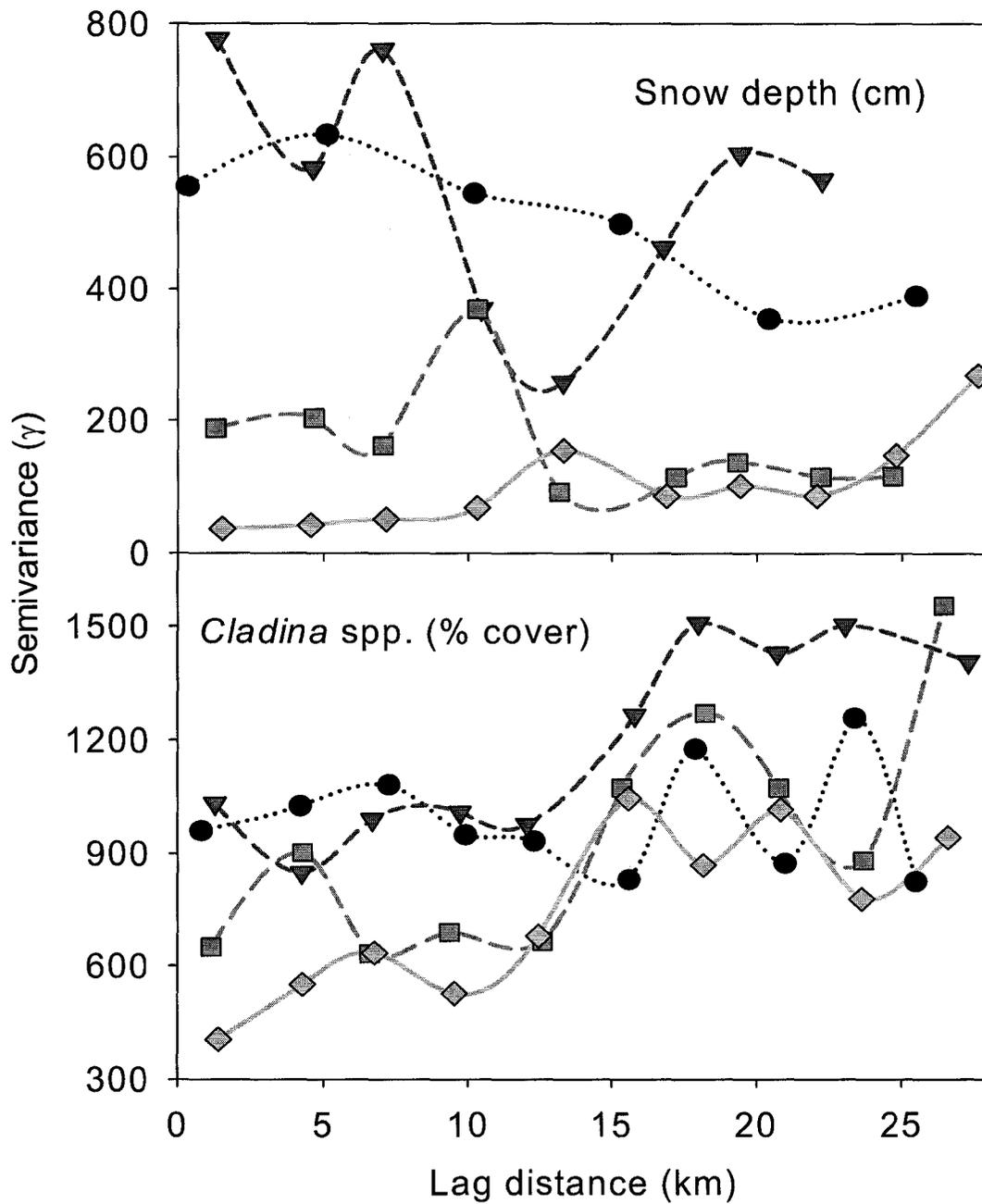
Figure 2.3: Variograms of a) snow depth (cm) and b) percent cover of Cladina spp. showing variability across separation distance between paired sample locations. Habitat selection is represented by the discrepancy between semivariance at crater (♦), feeding area (■), and travel route (▼) levels relative to the winter range (●) level.
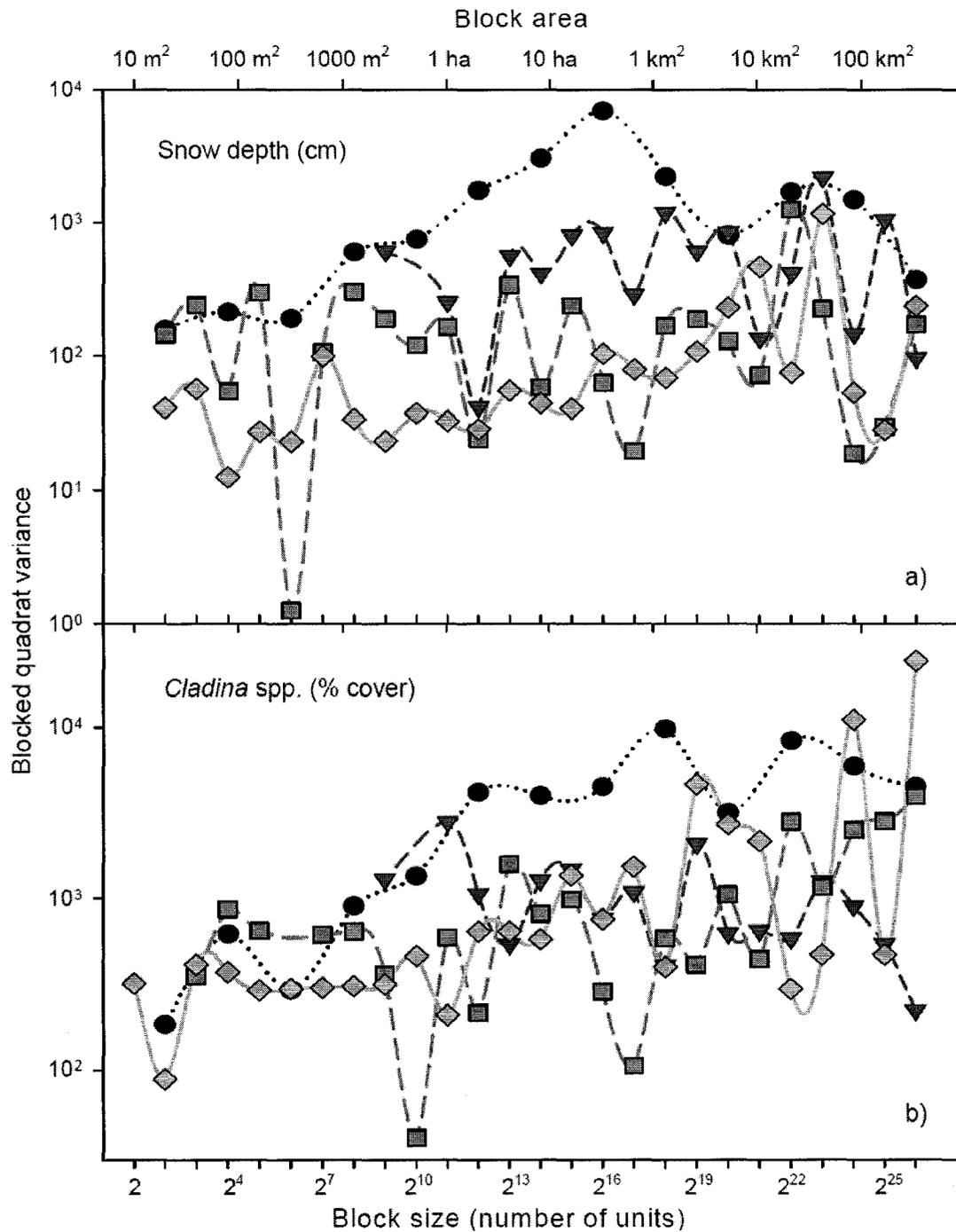
Figure 2.4: Blocked quadrat variance of a) snow depth (cm) and b) percent cover of *Cladina* spp. in relation to the number of units in each block and block area. Habitat selection is represented by the discrepancy between crater (⬦), feeding area (■), and travel route (▼) levels relative to winter range sites (●).

CHAPTER 3:

THE SPATIAL STRUCTURE OF HABITAT SELECTION: A CARIBOU'S-EYE-VIEW

Abstract

Evidence of habitat selection depends on analytical scale. More fundamental, habitat selection depends on organisms' perception of scale-dependent habitat heterogeneity. I investigated winter habitat selection of Newfoundland caribou (*Rangifer tarandus caribou*) as the response to heterogeneity and spatial variability of habitat. I quantified the spatial structure of habitat selected at four hierarchical levels along a continuum of spatial scales. I thereby avoided relying on arbitrary scales of analysis and explored habitat selection from the perspective of the organisms. Caribou consistently selected good habitat (greater cover of *Cladina* lichens and softer, shallower snow) such that they experienced reduced variability and patchiness of favoured habitat components in used relative to available sites. Caribou selected *Cladina* and shallow snow most at lag distances up to 13 km, which I interpreted as a perceptual range. By contrast, an increase in variability of *Kalmia* cover (despite greater mean cover) among selected sites revealed that this shrub was not selected. Caribou responded most strongly to the heterogeneity of snow depth at the scale of highest patchiness, 1 ha, which corresponded to the size of a feeding area. Similarly, much of the selective reduction in variability of favorable habitat components was accomplished at the feeding area level. However, the selective response to patchiness and variability extended to scales well beyond the dimensions of a feeding area, suggesting that behavioural levels may not adequately represent spatial scales. Habitat selection was stronger at successively finer levels, permitting a hierarchical

interpretation of behaviour. Among habitat variables, however, the scale domains of selection overlapped greatly, suggesting only weak hierarchical constraint. I suggest that caribou selected for *Cladina* cover and soft, shallow snow to make a trade-off between the potentially limiting effects of forage abundance and accessibility.

Introduction

Ultimately, habitat selection is the response to the relative fitness costs and benefits of environments, an attempt to escape the effects of limiting factors. Proximately, selection is the behavioural response to environmental cues at which individuals have the ability to perceive and respond to their environment (Hildén 1965, Hutto 1985). Habitat selection therefore depends on the range of scales perceived by organisms. By contrast, habitat use occurs at all scales and may not relate to animals' perception of habitat. An animal feeding on the leaves of a plant is simultaneously using that plant part, individual plant, plant patch, vegetation community, landscape, population range, species range, and so on, but may be selecting (i.e. using disproportionately to availability) at only one or several of those levels. Scale, therefore, is an intrinsic property of habitat selection.

Because studies of habitat selection conducted at only one scale often miss associations with habitat, and associations with habitat vary with scale (Schneider et al. 1987), habitat selection is now commonly assessed at multiple levels simultaneously. But such levels are usually chosen arbitrarily by the researcher and so may fail to represent selection from the perspective of the organisms (Wiens 1976, Thompson & McGarigal 2002). To identify selection from the organisms' perspective I investigated

the response to habitat along a spatial continuum, allowing the response of caribou to define the scale domains of selection.

Patchiness prevails in the environment (Kotliar & Wiens 1990), and this spatial structure should shape how organisms respond to habitat. For instance, animals should select habitat at scales at which the effects of limiting factors can be escaped most easily, such as by targeting resources at the dominant scales of patchiness. In this study, I begin by noting that when animals consistently select or avoid particular habitat components, selected habitats will be less variable in these habitat components than the available environment. I use variogram and coarse-graining analyses to test the prediction of habitat selection as a reduction in variance and a response to patchiness. These tools are prevalent as descriptors of pattern, but they have not yet been used to directly assess the process of habitat selection.

Multi-scaled habitat selection investigations usually employ a hierarchical framework (Johnson 1980, Senft et al. 1987), based on the assumption that selection at large scales constrains selection at small scales (O'Neill et al. 1989). Despite the widespread use of hierarchical procedures, the degree to which selection is constrained has generally not been tested (but see Poizat & Pont 1996). Alternatively, large-scale habitat selection patterns may result from smaller-scale decisions. For a given habitat component, I assess the degree to which selection is hierarchically constrained by the difference in selection among multiple levels of behaviour. I infer constraint when selection (assessed as a reduction in variance) occurs cumulatively at progressively finer levels, and reject the conclusion of hierarchy when selection is accomplished at a single level, such that variance is comparable between levels of habitat use. Various habitat

components may also be selected at different hierarchical scales, and I suggest that this constraint can be assessed as the discrete separation of scale domains (*sensu* Wiens 1989) at which selection occurs for different components. Constraint is inferred when scales of selection among habitat components are distinctly ordered, but when selection occurs within the same range of scales, hierarchy among components is rejected. Both within and among habitat components, testing the degree of constraint is valuable because it suggests differential importance among scales.

Scale-dependent habitat selection may result because the fitness costs and benefits of various habitat components vary with scale (Morris 1992). Individuals should strive to overcome factors limiting their fitness in the order of their importance. Rettie & Messier (2000) hypothesized that the importance of various limiting factors should be reflected by the coarseness of the scale at which individuals select habitat to reduce the effects of those factors. Thus the hierarchy of selection should reveal the hierarchy of limiting factors. Beyond this, I hypothesize that the relative importance of scales in overcoming the effects of limiting factors should be indicated by the degree of selection (difference in variance among levels) at those scales.

I test these predictions by applying new methods for detecting the degree and scale domains of habitat selection along a continuum of spatial scales to infer the role of structural habitat components in limiting a population of caribou (*Rangifer tarandus caribou*) in Newfoundland, Canada. Caribou are an ideal species for this investigation because their selection of habitat is easily observable as craters dug in the snow. Caribou are also a species of great interest for conservation and management in Newfoundland and Canada in general. Factors limiting caribou potentially include predation (Bergerud

1974, Rettie & Messier 2000), insect harassment (Walsh et al. 1992), disease (Lankester

& Fong 1998), snow conditions (Pruitt 1959, LaPerriere & Lent 1977, Adamczewski et

al. 1988), and food (Pruitt 1959, Bergerud 1972), notably *Cladina* lichens. Much work

on caribou has used coarsely scaled data produced by radio collars, and emphasized

predation pressure and broad habitat types (Rettie & Messier 2000, McLoughlin et al.

2005); I use fine-grained data emphasizing structural microhabitat selected directly by

caribou. I quantify habitat selection as a reduction of variability in key habitat

components in selected sites relative to those of the general environment and apply

descriptors of habitat heterogeneity at four levels of behaviour, from feeding microsites

to the population's winter range, across a continuum of spatial scales.

Methods

Data collection

I conducted field research in the winter range of the Middle Ridge caribou herd (47°55'N,

54°40'W; Mahoney 2000), in the maritime barrens ecoregion of east-central

Newfoundland, Canada (Meades & Moores 1989). The study area covered ca 600 km^2

and was characterized by poor soils and frequent ponds, bogs, low (ca 20 m high) hills,

and occasional rocky ridges. The winter range was characterized by generally low snow

cover (average depth across the study area was 26.6 cm).

I located caribou or their sign by searching on foot or by snowmobile from 3

February to 18 March 2005. Caribou dig craters in snow to gain access to food and these

were generally aggregated as feeding areas which in turn were connected by travel routes

and dispersed throughout the herd's winter range. I followed Schaefer & Messier (1995)

and assessed the structural habitat components at four hierarchical levels of behaviour: winter range (general environment sampled with systematic transects), travel routes (paths used by multiple caribou), feeding areas (aggregations of feeding microsites), and craters (feeding microsites identified by disturbed snow and plant or lichen debris).

At each sampling site, I measured nival conditions including snow depth and snow hardness using a ram penetrometer (a weighted hammer on a graduated guide-rod), and marked the locations. Because I could not assess lichen or other forage at the time caribou actually foraged, I assessed vegetation and soil characteristics at each site following regional snowmelt (25 May 2005 – 22 June 2005). Sampled characteristics included soil depth, measured with a graduated rod, and percent cover of herbs, lichens, mosses, shrubs, and graminoids within a 0.5 x 0.5 m quadrat. Herbs and shrubs were typically identified to the species level, lichens typically to genus; graminoids and mosses were treated as separate groups. I recorded percent cover as absent, 0-1%, 1-5%, 5-10%, 10-25%, 25-50%, or 50-100%. I used the midpoint of each class was used in statistical analyses. For craters, the crater area (mean = 0.41 m^2, SD = 0.48, n = 548) reasonably matched my choice of quadrat size and I used that measurement rather than cover within quadrats.

Winter range. Within the winter range of the Middle Ridge caribou herd, I established six linear transects, each 870 m in length with a northerly orientation and separated by five km. I employed a variable sampling step (0, 10, 30, 70, 200, 210, 230, 270, 400, 410 … 870 m) and at each step planted stakes, recorded coordinates by a handheld Global Positioning System (GPS; Garmin GPS III Plus), and took measurements at four sites (centre, plus 5 m west, south, and east of centre) for a total of

80 measurement sites along each transect. Varying the sampling step allowed me to

efficiently obtain data at sites a wide variety of distances apart and over a broad spatial

extent. For each site, I measured nival conditions two to three times throughout the

winter and averaged. There were no substantial temporal trends in snow cover during the

study. For non-nival variables, I established four additional east-oriented transects (with

sites at step center, plus 5 m north, west, and south).

Travel routes. I defined travel routes 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 travel route sites were recorded from

measurements taken at the nearest major point of convergence. I used a flagged nail and

GPS coordinates to mark the sites for later revisit.

Feeding areas. Across the landscape, craters were clearly clustered into feeding

areas. I defined feeding areas as a continuous aggregation of craters with the next nearest

crater by 50 m or more. For each feeding area, I established a transect connecting the

two most distant craters in the feeding area. As feeding areas were usually elliptical in

shape, this diameter typically bisected the primary feeding part of the area. I sampled the

centre of the closest clearly undisturbed site to a variable sampling step (0, 50, 70, 75,

125, 145, 150 m ...) along the transect from the edge of the feeding area, marked each

site with a nail, and recorded the GPS coordinates. I approximated the mean area of a

feeding area as half the squared transect length.

Craters. I defined craters as continuous areas of disturbed snow within which

caribou had fed, usually with scattered lichen or plant debris. Because the snow was

disturbed, I sampled undisturbed snow at the nearest point to the crater margin where

snow depth was equivalent to crater depth. Along the transect of greatest diameter of

each feeding area, I sampled the nearest clearly defined craters separated by a

systematically variable sampling step (0, 30, 45, 50, 55, 70, 100, 130, 145 m...)

beginning and ending with the first and last crater of the feeding area, respectively. I

marked each crater with 3 to 10 nails and recorded the GPS coordinates.

Data analysis

Principal components analysis. The multivariate environmental data were reduced to a

smaller number of components accounting for a large percentage of the variation by

performing Principal Components Analysis (PCA) of a correlation matrix using SPSS

(ver 14.0; SPSS Inc., 2005). Because PCA using a correlation matrix tends to be

sensitive to variables that occur infrequently, those not present in at least 10% of sampled

locations were excluded.

Hierarchical habitat analysis. To make general comparisons of habitat

components among the four behavioural levels (winter range to craters), I performed a

hierarchical analysis of variance (ANOVA) to determine the mean values across samples

at each level independently (PROC GENMOD, SAS ver 9.1; SAS Institute, 2003). I

assessed the significance between the means of each level at $\alpha = 0.05$.

Variograms. I constructed variograms to assess variability of each habitat

component in relation to separation distance within each behavioural level. Variograms

are widely used to assess environmental pattern (e.g. Webster & Oliver 2001), but I apply

them here to habitat selection by comparing variability at each of four levels of habitat

use. For each level, I plotted the empirical semivariance (γ) in sample sites over 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 half the sum of the squared difference between pairs (Matheron

1960) and I calculated it 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 x at the sampling location 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 *semi*variance) because the summation from 1 to n sampling

locations considers each pair twice in the calculation. I excluded lags where at least 30

pairs were not present.

Coarse graining. To quantify the spatial patchiness, or pattern intensity, of the

observed habitat components I analysed variability as a function of analysis detail (grain).

The absence of continuous data precluded the use of spectral analysis (Platt & Denman

1975) as recommended by Ripley (1978), so I used blocked quadrat variance (BQV)

following Greig-Smith (1952). I calculated BQV by delineating the study area into a grid

of contiguous units and then hierarchically grouped adjacent quadrats into blocks

doubling in size with each increment. Blocks in each progressively coarser delineation

were twice as large, and therefore half as numerous. I then applied a separate

hierarchical ANOVA (PROC GLM, SAS ver 9.1; SAS Institute, 2003) with each block size

as a nested level. I repeated this analysis at each behavioural level and interpreted peaks

in BQV as estimates of characteristic patch sizes.

Results

For the Middle Ridge herd, 16.0% of variation in the habitat data was explained by a moisture gradient (PC 1) with abundant *Cladina* spp. in drier sites and mosses and graminoids in sites with more frequent standing water (Figure 3.1). An additional 10.8% of the variation was explained by a gradient in snow depth and ericaceous shrubs (PC 2). Deeper snow was correlated with increased shrub cover, whereas *Empetrum nigrum* and non-abundant lichens (e.g. *Cladonia spp.*) were correlated with shallower snow, generally in exposed areas (Figure 3.1).

Caribou selected habitat at multiple hierarchical levels. At increasingly finer levels of behaviour, sampled sites were more similar and grouped as distinct nested subsets of available habitat at broader levels (Figure 3.2). Caribou selected sites with more *Cladina*, shallower snow, and less shrub cover in comparison to feeding areas. Similarly, sites measured at feeding areas relative to travel routes and winter range sites were richer in *Cladina* and had shallower snow (Figure 3.2).

Measurements of structural habitat components depended on the behavioural level (Table 3.1). Generally, means of variables favored by caribou were higher at finer behavioural levels. Significant differences between crater and winter range sites were evident for most variables. When comparing mean values in craters to those at other behavioural levels, broader levels showed an increasing number of variables that were significantly different.

Cover of *Cladina spp.* was significantly greater within feeding areas than along travel routes or in the available winter range (Table 3.1). Sites used by caribou were less

variable in cover of *Cladina* than those in the environment, but this difference depended on the separation distance between sites (Figure 3.3a). Percent cover of *Cladina* spp. was more similar in craters than in winter range sites at distances between pairs of 12 km and shorter, and this difference increased progressively at shorter lags. The variability of sites in feeding areas was nearly as low as that of craters at separation distances shorter than 12 km, but the variability of travel routes was similar to that of the winter range at shorter lags and more variable at longer lags. The blocked quadrat variance in *Cladina* spp. cover increased with coarseness of analysis to a plateau at areas 1 ha and greater (Figure 3.4a). Variance in craters also increased with scale, but more gradually. The difference between *Cladina* cover in craters and that across the winter range was greatest at the scales of greatest patchiness. No characteristic patch sizes of *Cladina* existed in craters.

Snow was significantly softer and shallower in craters than in feeding areas, and in feeding areas than on travel routes or the winter range (Table 3.1). Caribou selected shallower, softer snow at all scales examined (Figures 3.3b, c, 3.4b, c). Both the semivariance and blocked quadrat variance in snow depth and hardness were lower in craters than winter range sites at almost all scales. Use of shallow snow at the feeding area level accounted for selective reduction in variability at lags of at least 13 km, and additional selection occurred at the crater level across shorter lags (Figure 3.3b). The difference in variability in snow depth between craters and winter range sites decreased with lag distance. Snow depth in the winter range exhibited a characteristic patch size of about 33 ha, but selected sites at the travel route, feeding area, and crater levels showed no characteristic patch size but instead displayed trends of gradually increasing BQV

(Figure 3.4b). The BQV tended to decrease at the finer behavioural levels of feeding areas and craters.

For snow hardness, craters were consistently lower in semivariance than winter range sites across all separation distances (Figure 3.3c). Variability in snow hardness at the feeding area level decreased with increasing lag, and was lower than that of the winter range only at lags above 14 km. Variability in snow hardness along travel routes was greater than that sampled at the winter range level. BQV in snow hardness increased gradually with coarseness of delineation, with variance at coarser behavioural levels generally higher than at finer scales (Figure 3.4c).

Graminoids were correlated with hard snow conditions (Figure 3.1). Caribou avoid hard snow and thus appear to avoid graminoids at the levels of feeding areas and craters, regardless of spatial scales. I observed lower cover of graminoids in craters and feeding area sites than in travel route and winter range sites (Table 3.1). The variability in graminoids was also lower in selected sites than in those available across all lags and block sizes (Figures 3.3e, 3.4e). The semivariance of graminoid cover in the winter range increased with separation distance, but in craters was constant across scales, and the difference in semivariance between used and available sites therefore increased four-fold from the shortest to longest lags (Figure 3.3e). Variability in graminoid cover was lower in feeding areas than in craters at lag distances below 14 km and between that of craters and winter range sites at longer lags. The variance of graminoids increased with coarseness of analysis, with no characteristic patch size. It was consistently lower in craters than in winter range sites, but was lowest in feeding area sites (Figure 3.4e).

Although there was greater cover of *Kalmia* in selected sites than in those
available (Table 3.1), higher variability of *Kalmia* in selected sites indicates that it was
avoided. The variability in *Kalmia* was higher at all other behavioural levels relative to
the winter range across all lag distances (Figure 3.3d). This discrepancy increased at
pairwise distances above 18 km for each of the three sampling levels. Variance in
Kalmia spp. cover showed a characteristic patch size of about 1.3 km^2, as judged by a
maximum at this scale (Figure 3.4d). Unlike selected habitat components (*Cladina,*
shallow snow), variance in *Kalmia* spp. at finer behavioural scales was higher than at the
winter range level.

Discussion

Habitat selection is a multi-scaled phenomenon (Johnson 1980). The habitat components
selected by Middle Ridge caribou generally depended on the hierarchical level of
behaviour and spatial scale. Some habitat components, such as shallow snow, were
selected across all scales (Figures 3.3b, 3.4b). Habitat selection may also be viewed as a
behavioural process to reduce the effects of limiting factors (Rettie & Messier 2000). My
results support several studies (Pruitt 1959, Adamczewski et al. 1988, Schaefer and Pruitt
1991) that showed that lichens and snow conditions can be limiting factors for caribou. I
observed increased selective behaviour for *Cladina* and snow depth below a threshold of
about 13 km, and habitat selection was most prominent at the level of the feeding area.
My results confirm the importance of spatial scale in habitat selection studies. Increased
selective behaviour at characteristic scales of patchiness suggests heterogeneity may be
an underlying driver of multi-scaled habitat selection.

Species perceive and interact with their environments at different scales and in unique ways (Manning et al. 2004). Accordingly, predetermining discrete scales of analysis risks subjectivity (Johnson et al. 2002b), and detection of habitat selection depends on the scales at which data are collected and analysed (Schneider et al. 1987). To understand habitat selection from the perspective of organisms rather than merely of the researcher, the scales of research should therefore encompass the scales at which habitat selection is occurring. Without prior knowledge of the scales of selection, I let the organisms define the scales at which they respond to the environment from a continuum of scales. I strived to represent a caribou's-eye-view by describing the spatial structure of habitat selection using an objective set of behavioural levels, from crater to winter range.

My results largely supported my prediction that consistently selected habitat components would tend to exhibit reduced variance at the levels of selection. For instance, both semivariance and blocked quadrat variance were reduced at the crater and feeding area levels for *Cladina* and snow depth (Figures 3.3a, b, 3.4a, b), which exhibited significantly different means (Table 3.1). Habitat characteristics tended to not be selected at the travel route level, evidenced by non-significant differences in means relative to the available winter range and trends in variability and patchiness that were not easily distinguishable from the winter range.

The lags over which variance is reduced might provide additional biological information. For example, caribou responded to *Cladina* (as evidenced by a reduction in semivariance among selected sites) at lag distances up to 13 km, responded to snow depth at the crater level more than the feeding area level at lag distances up 12 km, and

responded to graminoids at the feeding area level more strongly than at the crater level at lag distances below 14 km (Figure 3.3e). Intriguingly, these distances are comparable to caribou responses to landscape disturbances. For instance, females of the Middle Ridge herd responded to areas disturbed by clearcut logging at distances of about 9 km (Schaefer & Mahoney 2006), woodland caribou in Ontario maintained at least a 12 km distance to disturbance (Vors 2006), and maternal wild reindeer in Norway (*Rangifer tarandus tarandus*) avoided a 10 km zone around a tourist resort (Nellemann 2000). I suggest that the correspondence among these response distances, reiterated by my variograms of winter habitat selection, may be the outcome of an effective perceptual range of *R. t. caribou*. Based on this consistency among studies, I recommend that conservation initiatives consider a buffer of at least 13 km beyond locations expected to be used by caribou.

Habitat selection at the feeding area level accounted for much of the response to the spatial structure of the environment (Figures 3.3, 3.4). *Cladina* is the most important winter food resource for Middle Ridge caribou (Mahoney 2000), and acquisition of these lichens appeared to occur by selecting feeding areas richer (Table 3.1), less variable (Figure 3.3a), and less patchy (Figure 3.4a) in *Cladina*. Additional selection occurred for craters consistently higher in *Cladina* (Figure 3.3a). However, the selection of *Cladina* occurred at spatial scales well beyond the dimensions of craters or feeding areas. While feeding areas had a maximum diameter of on average only 134 m, caribou responded to the variability in *Cladina* cover at lags up to 13 km (Figure 3.3a). Up to this distance, selected sites were more similar to each other than those available. Similarly, I estimated feeding areas to be on average 0.90 ha in size, corresponding to the scale above which

patchiness of *Cladina* cover was greatest, but *Cladina* in sites selected by caribou was less patchy even at much coarser grains (Figure 3.4a). In addition, I found that relative to the winter range sites, feeding area sites and craters had shallower, more similar snow depths, more similar but less cover of graminoids, and greater but more variable cover of *Kalmia*, and that these responses were evident across all spatial scales. Behaviour at the feeding area level was crucial to habitat selection, an observation that without an understanding of the spatial structure of habitat selection, might have led me to assume that the size of feeding areas was the chief scale of selection for this herd. In fact, habitat selection occurred over a much wider range of spatial scales, evidenced by reduced variability and patchiness in selected sites.

Habitat selection is a behavioural response not only to favored habitat components but the heterogeneous distribution of these components (Brown 2000, Stewart et al. 2000, Kie et al. 2002). The scale-dependence of habitat selection may result from the multi-scaled patch structure of habitat components. The way animals respond to patchy resources depends on the dominant scales of patchiness and the degree to which patchiness is perceived. Caribou typically responded to habitat components most at the dominant scales of patchiness, while often responding across a wide range of spatial scales (Figure 3.4). Snow depth was patchiest at a grain of 33 ha, whereas *Cladina* was patchiest at scales of 1 ha to the extent of the winter range. The greatest response to *Cladina* was at the smallest scales of substantial patchiness, namely about 1 ha. Because the importance of habitat structure can vary across scales (Turner et al. 1997, Krawchuk & Taylor 2003), heterogeneity may be the underlying cause of multi-scaled habitat selection.

I found that evaluating habitat selection as a reduction in variance can differentiate between selection for favoured habitat components and correlated but non-favoured components. Favoured habitat components should be more frequent and less variable in selected sites. In selected sites, *Kalmia* cover was higher (Table 3.1) but more variable (Figures 3.3d, 3.4d), and graminoid cover was lower (Table 3.1) but less variable (Figures 3.3e, 3.4e), patterns I interpreted as avoidance. Although Bergerud (1974) suggested that *Kalmia* and other shrubs help caribou detect lichen by creating air passages through deep snow, the increased variability in *Kalmia* cover I observed in selected sites suggests that it may not be favoured in low snow conditions (as in this study), probably because its woody stems can physically hinder accessibility and facilitate locally deeper snow. While graminoids do form part of the herd's diet, graminoids were associated with low, moist areas with deeper snow and were thus avoided due to inaccessibility.

Hierarchical habitat selection and limiting factors

Habitat selection by caribou was scale-dependent and can be viewed as a hierarchical behavioural process (Johnson 1980, Senft et al. 1987, Schaefer & Messier 1995, Rettie & Messier 2000, Griffith et al. 2002, Johnson et al. 2002a), such that selection was stronger and more focussed at finer behavioural levels. Sites sampled at finer levels of behaviour grouped as distinct subsets nested within the available habitat at broader levels (Figure 3.2), similar to the findings of Burkhardt et al. (1998). Caribou responded to two major gradients of environmental variation (moisture and snow cover) by honing in on sites with favoured habitat components at each successively finer behavioural level (Figure

3.2). Cover of these components selected by caribou also depended on behavioural level, a finding consistent with coarser-scaled studies (Rettie & Messier 2000, Ihl & Klein 2001, Mosnier et al. 2003). Mean values were higher at finer behavioural levels for favoured habitat components and lower for non-favoured habitat components (Table 3.1). Furthermore, an increasing number of habitat components in craters were significantly different relative to broader behavioural levels.

The scales at which selection occurs for a variety of habitat components may yield valuable information regarding the relative importance of limiting factors. Individuals should seek to escape limiting factors in the order of their importance. Rettie & Messier (2000) suggested that the scale of selection to escape a limiting factor indicates the relative importance of that factor, because more important factors should be selected at large scales if larger scales constrain smaller scales. However, assessing the importance of limiting factors based on the scales of selection rests on the assumption that selection among factors is hierarchical. Hierarchical habitat selection implies that large-scale decisions constrain those at smaller scales (O'Neill et al. 1989). If such constraint exists among selection decisions, and if selection for different habitat components occurs at different scales, then selection for fine-scaled habitat components may also be constrained. In such cases, more important selection decisions should be made at coarser scales, as Rettie & Messier (2000) suggested. For example, caribou may make long distance movements to avoid predation pressure and make smaller-scale feeding decisions only within the selected range (Rettie & Messier 2000). Yet the degree of constraint between scales has not been adequately tested. Alternatively, small scale selection patterns may propagate to large scales (Wiens 1989), for example with many

small-scale feeding locations making up a larger home range. Thus, large-scale selection patterns may be either the outcome of or constraint on smaller-scale selection. Dussault et al. (2005) suggested that animals should make trade-offs between multiple limiting factors when their effects occur at the same scales. I suggest that constraint among habitat components can be identified by distinct and separate scale domains of selection for different components.

In contrast to the results of Rettie & Messier (2000) but in agreement with those of Dussault et al. (2005) for moose (*Alces alces*), caribou selected habitat components at overlapping scale domains. Between *Cladina* and snow depth, only the latter was selected at long lags (Figure 3.3). However, at shorter lags (<13 km) selection for both variables was evident. I found that caribou attempted to evade deep snow conditions at all scales, and that forage was selected at smaller scales (Figure 3.3a, b). The overlapping scale domains of these two habitat components suggest that selection for *Cladina* was constrained only to a limited degree. Otherwise selection for *Cladina* could not have occurred until caribou had escaped the limiting effects of snow cover. This implies weak hierarchical constraint among habitat components, and in turn, a weak hierarchy in the importance of limiting factors. In such cases of weak constraint, the differential importance of these in affecting fitness is less clear, because there are potential advantages to habitat selection at both large and small scales. At large scales, infrequent choices such as seasonal migrations can achieve escape from certain limiting factors (Rettie & Messier 2000). At small scales, decisions and movements are more frequent, but are energetically less costly (Senft et al. 1987). Thus, I suggest that the

order of importance of limiting factors does not necessarily generate an ordered linear sequence of scales of selection among limiting factors.

Caribou selected habitat to minimize the negative effects of snow depth, but as snow could not be completely avoided at any scale, caribou selected for lichen cover as well within consistently low snow areas. Woodland caribou traded-off forage abundance with accessibility, consistent with Johnson et al. (2001), and scale-dependent tradeoffs in foraging have also been documented in other ungulates (Mysterud et al. 1999, Dussault et al. 2005). Clearly, selection to overcome several factors affecting fitness can occur simultaneously. These results underline the important limiting effects of snow depth, even in a herd experiencing relatively shallow snow (mean = 26.6 cm across the winter range). Others, using coarse-scale radiotelemetry data, suggest predation as a limiting factor for woodland caribou (e.g. McLoughlin et al. 2005), the effects of which I could not measure with my microhabitat data. Studies conducted at different scales tend to focus on different habitat selection processes, so scale of analysis may be the key to distinguishing among the effects of multiple limiting factors, such as predation and snow cover.

Animals should attempt to reduce the impact of limiting factors at the scales at which their effects are most easily overcome. When large scale selection constrains selection at smaller scales, animals should also attempt to overcome more important limiting factors at the larger scales (Rettie & Messier 2000). When large scale constraint is weak (such as constraint on *Cladina* selection by larger scale snow selection) 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). The importance of a scale in reducing the effects of limiting factors is indicated

by the relative degree of selection across scales for a given habitat component. Selection

for *Cladina* increased at smaller scales, indicating that smaller scales were more

important in meeting food requirements than larger scales.

Conclusions

The caribou's-eye-view – the spatial structure of response by caribou – revealed wide

scaling domains of selection that depended on habitat component. Yet the measured

response pointed towards typical scales at which caribou of this herd may perceive their

environment. A shift in response occurred at a scale of about 13 km. Habitat selection at

the feeding area and crater levels was paramount. Patch areas of 1 ha to 1 km^2 played an

important role in foraging. Multi-scaled selection for *Cladina* and favourable snow

conditions underline the importance of accessible forage to caribou. I stress the

importance of the scales of habitat selection in overcoming limiting factors and

recommend that they be considered when planning conservation initiatives. Future

studies should strive to represent the perspective of organisms by considering the spatial

structure of behavioural responses to heterogeneous environments.

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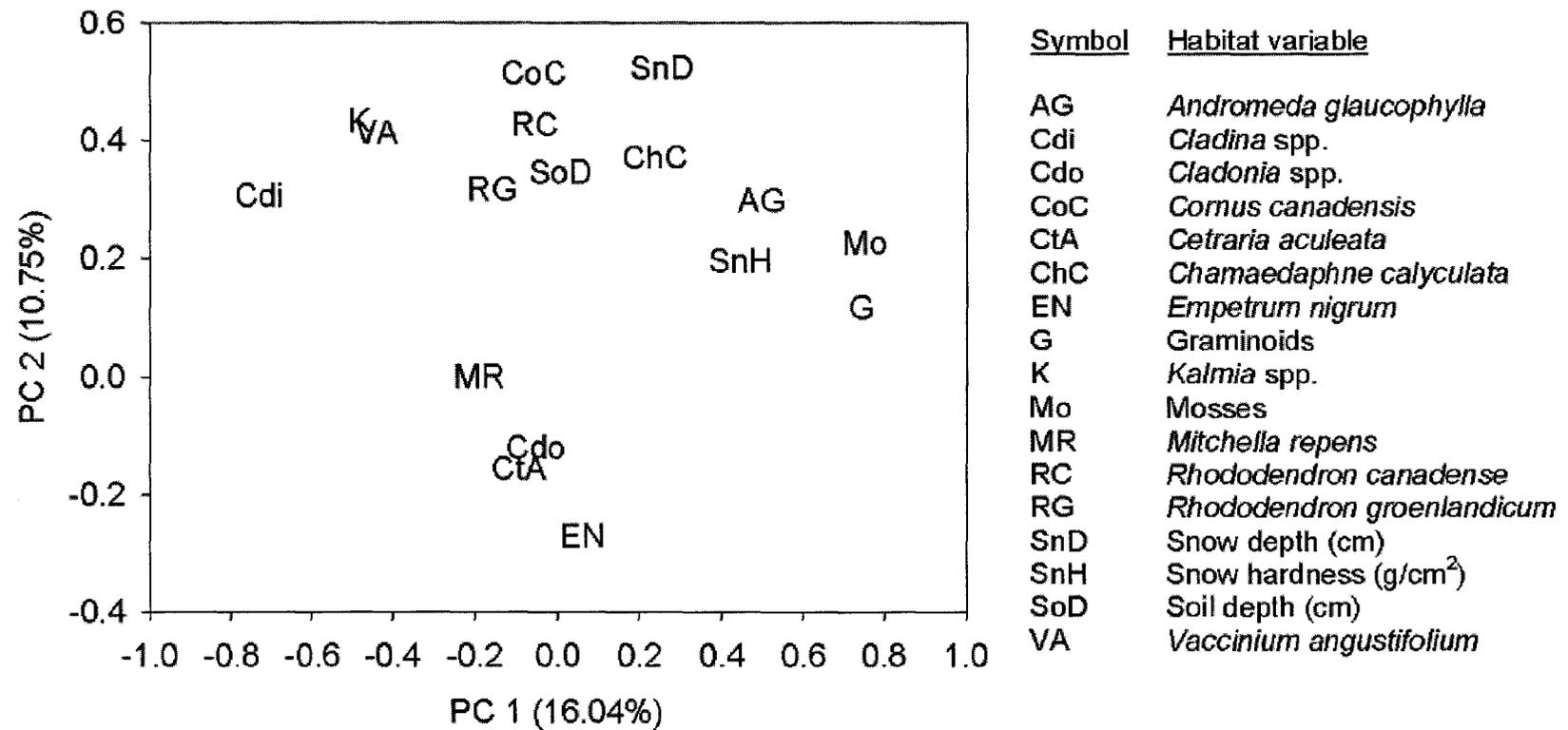
Figure 3.1: Principal components (PC) loadings plot. Percentages for each component indicate the percentage of variance explained by that axis. Variables were measured as percent cover unless specified.
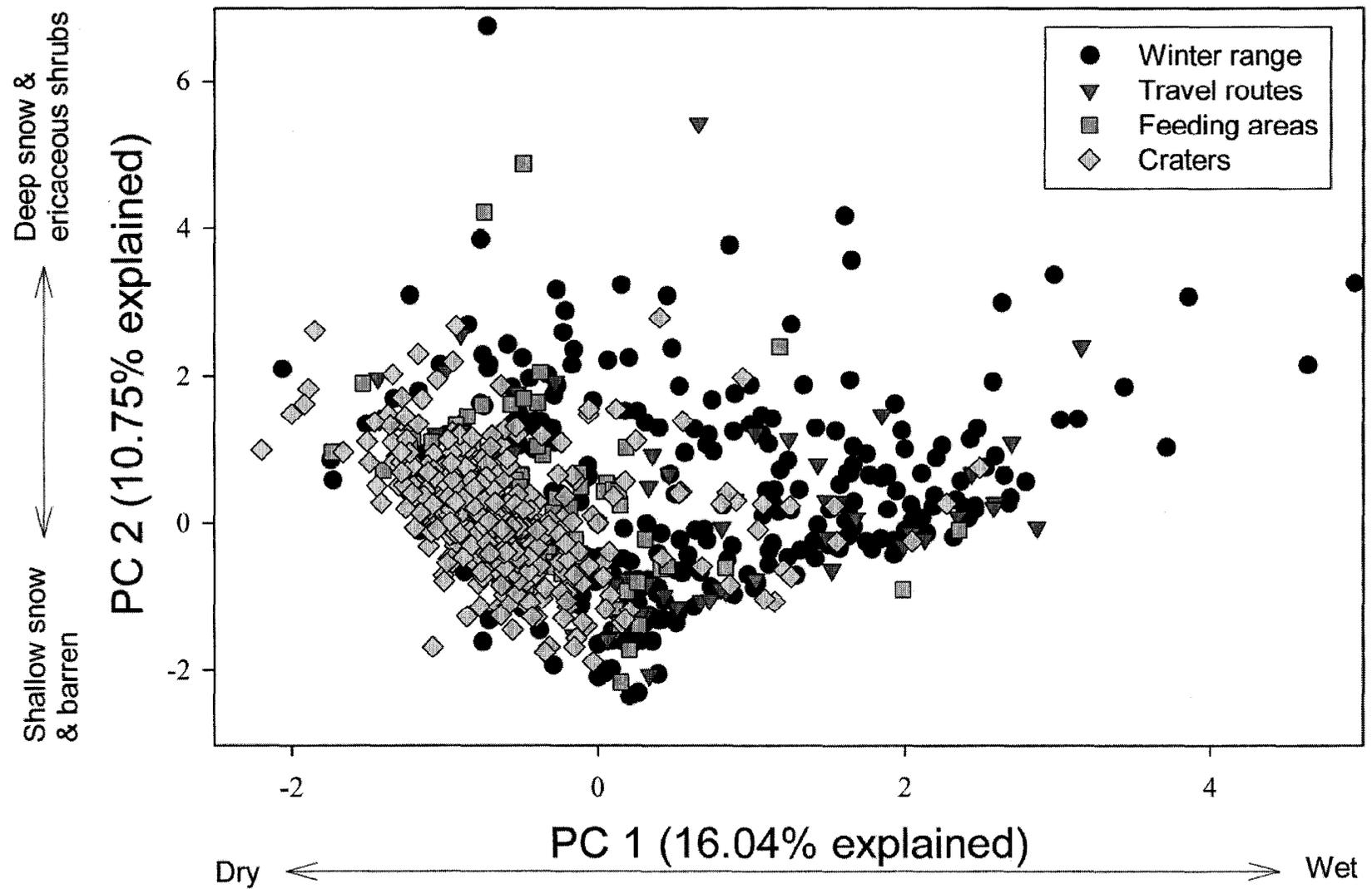
Figure 3.2: Principal component scores of sampling locations at four hierarchical levels of behaviour. The percentages indicate the percent of variance explained by each component. The environmental gradients were interpreted from Figure 3.1.

Table 3.1 : Mean habitat conditions across behavioural scales of selection for caribou in Newfoundland. Significant differences between behavioural scales (Cr = Crater, FA = Feeding Area, TR = Travel Route, WR = Winter Range) are indicated in bold (α < 0.05). Units are in percent cover unless otherwise stated.

|	Mean				p-value					
	Crater	Feeding Area	Travel Route	Winter Range	Cr - FA	Cr - TR	Cr - WR	FA - TR	FA - WR	TR - WR
Soil depth (cm)	42.81	31.69	32.04	33.00	**<0.001**	**<0.001**	**<0.001**	0.920	0.555	0.739
Snow depth (cm)	14.29	20.72	32.33	26.59	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.002**	**0.012**
Snow hardness (g/cm^2)	7.49	19.60	37.17	26.57	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.004**	**<0.001**
Andromeda glaucophylla	0.15	0.38	1.29	1.42	0.479	**0.004**	**<0.001**	0.055	**0.001**	0.743
Cetraria aculeata	1.32	1.13	0.94	0.67	0.653	0.486	**0.005**	0.779	0.287	0.612
Chamaedaphne calyculata	1.70	2.52	4.01	1.87	0.164	**0.002**	0.590	0.091	0.263	**0.003**
Cladina spp.	63.68	58.06	22.35	25.57	0.072	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.405
Cladonia spp.	2.15	1.09	1.38	1.68	0.097	0.339	0.168	0.757	0.346	0.708
Cornus canadensis	0.96	1.46	2.16	2.71	0.428	0.124	**<0.001**	0.451	**0.040**	0.473
Empetrum nigrum	2.28	3.53	6.30	3.83	0.369	**0.020**	**0.035**	0.182	0.824	0.150
Graminoids	2.46	1.94	19.83	12.97	0.807	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.009**
Kalmia spp.	19.14	23.38	11.01	8.44	0.051	**0.003**	**<0.001**	**<0.001**	**<0.001**	0.340
Mitchella repens	1.09	0.34	0.18	0.67	**0.032**	**0.039**	**0.025**	0.774	0.333	0.263
Mosses	4.03	5.02	27.98	19.15	0.705	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.006**
Rhododendron canadense	0.99	2.06	0.83	1.39	0.084	0.825	0.228	0.182	0.269	0.460
Rhododendron groenlandicum	3.76	5.15	2.18	2.81	0.113	0.150	**0.041**	**0.024**	**0.007**	0.562
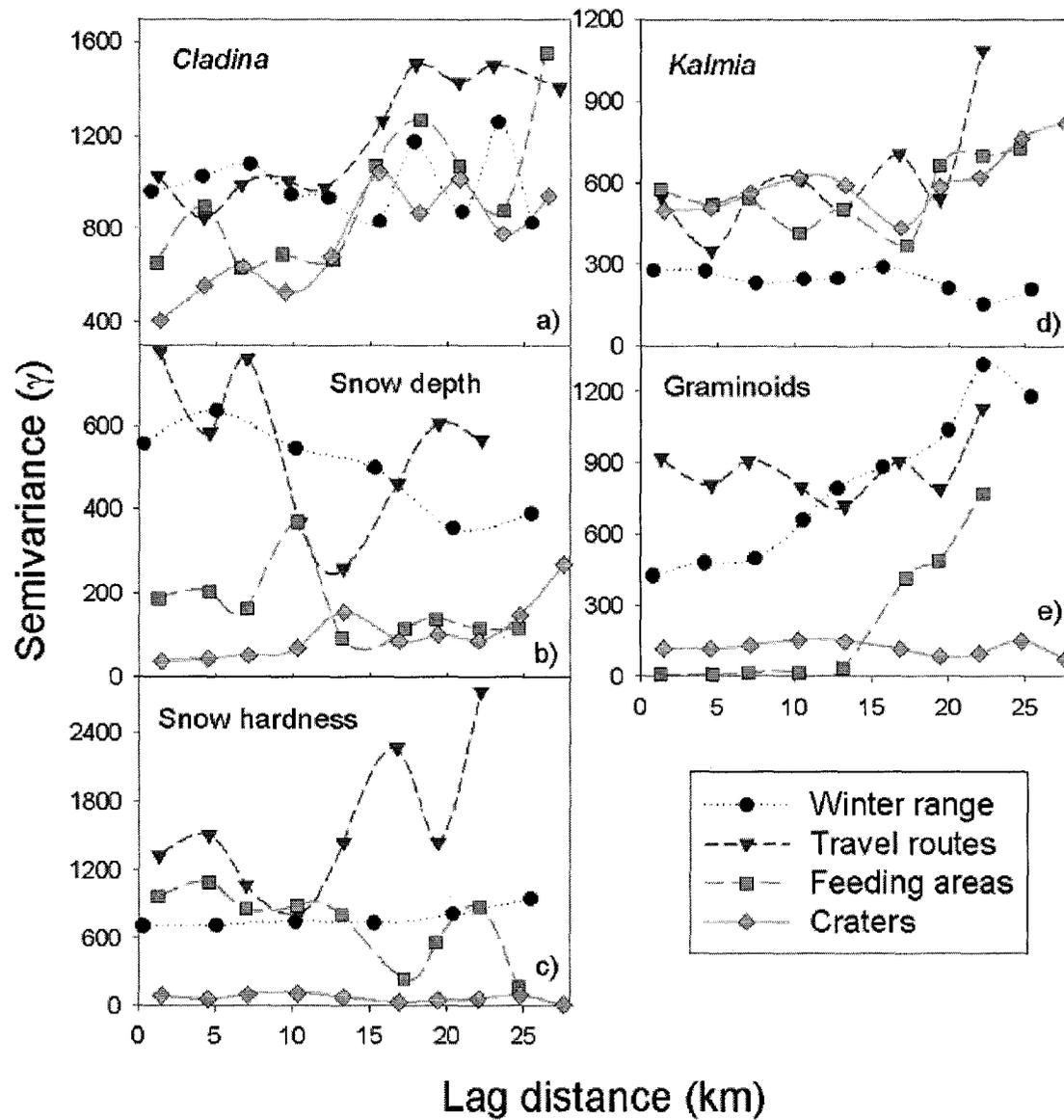
Figure 3.3: Semivariance in a) percent cover of *Cladina* spp., b) snow depth (cm), c) snow hardness (g/cm2), d) percent cover of *Kalmia* spp., e) percent cover of graminoids in relation to lag distance between sample pairs. Each panel shows four variograms, each representing a behavioural level at which habitat use was sampled. Habitat selection was interpreted as a reduction in semivariance at one behavioural level relative to the winter range level.
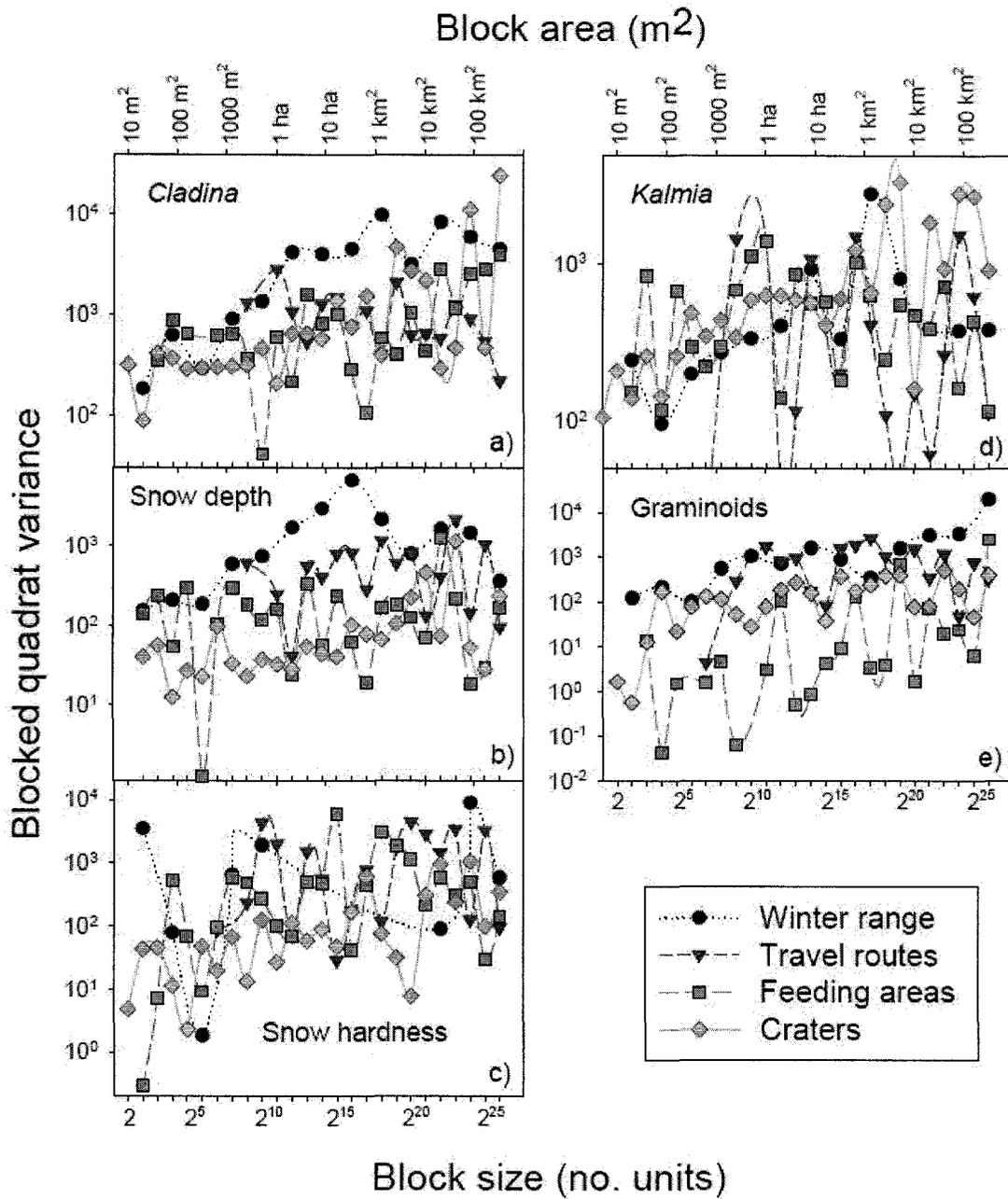
Figure 3.4: Blocked quadrat variance (BQV) of a) percent cover of *Cladina* spp., b) snow depth (cm), c) snow hardness (g/cm2), d) percent cover of *Kalmia* spp., e) percent cover of graminoids in relation to block size (number of units in each block) and block area. Each panel shows four trends, each representing a behavioural level at whch habitat use was sampled. Habitat selection was interpreted as a reduction in variance at one behavioural level relative to the winter range level.

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CHAPTER 4:

SUMMARY AND CONCLUSIONS

Conservation and management implications

Management of wildlife generally entails management of habitat. Habitat management,

in turn, presumes an understanding of the needs of species. These needs will be shaped

by fitness, which should be higher for populations in habitats that the species tends to

select. Habitat selection research is therefore an important component of the

management of wildlife populations.

Caribou selected favourable snow conditions across all spatial scales examined,

while selecting *Cladina* only at smaller scales. Snow depth averaged 26.6 cm and snow

hardness averaged 26.6 g/cm^2 across the winter range, and caribou dug craters in snow

with an average depth of 14.3 and hardness of 7.5 g/cm^2 – much lower than snow

conditions in habitats used by other caribou herds. For example, Brown & Theberge

(1990) reported caribou feeding in snow depths up to 125 cm and hardness values > 50

000 g/cm^2, though these are extreme and most caribou herds in the taiga are thought to

dig craters in snow of depth <60 cm and hardness <50 g/cm^2 (Miller 2003). The strong

selection for soft, shallow snow across all scales suggests that caribou cannot overcome

the negative effects of snow on food accessibility at any scale considered in this study.

Snow cover was a driving force behind habitat selection behaviour even at low snow

depths. Low snow areas tended to occur on hill tops, which also tended to display

abundant *Cladina* lichens and likely aided detection of predators. The extant predators of

Middle Ridge caribou include (black bears (*Ursus americanus*), coyotes (*Canis latrans*),

lynx (*Lynx canadensis*), and bald eagles (*Haliaeetus leucocephalus*), but (unlike for most populations of caribou) not wolves (*Canis lupus*; Mahoney & Virgl 2003). Greater research is needed to understand the effects of coyotes on winter habitat selection by caribou, where they are a newly introduced predator and active year-round.

Caribou responded most strongly to the environment at lags under 13 km, a response distance consistent with reports from other studies of caribou and reindeer (Nellemann et al. 2000, Schaefer & Mahoney 2006, Vors 2006). The 13 km range may be a function of the perceptual range (or ecological neighbourhood) at which caribou are sensitive to habitat, underscoring the need to investigate habitat selection from the organisms' perspective. The perceptual range is likely influenced by the sensory capacity, knowledge of the environment, as well as body size and inherent vagility of caribou (Mech & Zollner 2002). I recommend that conservation and management initiatives consider a buffer zone of at least 13 km from locations expected to be used. This stands in stark contrast to conventional habitat management for caribou – often at much finer scales, such as forest stands and buffers of 1000 m or less. I also suggest that future studies of caribou habitat selection that are unable to employ a continuum of multiple spatial scales in analyses consider using a scale of availability of up to 13 km. This response range suggests that caribou interact with the environment at much larger scales than might be concluded from traditional hierarchical habitat studies (e.g. feeding areas of diameter 134 m). Thus, anthropogenic disturbance in areas even beyond used habitats could affect caribou habitat selection by altering their perception of available habitat.

Caribou respond to heterogeneity at all scales – it is a fundamental pattern which facilitates habitat selection. Caribou habitat selection occurred most strongly at scales of high patchiness. Heterogeneity in habitat variables is likely generated by heterogeneous abiotic factors such as topography, soil conditions, and moisture, as well as biotic processes such as competition and dispersal of other species in the community (Stewart et al. 2000). Habitat heterogeneity should be conserved where possible, and functions of ecosystems which generate heterogeneity, such as natural disturbances, should be permitted to occur in moderation (Schaefer & Pruitt 1991).

Conclusions and future directions

In this thesis, I brought together two separate bodies 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. Habitat selection is increasingly recognised as a multi-scaled spatial phenomenon and spatial and geostatistical analyses are integrated into ecological methodology (Rossi et al. 1992, Dale 1999). I united the two with the observation that when animals consistently select good (or avoid bad) habitat, the variance of favoured habitat components in used sites is reduced. By comparing the spatial structure of habitat components in used and available sites (at several levels of behaviour), I step from patterns of spatial variability in the environment to a behavioural process in response to those patterns. I move from the spatial structure of habitat to the spatial structure of habitat selection.

I demonstrated the analysis of habitat selection as a reduction in variance along a continuum of spatial scales, and identified the behavioural levels at which selection was accomplished. Caribou selected habitat such that the variance of habitat components in selected sites was reduced, a result that emphasizes that animals are not only affected by total abundance of resources, but also the spatial pattern of resources (Wiens 1989). The accessibility of forage (indicated by snow conditions) drove selection at coarse scales but caribou made a trade-off between accessibility and abundance of the herd's primary winter forage (*Cladina* lichens) at finer scales. Selection for different habitat components can therefore occur simultaneously and the scale domains of selection for different habitat components can overlap (Dussault et al. 2005). Selection among habitat variables cannot be assumed to occur hierarchically, but if it does, the coarseness of the scale of selection can indicate the relative importance of habitat variables in escaping the effects of limiting factors (Rettie & Messier 2000). With only weak constraint, as I found in this study, the coarseness of the scales of selection may be influenced by other factors, such as the scales of patchiness of resources. The response to habitat was greatest at dominant scales of patchiness, implicating habitat heterogeneity as an underlying cause of multi-scaled habitat selection. A better understanding of the generation and maintenance of heterogeneity of caribou habitat is needed.

Caribou responded to the spatial structure of their habitat more strongly at scales under 13 km. This distance may be a function of the perceptual range of caribou, and the finding, along with the observation that habitat selection varied in degree across scales, suggests that scales of habitat selection vary in importance. More research is needed to understand the causes of scaling thresholds and shifts in habitat selection (With & Crist

1995). Another important future direction of research would be to determine the scales of selection of other important members of the ecological community, such as predators, competitors, and forage species – information that could shed light on interspecific interactions and effects of environmental heterogeneity on community assembly (August 1983). This study was limited to the scale of a single herd's core winter range. To understand fully the scale-dependent phenomenon of habitat selection, similar investigations need to be conducted in all seasons, and at scales up to the extent of the species range.

Several recommendations emerge from my findings. First, behavioural and spatial 'scales' are not necessarily synonymous; multi-scaled habitat selection studies should specify the type of scale being used, and when possible utilize spatial scales to facilitate comparisons across studies and taxa. Second, researchers should consider habitat selection as a reduction in variance of habitat components, rather than correlations with habitat components, to avoid cross-scale correlations that can lead to misinterpretation of the relative strength of habitat selection among variables. Third, future studies should attempt to represent habitat selection from the perspective of organisms rather than the researcher.

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