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Research article

Quantifying patch distribution at multiple spatial scales: applications to wildlife-habitat models

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Abstract

Multiscale analyses are widely employed for wildlife-habitat studies. In most cases, however, each scale is considered discrete and little emphasis is placed on incorporating or measuring the responses of wildlife to resources across multiple scales. We modeled the responses of three Arctic wildlife species to vegetative resources distributed at two spatial scales: patches and collections of patches aggregated across a regional area. We defined a patch as a single or homogeneous collection of pixels representing 1 of 10 unique vegetation types. We employed a spatial pattern technique, three-term local quadrat variance, to quantify the distribution of patches at a larger regional scale. We used the distance at which the variance for each of 10 vegetation types peaked to define a moving window for calculating the density of patches. When measures of vegetation patch and density were applied to resource selection functions, the most parsimonious models for wolves and grizzly bears included covariates recorded at both scales. Seasonal resource selection by caribou was best described using a model consisting of only regional scale covariates. Our results suggest that for some species and environments simple patch-scale models may not capture the full range of spatial variation in resources to which wildlife may respond. For mobile animals that range across heterogeneous areas we recommend selection models that integrate resources occurring at a number of spatial scales. Patch density is a simple technique for representing such higher-order spatial patterns.

Introduction

Ecologists are beginning to develop an appreciation for the influences of spatial and temporal scale on ecological processes (Wiens 1989; Levin 1992; Dungan et al. 2002). Although we recognize that ecological phenomena vary in space and time, we struggle to identify the effects of that variation on the processes of interest. Wildlife ecologists are not immune to the challenges of scalar relationships, especially given the wide-ranging nature of many of their study species (Bergin 1992; Schaefer and Messier 1995; Saab 1999; Johnson et al. 2002a). Their goal is often an understanding of animal fitness as it relates to population productivity, but the complexity of the problem results in studies that address one or two scales of analysis assumed to correspond with some ecologically meaningful scale. Less typical are examples integrating behaviors across scales or attempts to delineate ecologically based breaks in scalar processes (Viswanathan et al. 1996; Johnson et al. 2002a).

A common objective for wildlife studies is the identification of important resources which may include specific diet items or, more generally, habitats which constitute the broad range of life requisites (Hall et al. 1997). For some study designs, a differential ratio of used to available resources suggests selection and importance of a particular resource. Recognizing that selection may vary according to the definition of availability, studies are conducted at several discrete spatial and temporal scales (McLoughlin et al. 2002). Researchers have looked to Johnson's (1980) hierarchical orders of selection to define those scales of analysis. Others have analyzed selection at a number of arbitrary scales searching for patterns or changes across scale (Apps et al. 2001).

Depending on species and environment and contingent on the correct definition of scale, resource selection studies conducted at a number of discrete orders or scales of selection can be more informative than single scale designs. However, understanding and inferences of multiscale studies are limited by several fundamental flaws in study design, analysis, and conceptualization of the underlying processes. First, it is assumed that animal movement and behavior is related to individual patches of resources as defined in a GIS. Researchers often ignore the fundamentals of landscape ecology and assume that patches of resources occur in isolation of other and like patches. For many systems, vegetation will scale in response to climate or topography, processes that may not influence the movements and behavior of the study species directly (McIntyre and Wiens 2000). The patch is likely only a representative resource unit across small homogenous study areas with little regional gradient in vegetation. Second, discrete multiscale resource selection analyses provide little empirical insight into the relative importance of habitats at each scale. Statistical tests, selection coefficients, and measures of precision allow one to infer selection or avoidance of habitats at each scale, but there is no means to compare the strength of selection across scales. With the exception of guiding hypotheses, managers are left to prioritize the management or conservation of resources identified at each scale (Rettie and Messier 2000). Such problems are especially apparent when selection coefficients are used to map areas for conservation emphasis (Mladenoff et al. 1995; Carroll et al. 2001). Third, there is good reason to question the ecological premise upon which most discrete multiscale resource selection studies are based. Such studies assume that selection is hierarchical and that one scale of selection is conditional upon another (Johnson 1980). This may be a necessary expectation for statistical tractability, but it fails to represent cross-scale linkages. In reality, it is unlikely that selection at any one scale is independent of any other (Huston 1999).

We developed and assessed resource selection models that integrated vegetation resources distributed at multiple spatial scales. As our working hypothesis, we expected wide-ranging species to select vegetative resources distributed as patches and collections of patches aggregated across regional areas. To explore that relationship, we evaluated vegetation types found across a 191 000-km^2 area of the Canadian central Arctic for multiple patterns or scales of distribution. We used measures of patch density to parameterize the distribution of vegetation available to Arctic wildlife at scales greater than the individual patch, which we defined as a single or homogeneous collection of pixels representing 1 of 10 unique vegetation types. We included variables for vegetation occurrence at the scales of the patch and region in resource selection models for barren-ground caribou (*Rangifer tarandus groenlandicus*), wolf (*Canis lupus*), and grizzly bear (*Ursus arctos*). For each species, we identified the most parsimonious resource selection model inclusive of covariates for vegetation parameterised at the scale of the patch, the region (i.e., patch density), and both the patch and region. Selection of the model including terms for vegetation distributed at the scale of the patch and region provided evidence supporting our working hypothesis.

Methods

Study area description

The study area was centred at Contwoyto Lake (65° 30′ N, 110° 30′ W) approximately 400 km northeast of Yellowknife, Northwest Territories, Canada and encompasses 191 000 km^2 of the Taiga Shield and Southern Arctic ecozones (ESWG 1996; Figure 1). Treeline, the absence of open stunted forests of black (*Picea mariana*) and white spruce (*P. glauca*), demarks the northern extent of the Taiga Shield. Permafrost, forest fires, and soil productivity dictate the

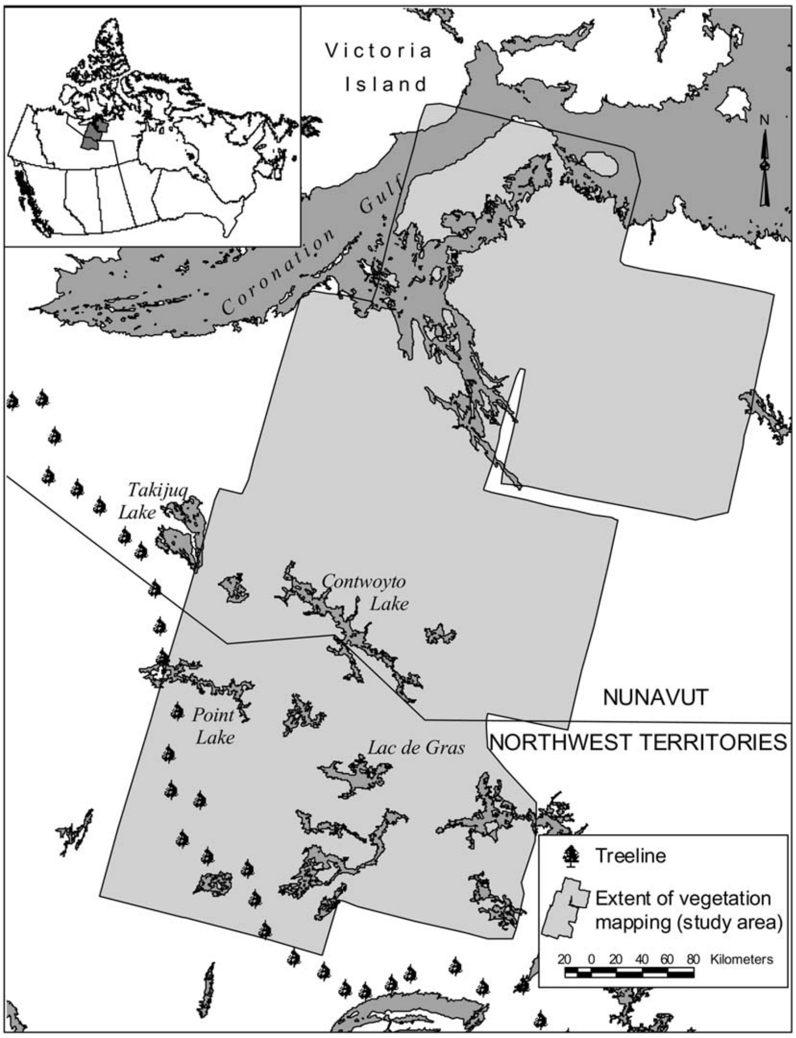


Figure 1. Location of study area across the Canadian central Arctic. Treeline represents the northern extent of coniferous forest.

mosaic of plant communities found across that area. Forested sites are characterised by white and black spruce, pine (*Pinus banksiana*), and in the south larch (*Larix laricina*). Understory is dependent on site productivity, but typically consists of some combination of lichen and shrub. Wet, riparian, or recently disturbed sites are devoid of tree cover and accommodate plant communities dominated by sedge (*Carex* spp.), birch (*Betula* spp.), willow (*Salix* spp.), and alder (*Alnus* spp.). Peatlands occur across wetland areas of discontinuous permafrost.

The majority of the study area is contained within the Southern Arctic ecozone. Landform geomorphology was shaped by past glacial actions and includes esker complexes, boulder moraines, outwash aprons of sand and gravel, glacial erratics, and raised ridges of ancient beaches. Permafrost is continuous through the zone and numerous lakes dot the landscape. Drainages are the most productive growing sites accommodating birch and willow of 2–5 m in height. Vast shrub communities of willow, shrub birch, and Labrador tea (*Ledum decumbens*) dominate areas with adequate soil development. Extensive mats of lichens, mosses, and low shrubs are found across exposed rocky sites.

Defining scale

Vegetation is distributed as patches within an environmental matrix of unsuitable growing condi-

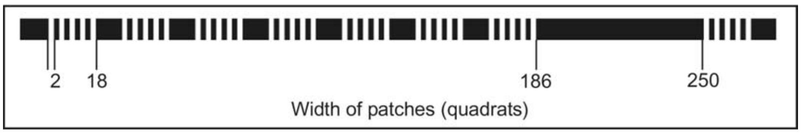


Figure 2. Simulated data representing hierarchically structured patches (white) occurring at the 2nd, 18th, and 187th quadrat.

tions. Patch size and aggregation is dictated by a number of factors including competitors, nutrient and moisture conditions, climate, disturbance history, and topography (Bengtsson et al. 1994). Often, the spatial pattern of patches occurs as an integrated nested hierarchy from individual plants, to groups of individuals of the same species, to collections of species that share a similar ecological niche and vary in prevalence across an ecological gradient defined by coarser scale factors (Diaz et al. 1998; Pausas and Austin 2001; Francis and Currie 2003). Animals will choose individual patches at some scale in the hierarchy to access vegetative or proteinaceous foods or avoid predators and competitors. Within a regional context, animals wishing to maximise the availability of resources or minimise intra and interspecific interactions may choose areas dominated by patches of a particular vegetation type. Our analyses were conducted at two spatial scales within this hierarchy: the patch and the region. A patch was a single or homogeneous collection of pixels representing one vegetation type. Minimum patch size was the 25 × 25-m (1 ha) grain of the raster vegetation maps; extent varied depending on vegetation type, but was limited to the mapped area. The regional scale represented the density of patches of like vegetation types calculated using a moving window algorithm. The size of the moving window was a function of the spatial patterning of patches of each vegetation type.

A number of techniques are available for exploring patterns in spatial data. Based on the recommendations of Dale (1999; 2000), we used three-term local quadrat variance (3TLQV) to identify various scales of pattern for vegetation found across our study area (Rosenberg 2002). Application of 3TLQV first requires the delineation of random transects across the vegetation type of interest. For each quadrat, or in this case pixel, along the transect, an overlapping moving window consisting of three terms or blocks of size *b* calculates a variance (Dale et al. 2002). The average variance across all pixels is the squared difference of the sum of the first and third blocks minus two times the sum of the second (Equation 1).

$$V_3(b) = \frac{\sum_{i=1}^{n+1-3b}\left(\sum_{j=i}^{i+b-1} x_j - 2\sum_{j=i+b}^{i+2b-1} x_j + \sum_{j=i+2b}^{i+3b-1} x_j\right)^2}{8b(n+1-3b)} \tag{1}$$

The moving window progresses across the transect multiple times successively increasing the size (*b*) of the three blocks during each iteration. The average variance is calculated and plotted for a range of block sizes or scales. Peaks in variance relative to block size indicate the dominant spatial scales of patch aggregation and distribution for the vegetation type bisected by the transect. For our analyses, each vegetation type was mapped as a simple binary layer of 1s and 0s. A patch was identified as a collection of 1s and the supporting matrix was identified by 0s.

Given the range of techniques available, we first explored 3TLQV to ensure that we could identify predefined scales of pattern. We simulated data consisting of patches in a hierarchy of three successively larger scales. Patterns of alternating 1s and 0s represented patch boundaries at the 2nd, 18th and 186th location repeated across a transect of 1000 quadrats (Figure 2). We used a randomization procedure to illustrate the magnitude of that spatial pattern. Locations of quadrats for the simulated data were randomly reassigned and the 3TLQV statistic was recalculated. The randomization procedure was repeated 500 times and the mean and 95% confidence intervals for the variance statistic were calculated for each block size.

For our analyses of resource selection, vegetation data were derived from a supervised classification of a number of Landsat Thematic Mapper images (25×25-m pixels; Matthews et al. 2001). To ensure statistically tractable resource selection models, we recombined the 23 original vegetation classes into 10 super classes (Table 1). We created binary images and randomly situated 10 transects across the range of

Table 1. Vegetation types used to model resource selection of caribou, wolves, and grizzly bears across the Canadian central Arctic.

Vegetation Type	Description
Esker density/patch[1]	sparsely vegetated sand and gravel esker complexes
Forest density/patch	continuous or discontinuous forested areas of dwarf white spruce, black spruce, and tamarack
Heath rock density/patch	open mat heath tundra interspersed with bedrock and boulders
Heath tundra density/patch	closed mat of heath found on moderate to well drained soils on upland areas
Lichen veneer density/patch	windswept, dry, flat topography covered with a continuous mat of lichen
Low shrub density/patch	extensive areas of low birch and willow found on moist well-drained soils
Peat bog density/patch	mosaic of uplands and lowlands with fens, bogs, mixed-wood forest, and peatlands
Riparian shrub density/patch	active stream courses or areas of water seepage with a shrub layer of birch, willow, and alder
Rock association density/patch	large areas of windswept bedrock or boulders with little vegetative cover
Sedge association density/patch	wetland complexes of wet sedge meadow and drier hummock sites

[1] Vegetation was modeled at two scales: the percent area per type and the mean density representative of the regional distribution of each vegetation type.

each vegetation type. We assumed that the dominant ecological gradient occurred from south to north and thus we oriented transects in that direction. Transect length varied (170–295 km) according to the geographic distribution of each vegetation type across the study area. We used 3TLQV to quantify the average variance for each scale of heterogeneity (b) for each type. Because of computational constraints analyses were conducted at a pixel resolution of 100×100 m. We plotted the median variance for the 10 sample transects and identified the major peak in variance as one scale at which availability of vegetation differed beyond that of individual patches. We used that scale (i.e., distance) to identify the length and width of a moving window which calculated the density of pixels for each vegetation type across the study area. Density of vegetation pixels served as a covariate by which to evaluate selection by our focal species for aggregations of patches at the regional scale.

Statistical definition of resource selection

We used resource selection functions (RSF) to quantify the relationship between the observed seasonal distribution of caribou, wolves, and grizzly bears and covariates representative of vegetation at the patch and regional scale (Table 1). A RSF is any mathematical function that is proportional to the probability of use of a resource or habitat unit (Manly et al. 2002). Typically, an RSF consists of a number of coefficients (β_i) that quantify selection for some environmental variable (Equation 2).

$$w = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_i x_i) \qquad (2)$$

Coefficient sign and strength is a function of variation in the distribution of environmental features measured at a sample of animal locations and a comparison set of random sites.

Resource selection analyses were based on animal locations collected during previous studies of caribou, wolf, and grizzly bear (Gunn et al. 2001; Walton et al. 2001; McLoughlin et al. 2002). All animals were fitted with satellite collars which remotely calculated and transmitted locations with an error radius of 150, 350, and 1000 m (Ballard et al. 1995). The geographic extent of capture efforts, relocation frequency, and the distribution of monitored animals varied amongst studies. In total, 28 individual female caribou of the Bathurst herd were collared and monitored from April 1996 to December 2000. Animals were fitted with satellite collars which, depending on season, transmitted locations daily, at 5-day intervals or weekly. Twenty-three wolves in 19 different packs were captured and monitored between June of 1997 and August 1999. Location interval was typically 24 h during summer and, depending on year, 4, 5 or 14 days for other months. Between June 1995 and June 1999, 42 female and 39 male grizzly bears were captured and monitored. Collars were programmed to transmit locations every two days.

We used our understanding of the focal species to identify ecologically relevant seasons (Johnson and Boyce 2004). Our intent was an analysis of the variation in resource selection across spatial scales not a complete assessment of seasonal resource selection patterns. Therefore, for each species we developed resource selection models for the season with the greatest number of animal relocations. To control for the possible confounding effects of location quality, we used only those locations with an expected error radius of 350 m.

We used conditional fixed-effects logistic regression – also known as discrete choice, paired and matched case-control logistic regression – to estimate coefficients for the RSF analyses. Fixed-effects logistic regression allows one to statistically control for responses that characterize clustered data (Pendergast et al. 1996; Hosmer and Lemeshow 2000; Compton et al. 2002; Manly et al. 2002). In this case, we clustered the fixed effects regression on each animal location to statistically control for temporal and spatial variation in resource availability. Each animal location was paired with five randomly selected comparison sites that served to quantify the availability of vegetation. We sampled comparison sites from within a circle that was centred on the preceding animal location, and had a radius equal to the 95th percentile movement distance for that particular relocation interval (e.g., 48 h, 2 day etc.) for that species (Arthur et al. 1996). We considered the resource selection models to be representative of the range of behaviours the monitored animals demonstrated over their mean relocation interval. Mean time between relocation was 272.09 (SE = 57.47), 39.02 (SE = 10.50), and 49.52 (SE = 1.82) hours, for caribou, wolves, and grizzly bears, respectively.

We used a logit link function to relate vegetation covariates to the dependent variable of used and random locations (Hardin and Hilbe 2001). Used and available resources were sampled from under an error polygon centered on the focal location with a radius equal to an assumed accuracy of 350 m. Covariates represented the percent occurrence and mean density of each vegetation type for the patch and regional scales, respectively. Although our models represented the distribution of vegetation at two spatial scales, the scale of resource selection was defined by animal movements and associated availability radii.

Model development, selection, and evaluation

For each species, we developed three resource selection models, which included covariates for vegetation parameterised at either the scale of the patch, the region (i.e., density) or both the patch and region. We used the Akaike information criterion difference adjusted for small sample sizes (AIC_c Δ), and Akaike weights (w) to evaluate and choose the most parsimonious model of the three for each species (i.e., the fewest variables to explain the greatest amount of variation). Akaike weights provide a normalised comparative score for all specified models and are interpreted as the approximate probability that each model is the best model of the set of proposed models (Anderson et al. 2000). For confirmatory purposes, we present log likelihood χ^2 statistics for assessment of overall model fit. Also, we evaluated the predictive success of each model. We applied a *k*-fold cross validation procedure five times, withholding 20% of the data during each iteration (Boyce et al. 2002). A spearman-rank correlation was used to assess the relationship between predicted occurrence for withheld animal locations and their frequency within 10 ordered bins of equal size as defined by the range of predicted data. A predictive model will have a strong mean correlation indicating a greater number of withheld locations in bins with relatively larger values. We used 95% confidence intervals to assess the strength of effect of each predictor covariate on the dependent variable. We used the Pregibon Δ β and leverage (i.e., hat) statistics as well as the Hosmer and Lemeshow Δ χ^2 statistic to identify cases and clusters that had a large influence on the parameters of the model (Hosmer and Lemeshow 2000). We assessed each model for excessive collinearity (Menard 1995).

Results

In agreement with our expectation, application of 3TLQV to our simulated data indicated three scales of pattern (Figure 3). Maximum average variance across all scales peaked at a window size (b) of 2, 14, and 121. The latter two scales drifted from the true scale we defined at the 18th and 186th quadrats on the transect (Dale 1999). Randomization of those data resulted in a near constant mean variance increasing linearly from 0 to 0.051 across window sizes (Figure 3). Serving as a null model, the randomization procedure illustrated the magnitude of the spatial pattern in the scaled data.

Results of the 3TLQV analyses for each of the 10 vegetation types revealed patterns we assumed represented various scales of patch structure across the study area. The strength of spatial patterning differed among the vegetation types; heath tundra and esker demonstrated the highest and lowest peaks in variance, respectively (Figure 4). The magnitude of

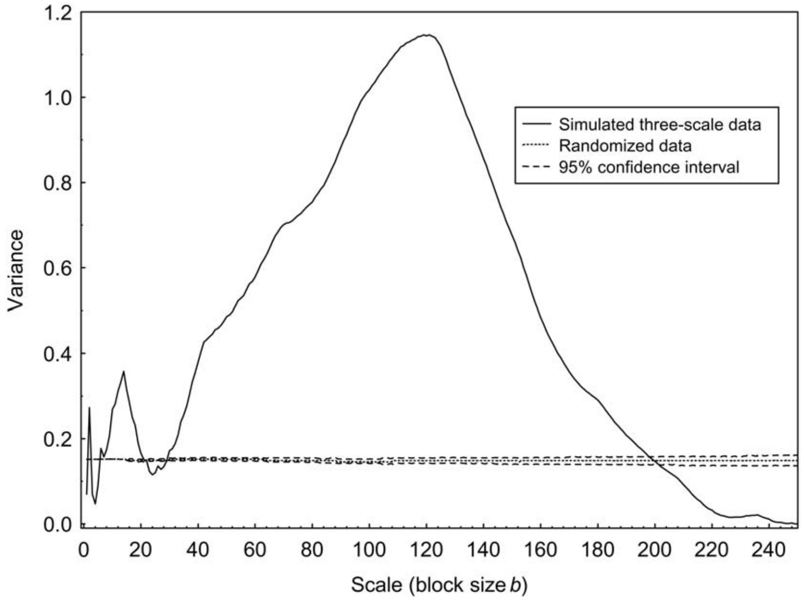


Figure 3. Variance of simulated data with three scales of structure (see Figure 2) calculated using 3TLQV. For comparison purposes the mean variance and 95% confidence intervals were calculated for the simulated data randomised 500 times.

results also were variable across transects for each vegetation type, but in general patterns were consistent across replicates. In some cases, graphs suggested a number of scales of vegetation patchiness to which our focal species might be influenced. For instance, heath rock and lichen veneer demonstrated several peaks in variance. The relationship was less complex for other vegetation types such as heath tundra (Figure 4). We used the scale at which the variance was greatest to calculate patch densities for each of the vegetation types. Those peaks occurred at the following distances: esker = 73 km; forest = 64.1 km; heath rock = 40.5 km; heath tundra = 55.2 km; lichen veneer = 17.7 km; low shrub = 42.2 km; peat bog = 11.6 km; riparian shrub = 77.2 km; rock association = 97.4 km; and sedge association = 94.9 km.

We used 377, 666, and 633 animal relocations to generate candidate resource selection models for caribou, wolves, and grizzly bears, respectively. AIC weights suggested little model selection uncertainty and strong evidence that the most parsimonious models were the best of their respective sets (Table 2). The most parsimonious model for caribou during the post-calving season (15 June–31 August) consisted of covariates for density of vegetation patches representing the distribution of the various vegetation types at the regional scale (Table 2). That model was statistically significant and suggested that caribou selected portions of the study area dominated by the lichen veneer, heath tundra, and rock vegetation types (Table 3; $\chi^2(10) = 87.21$, $P < 0.001$). Predictive capacity of the three models ranked equally with the results of the AIC analyses. Although differences were small, the mean Spearman rank correlation across 5 replicates was greatest for the vegetation density, followed by the vegetation patch and density, and finally the vegetation patch model (Table 2).

During denning (18 April–3 November), resource selection by collared wolves was best explained by a model consisting of vegetation covariates quantified at the patch and regional scales (Table 2; $\chi^2(18) = 144.35$, $P < 0.001$). That model also was the most predictive of the three (Table 2). The model consisting exclusively of patch-scale covariates was more parsimonious and predictive than a model representative of regional-scale selection, but fell well below the more complex multiscale model. Coefficients suggested that wolves selected for areas dominated by the heath rock and heath tundra vegetation types and patches of sedge, lichen veneer, and rock (Table 3). The esker vegetation type was important at both scales, but confidence intervals indicated imprecision in coefficient estimates.

Resource selection by grizzly bears during early summer (21 June–31 July) was best modeled using

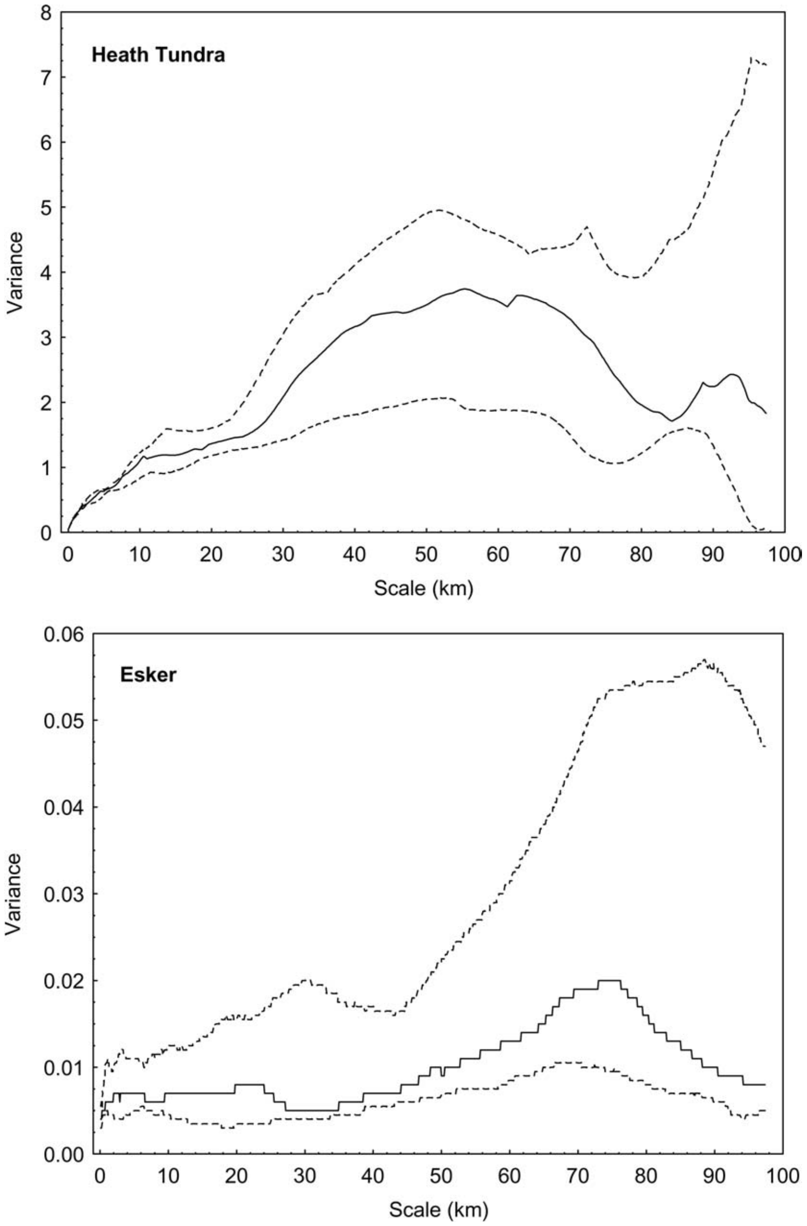
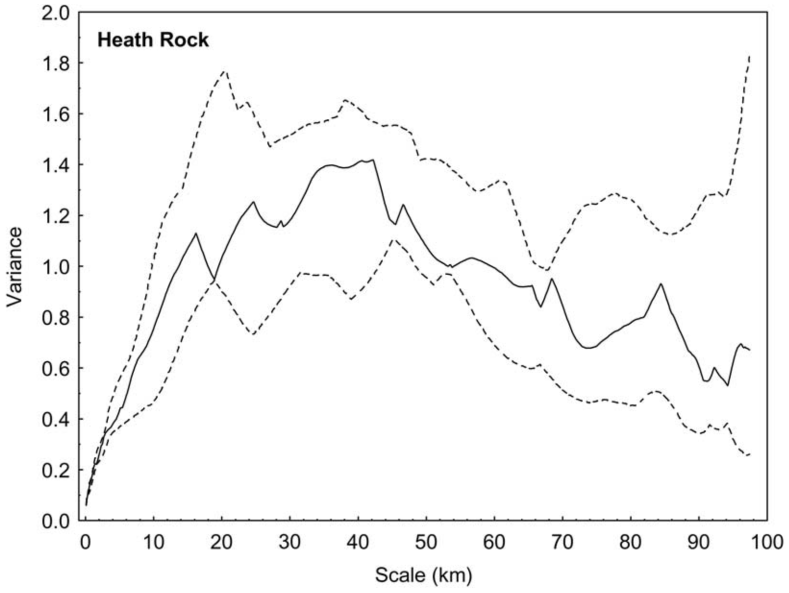


Figure 4. Median variance and interquartile range calculated using 3TLQV for 10 transects randomly oriented across the heath tundra, esker, heath rock, and lichen veneer vegetation types.

patch and density covariates (Table 2). The most parsimonious model was statistically significant and the best predictor of bear occurrence ($\chi^2(20)=99.94$, $P < 0.001$; $\bar{r}_s = 0.701$). Bears selected areas with a high density of patches of the esker and low shrub vegetation types and a low density of forest and sedge patches (Table 3). Holding vegetation density statistically constant, monitored bears also were associated with patches of heath tundra, low shrub, riparian shrub, and sedge.

Discussion

We are not the first to recognize the role of scale in understanding and predicting ecological processes. Senft et al. (1987) concluded that '...useful foraging



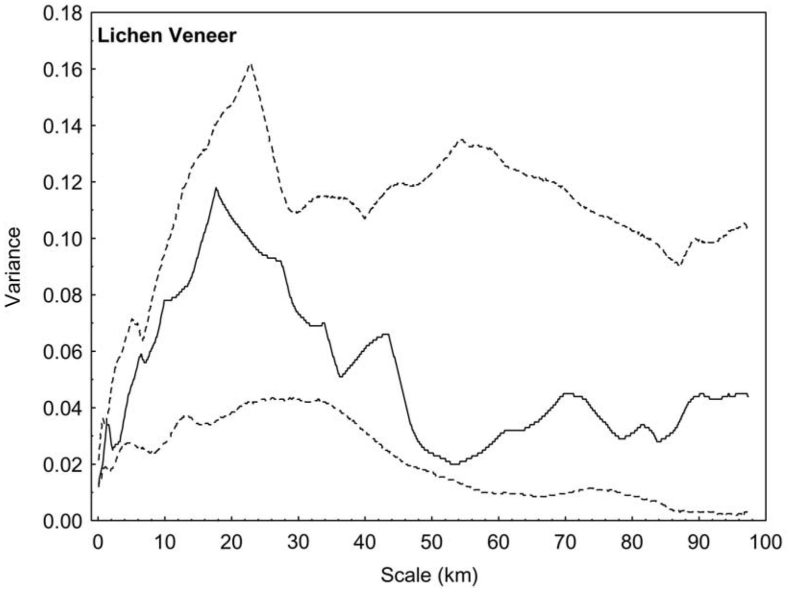


Figure 4. Continued.

theory must explain how foraging behaviour varies with ecological scale.'; Wiens (1989) stated that we '...must go further, to consider scaling issues as a primary focus of research efforts.'; and Levin (1992) asserted that '...it is (scale) I will argue, the fundamental conceptual problem in ecology, if not in all of science.' Consistent with these seminal works are dozens of empirical studies that concluded with statements advocating the necessity of multiscale approaches. Although many of these studies were premised on hierarchical designs, relatively few implemented methods that allowed for an integration and analysis of processes across scale (but see Morris 1987; Johnson et al. 2001; Bakker et al. 2002). Wildlife ecologists often refer to Johnson's (1980) orders of selection when conducting multiscale habitat selection studies. The focus of that much cited work has been largely forgotten, but researchers continue to premise their inferences on several discrete orders or scales of selection that approximate use of a study

Table 2. Mean Spearman rank correlation ($\bar{r}_s$) as an index of predictive success and differences in Akaike's information criterion (AIC_c) scores (Δ) and AIC_c weights (w) for candidate selection models developed for monitored caribou, wolves, and grizzly bears of the Canadian central Arctic.

					Prediction	
Species	Model	k	AIC_c Δ_i	AIC_c w_i	$\bar{r}_s$	SE
Caribou	Vegetation patch	11	42.46	< 0.001	0.683	0.063
	Vegetation patch + Vegetation density	11	4.51	0.095	0.689	0.105
	Vegetation density	21	0.00	0.905	0.706	0.066
Wolf	Vegetation density	10	79.94	< 0.001	0.538	0.058
	Vegetation patch	10	41.46	< 0.001	0.648	0.119
	Vegetation patch + Vegetation density	19	0.00	1.000	0.734	0.062
Grizzly Bear	Vegetation patch	11	26.14	< 0.001	0.664	0.102
	Vegetation density	11	13.81	0.001	0.468	0.144
	Vegetation patch + Vegetation density	21	0.00	0.999	0.701	0.066

Table 3. Coefficients (β) and 95% confidence intervals from the most parsimonious resource selection models for monitored caribou, wolves, and grizzly bears of the Canadian central Arctic.

	Caribou		Wolf		Grizzly Bear	
Covariate	β	95% CI	β	95% CI	β	95% CI
Esker den.	− 4.188	− 18.561 10.185	10.236	− 4.179 24.652	21.674	11.288 32.059
Esker patch	NI[a]	NI	0.029	− 0.004 0.063	− 0.006	− 0.032 0.021
Forest den.	1.272	− 3.988 6.533	3.638	− 6.135 13.411	− 34.788	− 57.181 − 12.395
Forest patch	NI	NI	0.026	− 0.019 0.071	0.055	− 0.013 0.124
Heath rock den.	0.108	− 3.546 3.762	8.242	5.166 11.317	− 1.548	− 4.033 0.937
Heath rock patch	NI	NI	− 0.005	− 0.010 0.001	0.005	< -0.001 0.011
Heath tundra den.	4.256	0.962 7.551	7.443	4.226 10.661	− 0.761	− 3.257 1.735
Heath tundra patch	NI	NI	< 0.001	− 0.003 0.004	0.006	0.001 0.010
Lichen veneer den.	11.114	7.642 14.586	− 8.362	− 17.264 0.540	− 3.445	− 7.487 0.597
Lichen veneer patch	NI	NI	0.027	0.001 0.053	− 0.005	− 0.023 0.013
Low shrub den.	4.168	− 0.675 9.011	NI	NI	2.598	0.367 4.829
Low shrub patch	NI	NI	NI	NI	0.010	0.001 0.019
Peat bog den.	− 16.737	− 44.865 11.391	18.597	− 0.049 37.244	− 1.123	− 11.269 9.023
Peat bog patch	NI	NI	0.022	− 0.110 0.153	0.019	− 0.031 0.068
Riparian shrub den.	− 10.445	− 21.706 0.816	− 1.014	− 7.583 5.555	1.194	− 2.855 5.244
Riparian shrub patch	NI	NI	0.020	− 0.008 0.048	0.027	0.007 0.048
Rock den.	3.047	1.152 4.942	− 3.501	− 7.333 0.332	1.320	− 0.660 3.300
Rock patch	NI	NI	0.018	0.006 0.031	0.005	− 0.004 0.013
Sedge den.	3.383	− 1.041 7.806	− 0.595	− 5.437 4.248	− 4.580	− 9.012 − 0.148
Sedge patch	NI	NI	0.031	0.024 0.039	0.010	0.004 0.017

[a] covariate excluded during model selection process or absent from range of monitored animals.

area, home range, patches within the home range, and food items within patches. Assuming that those orders are meaningful to the study species, effects measured at multiple scales in a discontinuous hierarchy illuminate differences in resource importance, but fail to enlighten mechanisms that vary continuously across scales (Andrzejewski 2002). Although the absence of an organism or nonlinearities in the importance of a resource suggests a holon, many processes and systems function along a scalar continuum (Allen and Starr 1982). In the context of animal behaviour, we can define selection of a regional area for a particular individual or population, but that observed distribution is likely a function of activities occurring at a number of interconnected scales from components of plants, to plants, to patches of plants and upwards. Patch density is a straightforward summary measure of vegetation distribution and aggregation that occurs at one scale greater than the patch, as identified by our GIS. In conjunction with a generalized linear model, measures of vegetation density allow researchers to objectively integrate and assess multiple scales of patchiness within resource selection models.

Our application of patch density to seasonal resource selection models for caribou, wolf, and grizzly bear suggested that wide-ranging species respond to vegetation at scales greater than the patch. Integrated multiscale models not only account for a greater percentage of variation in resource selection, but allow one to assess nonlinearities in selection across scale. When interpreting such models one must consider that each coefficient represents the effect of a covariate while holding other covariates statistically constant (Hardin and Hilbe 2001). Thus, we may model avoidance or selection of a vegetation type across scales or observe selection at one scale and avoidance at another. The latter would suggest a nonlinear scalar response. Grizzly bears, for example, demonstrated avoidance of areas of the study area dominated by sedge, but when ranging across those areas selected for patches of that vegetation type. Interactions across scale can be challenging to interpret, but nonlinearities in natural systems should not be unexpected (Pascual and Levin 1999).

Quantification of regional scale vegetation covariates was dependent on the identification of distances over which vegetation layers in our GIS demonstrated scalar patterns. A number of alternative techniques are available for exploring patterns in spatial data including lacunarity, fractal, spectral, and wavelet analyses (Ripley 1978; Palmer 1988; Plotnick et al. 1993; Dale and Mah 1998; Dale 1999). Variation in the results of pattern analyses conducted with different techniques, but similar data and objectives, highlights the necessity of considering a range of approaches (Perry et al. 2002).

We observed some variation in results among replicates for each vegetation type. Scale drift and resonance also obscured the true patterns of variance (Dale 1999). Inferences to patterns of vegetation across the central Arctic study area are imprecise and predictions specific to absolute values of vegetation density should be interpreted carefully. However, resource use versus availability analyses model relative differences in patch density between animal and paired random locations and thus should be robust to such sources of imprecision. Nine-term local quadrat variance (9TLQV) is similar to 3TLQV except that variance calculations occur in two dimensions across a surface (Dale 1990). Such an approach eliminates the need for multiple transects and is likely a superior technique for mapped vegetation data. Lengthy computation time prevented application to our large study area.

We modelled the influence of vegetation on resource selection at two scales. Results of the 3TLQV analyses, however, suggested that several scales of patchiness characterized some vegetation types. Researchers may wish to investigate the inclusion of vegetation covariates quantified at alternative or additional scales. Such higher order models should be evaluated for excessive collinearity, a condition that will reduce model parsimony and inflate standard errors (Menard 1995). We also anticipate that some resources will fail to demonstrate scales of aggregation beyond the individual patch. The esker vegetation type occurred as narrow linear features across the study area. Variance measures for that type were relatively small suggesting that the individual patch was the dominant scale of pattern (Figure 4).

Density measures also may serve as a scale-sensitive index of the distribution of environmental features other than vegetation. Resource selection models designed to assess disturbance responses of carnivores often incorporate road density as an index of human occurrence (Mace et al. 1999; Merrill et al. 1999; Carroll et al. 2001). Typically, that measure is calculated as the length of road within an arbitrary area of 1 km^2. At coarser scales, animals may orient their seasonal distribution to avoid areas of high road density. As with vegetation, alternative scales of measurement would capture such relationships. Animal movement parameters or home range estimates could guide the size of moving windows used to quantify the density of human disturbance features at scales larger than a 1-km^2 area (Blundell et al. 2001).

Vegetation density is just one approach for addressing the influence of landscape pattern on animal movement and patch occupancy. Numerous techniques and associated software programs are available for quantifying the shape, spatial configuration, and diversity of patch types (Baskent and Jordan 1995; McGarigal and Marks 1995; Gustafson 1998; Mladenoff and DeZonia 1999). Such metrics are applied to resource selection studies, but the bewildering choice and often high correlation among indices suggests that inclusion within models should be carefully guided by the research question and ecology of the system being studied (Riitters et al. 1995; Saab

1999; Johnson et al. 2002a; Kie et al. 2002; Fernandez et al. 2003).

Scale is an often used, but poorly defined and understood term (Csillag et al. 2000). Scaling principles can be applied to a number of research constructs and, therefore, need to be considered context specific. When representing scalar processes, one could consider the scale of the phenomenon or the scale of measurement, statistical summary, and modelling (Turner et al. 1989; Dugan et al. 2002). Behavior, for example, is a nonlinear phenomenon based scalar process: animals choose different resources relative to specific activities (Johnson et al. 2002b). Our definition of used and available habitats encompassed a wide range of selection behaviors that occurred over numerous observation periods. Thus, our data did not allow us to control for variation in behavioral or observational scales.

Our definition of resource availability was a function of the frequency of animal observation and likely influenced model results. Caribou were relocated less frequently and, therefore, had a larger area from which to sample available vegetation. Congruent with those measures, the model consisting of regional vegetation covariates was the most parsimonious and the best predictor of resource selection by monitored caribou. Measured patterns in vegetation data also were influenced by scales of observation and methods of analysis. The 3TLQV analyses were conducted at a grain of 100 m and an extent that did not exceed the distribution of each vegetation type across the 190 000-km^2 study area. Furthermore, the GIS data represented one scale of patch that was a function of spectral reflectance, sensor resolution, the supervised classification protocol, and interpretation by operators.

Landscape ecology is evolving. A discipline once largely focused on describing pattern now recognizes the importance of relating pattern to process (Hobbs 1997). Habitat ecologists can apply many of those lessons to their area of study. Here, we related animal movements recorded across a large ecologically diverse area to vegetation occurring at two spatial scales. Unlike other studies, scale was not a function of the availability of individual patches, but instead represented the aggregation and distribution of patches across space. Where others have noted a discrepancy between pattern and process, model fit for the three focal species indicated that resource use was correlated with vegetation patchiness (McIntyre and Wiens 2000).

Our approach is easily implemented and will provide added insight into the distribution of habitat resources and the response of animals to resources occurring at multiple spatial scales. Patch density as an index of scale also offers distinct advantages to conservation planning. Model results provide quantitative evidence of the importance of responses at each scale and coefficients from each scale are included in single predictive resource selection models which can be used to map and identify high-quality habitats (Mladenoff et al. 1995; Carroll et al. 2001). However, more work is needed to develop unified theories and methods for habitat ecology as well as a greater appreciation for the confounding effects of variation in scale as a true product of the process of interest and an artifact of our observations (Levin 1992). Although we integrated the responses of animals at two scales of resource availability, an understanding of finer and larger scale factors, such as feeding site selection and metapopulation dynamics, is necessary to place results in the larger ecological and evolutionary context. We acknowledge that complete integration of animal-resource responses is untenable. Individual studies within a discontinuous hierarchy still have a role in understanding complex ecological phenomena.

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