

ANIMAL MOVEMENTS AND LANDSCAPE PATTERN:  
IMPLICATIONS FOR ASSESSING HABITAT USE

by

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## Abstract

To understand ecological processes, it is important to study observed patterns at appropriate scales. Patterns of habitat use by animals have a spatial dimension that is usually ignored in analyses of habitat selection and preference. Hence, I studied the interaction between animal movement behaviour and landscape pattern, across a variety of spatial scales. The purpose of the study was to determine how these variables affect our ability to make inferences about the habitats used by animals.

I simulated the movements of animals on maps of real and simulated landscapes. I modelled movements that were either insensitive or sensitive to the underlying distribution of habitats. The unequal proportions of different habitat types had the greatest influence on measures of habitat use and preference, but measures were also affected by the scale of animal movements, the affinity of animals for different habitats, the size and arrangement of habitat patches, and the method of analysis.

Changing the scale of animal movements by varying the daily distances that simulated animals moved, had little effect on the mean use of different habitats, but scale affected the variance of habitat use among simulated animals. Small-scale movements produced the largest overall variances, and variances were greatest for the most abundant habitats. The correlation between variance in habitat use and proportions of habitat types was an expected result, although previous researchers have not assessed the implications of the correlation. Spatial effects were evident primarily where home ranges were less than about ten times the median size of habitat patches on the landscape.

The relationship between variance in habitat use and scale of animal movements was similar among all simulations. Regions where variance did not change with scale were next to a region

where variance changed monotonically with scale (log-transformed). This suggested the existence of 'domains of scale' or regions where a given property (in this case, variance in habitat use) changes predictably with scale. Characteristics of these regions were a function of the proportions of habitat types on the landscape, the size and arrangement of habitat patches, and of the variances associated with other parameters of the model. Domains were not separated by sharp discontinuities; higher variances among variables such as home range size and patch size, as well as the random placement of simulated animals tended to make scaling properties less distinct.

Preference analyses often distorted the true habitat affinities of simulated animals. These distortions were partly due to the unit-sum constraint which affected measures of both habitat use and availability (measures for different habitat types summed to one), and the analyses used to compare them. However, landscape pattern also affected the ability to make accurate inferences about habitat preference. The proportions of different habitat types, as well as their patch sizes and arrangement, constrained the ability of animals to exploit habitats according to their affinity for habitats. These constraints were reflected in the results of preference analyses, which rarely detected strong preference for rare habitat types, even when animals had a high affinity for those habitats. This result depended on the inability of simulated animals to learn the locations of high quality patches.

I analysed radio telemetry data collected on grizzly bears (*Ursus arctos*) in the Flathead Valley, British Columbia to examine the degree to which landscape characteristics could produce similar patterns of habitat preference in real and simulated animal movement data. Results suggested that simulated animals that did not discriminate among different habitat types could have rank orders of habitat preference similar to that observed in the actual grizzly bear data, but only when the movements of simulated animals were determined by a spatially-

explicit model. However, there was a 'boundary effect' in the spatially-explicit simulations that was largely responsible for the fit between simulated and actual data. The magnitudes of preference and avoidance of habitats were greater in the bear data than in the simulated data. Additional simulations based on a model of grizzly bear habitat capability revealed that methods of analysing preference differed in their ability to reflect the habitat affinities suggested by the bear data.

These results underline the importance of considering the spatial dimension of habitat use data when mapping habitats, developing data collection protocols, and interpreting results.

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## Quotation

“Ecology is the science which says what everyone knows,  
in language that no one understands”

*Charles S. Elton*  
*Animal Ecology 1927*

## Chapter 1. General Introduction

Descriptions of wildlife habitat that account for both the arrangement and amounts of different habitats are beginning to emerge in wildlife studies (McGarigal and Marks 1995, Roseberry and Hao 1996). The distribution of resources in space is one of the factors that determines the distribution and abundance of species, and to understand ecological processes often requires an examination of spatial patterns at appropriate scales (Wiens and Milne 1989, Dunning *et al.* 1992, Milne *et al.* 1992, Thomson *et al.* 1996). There is also the practical issue for researchers conducting wildlife studies with radio telemetry, that the spatial pattern of available habitats and the scale of animal movements may affect the results of habitat use analyses (Porter and Church 1987, Shulz and Joyce 1992, Turner *et al.* 1993, Arthur *et al.* 1996, Wilson *et al. in press*).

Issues of spatial pattern and scale can be articulated within the context of the emerging field of landscape ecology (Forman and Godron 1986, Turner 1989). A basic principle of this discipline is that the arrangement of landscape elements may regulate the distribution of organisms, resources, and energy (Milne *et al.* 1989). Here, I define a 'landscape' as an area that is spatially heterogeneous with respect to the resources an animal requires, is larger than an average home range, but smaller than the regional distribution of a species (Turner and Gardner 1991, Dunning *et al.* 1992). Therefore, a landscape is a species-specific area large enough to be used by several individuals, but not large enough to be considered a regional population. This is a size that corresponds to the study areas that many wildlife researchers use.

Landscape ecology provides a framework for understanding the manner in which smaller-scale processes are influenced and/or constrained by larger-scale phenomena (O'Neill *et al.* 1988b), and whether there are emergent properties that are at least partly independent of the

smaller-scale behaviour (Levin 1992). In this thesis, I defined the smaller-scale behaviour by the daily movements of individual animals. Describing habitat use generated by animal movements has been a central theme of modern ecology and in particular, of wildlife ecology and management (Neu *et al.* 1974, Johnson 1980, Arthur *et al.* 1996). The larger-scale constraints that I consider are those imposed by the amounts and arrangement of habitats across a landscape. While biologists have commonly incorporated measures of habitat availability in their analyses (Neu *et al.* 1974, Johnson 1980, Alldredge and Ratti 1986, Aebischer *et al.* 1993), rarely have they considered habitat juxtaposition, interspersion, and other aspects of landscape structure.

Studies that have examined habitats available to animals in a spatially-explicit manner have found that habitat patch size and the extent of study areas can affect measures of available habitat (Porter and Church 1987), and that considering available habitat in the context of animal mobility can generate predictions different from those produced by a spatially-neutral model (Shulz and Joyce 1992, Wilson *et al. in press*). It is important to understand the applicability of this results to habitat use studies in general.

### ***Modelling Wildlife-Habitat Relationships***

Habitat use is often measured by comparing an index of use (either the number or proportion of animal locations, or the proportion of an estimated home range, contained within different habitat types) to a measure of habitat availability (Alldredge and Ratti 1986). Johnson (1980) introduced the concept of a hierarchy of selection, and classified the largest (or *first*) order of selection as the selection of a species range, and the smallest (or *fourth*) order as selection of individual bites by animals. In this hierarchy, the larger-scale selection behaviour constrains choices available at smaller scales, however, most analyses (including Johnson 1980) assume

that the nature of this constraint is limited only to the quantity of different habitats included in the analysis; the spatial characteristics of the habitats within the study area are not considered.

It is difficult to determine the role of spatial characteristics in generating habitat use results with data from field studies because the true behaviour of sampled animals is not known. However, models of animal movements allow the study of spatial effects where animal behaviour is known and where locations can be sampled and habitat maps generated without error. I examined habitat use in a spatially-explicit context by using 'individual-based' models of animal movements (Judson 1994). This modelling method attempts to simulate the behaviour of individuals based on relevant decision rules, and to build the dynamics of systems by simulating many animals. The focus is on the resulting broad-scale patterns, in this case the distribution of animal locations, rather than the details of the fine-scale behaviour (*i.e.* the movements of individuals). It is not assumed that complex rules defining fine-scale behaviour do not exist, but rather that they do not significantly influence broader-scale patterns (Levin 1992). Therefore, the goal is not to capture all the decision rules used by animals moving through landscapes, but to use the simplest possible model to generate broad-scale patterns that are consistent with those observed in the field (Levin 1992, Starfield 1997).

An individual-based model of animal movements is a novel approach to studying the effects of spatial variables on habitat use. More commonly, models of habitat selection attribute no behaviour to individuals and assume that locations will be distributed according to the suitability of habitat patches, regardless of the distribution of habitats or of the mobility or energetics of animals (Lima and Zollner 1996).

My models were based on random walks (Kareiva and Shigesada 1983, Bovet and Benhamou 1988, Marsh and Jones 1988, Johnson *et al.* 1992, Gross *et al.* 1995), which have been used in ecology to characterise and simulate the movements of animals (Kareiva and Shigesada 1983,

Johnson *et al.* 1992, Gautestad and Mysterud 1993, With 1994, Gross *et al.* 1995, Boone and Hunter 1996) and to analyse search paths in the context of foraging theory (*e.g.* Pyke 1978, 1983).

Random walk models in biology have been based on either discrete or continuous movements (McCulloch and Cain 1989). Discrete models characterise animal paths as a distribution of step lengths and turning radii (Kareiva and Shigesada 1983, Wiens and Milne 1989, Johnson *et al.* 1992, With 1994, Nams 1996). In contrast, continuous or diffusion models generate movements in a cell-to-cell fashion, at a scale equal to the grain of the map and the time necessary to traverse a cell (Turner *et al.* 1993, Boone and Hunter 1996). These models have been used to simulate animal dispersal movements, usually on artificial landscapes consisting of a random grid of resource and non-resource sites (*e.g.* Gardner *et al.* 1989, Turner *et al.* 1993).

Animal movement models based on random walks are 'information free'; that is, animals have no information about surrounding habitat and cannot learn, although they are usually given the ability to instantly assess the value of a patch upon arrival. By contrast, most methods of modelling habitat use assume that animals have perfect information about all available habitats and have no need to learn (Lima and Zollner 1996). Which approach is more useful is open to debate, but following one set of assumptions or the other may affect the inferences made about habitat use. I used simulation models to compare results based on these sets of assumptions.

In this thesis, I use both discrete and continuous correlated random walk models to examine the effects of spatial variables on measures of habitat use. The goal is to generate system-independent relationships between the spatial characteristics of location and habitat data, and the inferences made about habitat use by animals. There are many variables with spatial consequences that are at least partly under the control of researchers. These include the

frequency of animal relocation, the number of habitats mapped, and average habitat patch sizes. As a result, data collection protocols have spatial consequences, and a better understanding of the relationship between spatial variables and habitat use measures will assist researchers in designing better studies, and in interpreting results that can lead to better management prescriptions and policies.

In Chapter 2, I describe the characteristics of the landscapes that I use in subsequent chapters. In Chapter 3, I use a discrete movement model, insensitive to the distribution of habitats, to investigate the effects of landscape characteristics on habitat use. This is an application of a 'null model', which allows the inference of a particular mechanism by generating patterns that are expected in the absence of the mechanism (Lewin 1983, Gotelli and Graves 1996). In this case, I use habitat-insensitive simulations of animal movements to generate expected patterns of habitat use, in the absence of habitat selection (see Arthur *et al.* 1996 for a similar application). I simulate the movements of animals, at different scales, on maps based on both real and random landscapes, to examine and characterise these interactions.

In Chapter 4, I develop a continuous movement model that is sensitive to the underlying value of habitat types. My objective is to predict ways in which affinities for different habitats interact with landscape characteristics to produce patterns of habitat use across spatial scales.

Finally in Chapter 5, I examine radio telemetry data collected on grizzly bears (*Ursus arctos*) in the Flathead Valley, British Columbia, and investigate patterns of habitat use from the perspective developed in the previous chapters. Grizzly bears provide an excellent opportunity for examining landscape effects, primarily because they move at scales similar to those at which we often produce multipurpose maps. Also, a long-term study in the Flathead Valley has provided a large dataset of telemetry locations on many ( $n = 116$ ) grizzly bears (McLellan 1989, F. Hovey, unpubl.), and contributed to the map upon which many of my simulations were based

(Lea *et al.* 1988, Fuhr and Demarchi 1990). In the chapter I investigate the degree to which landscape variables can produce similar patterns of habitat use in both real and simulated data, despite the oversimplifications used in simulating animal movements. This provides an example of broad-scale patterns (*i.e.* habitat use) emerging from processes with dissimilar fine-scale behaviours (actual and simulated movements; Levin 1992, Wiens and Milne 1989).

## Chapter 2. Habitat Maps

### Introduction

In this chapter, I describe the habitat maps on which I base animal movement simulations. The maps were originally generated from a grizzly bear habitat capability model (Fuhr and Demarchi 1990) for the Flathead Valley, BC (49° N, 114° 85' W; for details of the study area see McLellan 1989), and consist of four habitat types that correspond to different classes of habitat quality for grizzly bears. I used the maps only because they provided good examples of landscapes often encountered in habitat use studies.

I first outline the general methods used to adapt the maps for my purposes, and then characterise them with common landscape indices. Finally, I discuss the usefulness of different indices for describing landscape structure in the context of habitat use studies.

### Methods

Three seasonal maps (spring, summer, fall) were used for the simulations, and each contained four habitats that I arbitrarily labelled h1, h2, h3, and h4. The maps covered approximately 1100 km<sup>2</sup> at a resolution of 50 m<sup>2</sup>. I generated an additional map by reclassifying two of the habitat types into one on the fall map ('3-habitat fall map').

I also generated 'random' landscapes (With 1997) that had the same habitat proportions as the original fall map (chosen arbitrarily from the three seasonal maps). To generate these maps, each pixel was pseudorandomly (*i.e.* by a computerised random number generator) assigned a value between 0 and 1, and pixels were then classified into the four habitat types according to pixel value, such that values between 0 and 0.127 were assigned to habitat h1 (to correspond to the 12.7% of the fall map that was comprised of habitat type h1), values between 0.12701 and 0.754 were assigned to h2, and so on. The result of this exercise was a map that contained

several thousand very small patches, many no larger than a single 0.25 ha pixel. I increased the average patch sizes by first contracting the map by repeatedly removing every other pixel until I had maps that were smaller than the original by factors of 4 and 10. I then expanded these two maps to their original size by repeatedly duplicating pixels. This resulted in maps with patches that were, on average, 4 and 10 times the size of patches on the initial random map, and that had similar proportions of habitats as the fall map, but that differed in other landscape characteristics. I labelled these maps 'random a' and 'random b' respectively.

Map files were maintained in *Idrisi 4.1* (Clark University Graduate School of Geography, Worcester, MA). Landscape characteristics were calculated with *Fragstats 2.0* (McGarigal and Marks 1995), and I used the program's definitions of interspersion/juxtaposition, and contagion indices to quantify landscape pattern (Appendix I). *Fragstats'* interspersion/juxtaposition index is a measure of the intermixing of habitats based on patch adjacencies. It measures the degree of patch type interspersion. Higher values indicate greater interspersion; that is, patch types are more equally adjacent to each other. The contagion index is based on pixel adjacencies and measures the extent to which patch types are clumped or aggregated. As such, contagion measures both patch interspersion and dispersion (the spatial distribution of habitat patches). Higher contagion values result from landscapes with few large, contiguous patches.

## Results

The landscape characteristics of the maps that I used were dominated by the h2 habitat type, with the proportions of other habitats varying among seasons (Table 1). In general, the broad patterns of habitat arrangement were similar across the three seasons (Figure 1), because the biogeoclimatic characteristics of the Flathead Valley are dominated by the valley's topography (Lea *et al.* 1988).

**Table 1.** Common landscape statistics for the habitat maps used in the movement simulations. In addition to the three seasonal maps, the two rarest habitat types on the fall map were combined to produce a fourth seasonal map. 'Random' maps that had the same habitat proportions as the fall map were also generated by randomly assigning pixels to one of the four habitats.

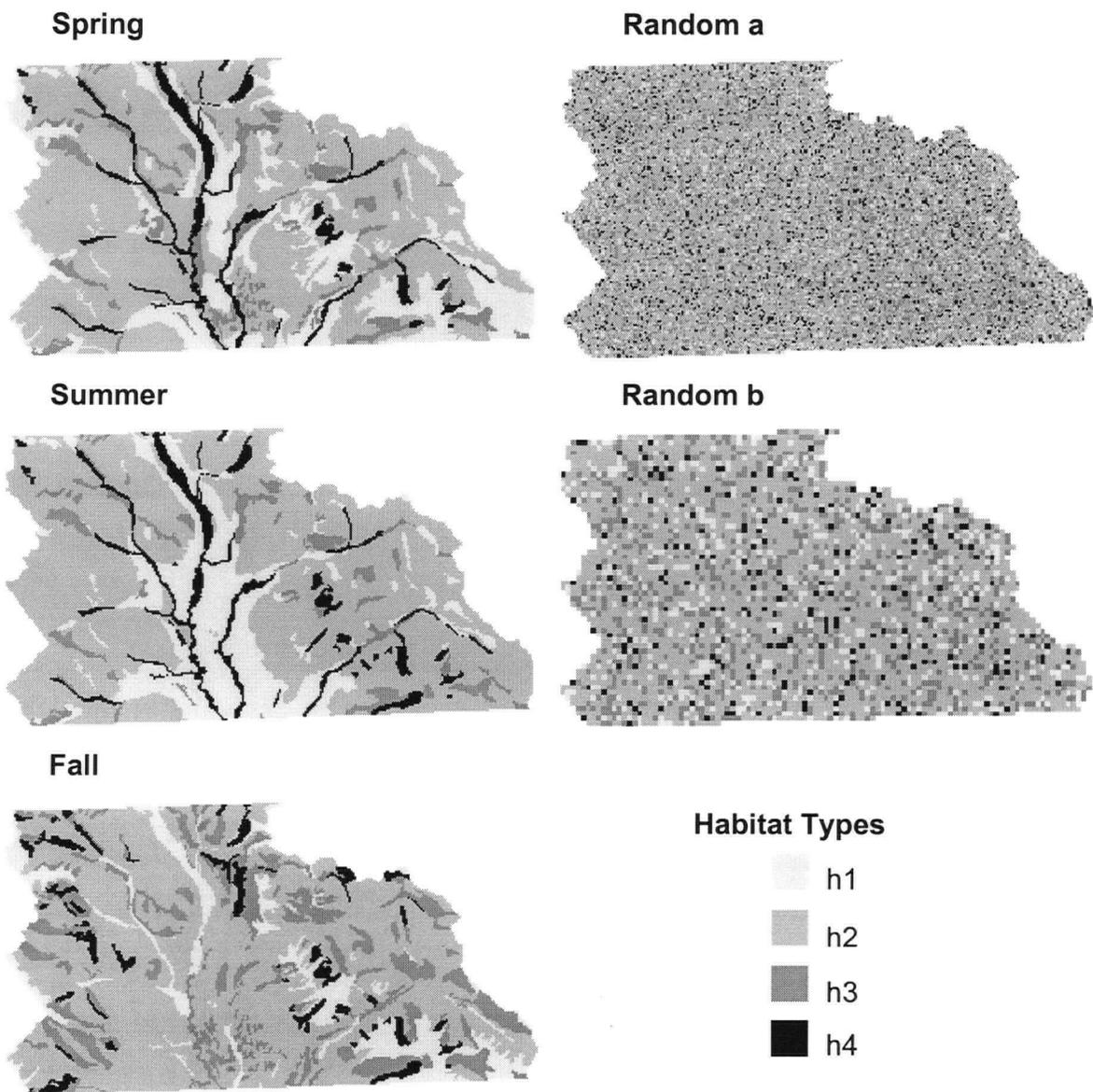
habitat characteristics	Maps					
	Spring	Summer	Fall	Fall 3-habitat	Fall random a <sup>1</sup>	Fall random b <sup>2</sup>
<b>h1</b> % landscape	23.0	20.8	12.7	12.7	12.6	12.9
# of patches	69	56	37	37	1961	315
mean size (ha)	366.7	408.2	378.0	378.0	7.1	45.0
patch size CV <sup>3</sup> (%)	226.9	324.9	208.4	208.4	78.6	82.7
<b>h2</b> % landscape	62.0	65.8	62.7	62.7	62.4	62.7
# of patches	32	16	20	20	18	3
mean size (ha)	2126.9	4521.0	3445.4	3445.4	3811.1	22983.3
patch size CV <sup>3</sup> (%)	234.9	191.7	239.8	239.8	411.2	141.0
<b>h3</b> % landscape	8.4	6.2	19.0	24.5	19.4	19.2
# of patches	68	43	111	113	2023	314
mean size (ha)	135.3	159.4	188.9	238.6	10.5	67.4
patch size CV <sup>3</sup> (%)	109.7	99.7	131.3	153.6	113.5	112.1
<b>h4</b> % landscape	6.6	7.1	5.5		5.6	5.1
# of patches	26	31	47		1189	185
mean size (ha)	280.7	252.0	127.7		5.2	30.5
patch size CV <sup>3</sup> (%)	236.1	243.2	94.6		48.4	45.0
<b>landscape characteristics</b>						
median size (ha)	85.0	80.4	84.3	105.0	4.0	25.0
mean size (ha)	563.4	752.5	511.0	646.2	21.2	134.5
patch size CV <sup>3</sup> (%)	392.8	435.7	531.6	471.9	1485.5	1787.7
inters./jux. <sup>4</sup> (%)	86.7	86.6	79.3	80.9	78.9	78.0
contagion <sup>4</sup> (%)	56.2	59.8	55.6	50.9	44.6	54.0

<sup>1</sup>same habitat proportions as 'fall' map, but pixels were randomly interspersed, then resampled to increase patch sizes by a factor of 4 -- see Methods

<sup>2</sup>same as 'random a', but resampled to generate patches 10 times in size -- see Methods

<sup>3</sup>CV = coefficient of variation

<sup>4</sup>inters. = interspersion, jux. = juxtaposition -- see Methods and Appendix I for definitions and equations



**Figure 1.** Maps used in simulations. Random maps had the same proportions of habitat types as the fall map.

For the two random maps ('a' and 'b'), average patch size was much smaller than that for the seasonal maps, and patches were much more numerous, except for h2 (Table 1). The random interspersion of different habitats resulted in large numbers of small patches within a matrix of the most common habitat type. Further resampling of the map by factors larger than 10 did little to alter this effect.

Although the fall and random maps looked very different (Figure 1), landscape indices of patch arrangement (interspersion/juxtaposition and contagion) were similar.

### Discussion

Measures of patch size and amounts of habitat were useful for describing differences among maps, while measures of patch arrangement were relatively insensitive to visually dissimilar maps. Landscape indices must be interpreted with caution because many are not independent (*c.f.* O'Neill *et al.* 1988a) and different statistics change in different ways with simple changes in scale (Turner 1989, Turner *et al.* 1989c).

Simple measures such as mean patch size can be misleading because distributions of patch sizes are rarely normal; small patches are usually more common than large patches. The picture is further clouded by landscapes with several types of habitats. The same statistic can vary among habitat types on the same landscape (although not independently), and often the same statistic is used to characterise an entire landscape (*e.g.* measures of mean patch sizes and dispersions).

In general, the similarities among characteristics of the different landscapes were surprising, particularly the similarities between landscape-wide measures of the patch arrangement for real and random maps. However, the interspersion/juxtaposition and contagion indices calculated by *Fragstats* are strongly affected by the proportions of the different habitats on a landscape

(Riitters *et al.* 1996). For example, I generated a random test map with equal proportions of four habitat types. The interspersion/juxtaposition index was 100%, and the contagion index was 25%. By contrast, random habitat maps with unequal habitat proportions such as those that I used for analysis (Table 1), had lower interspersion/juxtaposition and higher contagion values. The arrangement of patches on the maps were random and, therefore, the interspersion/juxtaposition values were the maximum and the contagion values the minimum possible for the habitat proportions that I used. Interspersion/juxtaposition and contagion are less sensitive to different patch arrangements when the amounts of habitats among maps are similar. These results underline the importance of using appropriate landscape indices for the properties of interest, and interpreting common landscape statistics with caution.

The consideration of four habitat types in this study rather than the more common two-habitat design (Gardner *et al.* 1989, Turner *et al.* 1989b, Milne *et al.* 1992, Wiens *et al.* 1997) make the interpretation of landscape characteristics more difficult. From the perspective of animal habitat use, a four habitat design is a better representation of the habitat faced by most animals (With 1997). Four habitats is still a simplification, and ignores within-patch heterogeneity. Habitat use studies are often restricted to 4 - 7 habitat types to simplify analyses (Alldredge and Ratti 1986).

## Chapter 3. Effects of Scale and Landscape Pattern on Habitat Use

### Introduction

It is important that we measure phenomena at appropriate scales for the ecological process of interest (Burrough 1981, Addicott *et al.* 1987, Wiens and Milne 1989, Dunning *et al.* 1992). A number of techniques have been developed to sample and analyse interactions between animal behaviour and habitat (*e.g.* Neu *et al.* 1974, Johnson 1980, Aebischer *et al.* 1993, Arthur *et al.* 1996), but while frequently recognised, consideration of the spatial dimension of wildlife-habitat relationships is rarely addressed in study designs or analysis techniques (*c.f.* Porter and Church 1987, Shulz and Joyce 1992, Otis 1997).

Here, I consider 'spatial dimension' to be the spatial relationships among the sample of animal locations that we use to characterise habitat use behaviour, and among the habitat patches that comprise available habitat. These relationships arise from both *scale* and *pattern*. The scale of animal movements is defined by the distance between sample locations, and is a function of both ecology (*e.g.* body size, food habits, physical characteristics of habitat) and data collection (*e.g.* relocation frequency). The pattern of animal movements refers to the description of sampling points in relation to each other in space. The scale of a landscape is a function of the sizes of its habitat patches, while landscape pattern is defined by the spatial relationship among patches.

The influence of spatial variables on habitat use measures has remained largely unstudied for two general reasons. First, the computer hardware and software required to examine spatial relationships has only recently become widely available (McGarigal and Marks 1995). Second, the consideration of spatially-correlated variables complicates statistical analysis. For example, a standard technique in wildlife field research is to sample animal locations widely separated in

time to ensure locations are spatially independent (*i.e.* no autocorrelation; Swihart and Slade 1985). This is done to meet assumptions of statistical tests (Swihart and Slade 1985, White and Garrott 1990, Legendre 1993), which assume that each animal location represents an independent choice taken from all available habitats (Arthur *et al.* 1996). This assumption requires that animals have a knowledge of, and are able to move with negligible cost among, all habitats within the area under study (Rosenzweig 1981, Arthur *et al.* 1996). Following these assumptions, there can be no spatial effects by definition. The time and cost of moving between patches are the restrictions that give rise to spatial effects (Arthur *et al.* 1996).

Aebischer *et al.* (1993) questioned the need to eliminate autocorrelation among sample locations by arguing that doing so is only necessary if the experimental unit of tests is erroneously assigned to radio locations rather than to animals. Where the experimental unit is properly assigned to animals, individual locations serve only to approximate the habitat use of animals (although problems occur if sampling frequency varies within animals). Of course, for each individual, its locations *are* autocorrelated, and using sampling methods to ensure that autocorrelation is not statistically significant may obscure the real patterns of interest (Meentemeyer and Box 1987, Legendre 1993, McNay *et al.* 1994, Reynolds and Laundré 1990).

When characterising habitat use and availability in a spatially-neutral manner, the assumption is that little information is lost by ignoring the spatial component of data. However, the effects of this assumption are largely unknown. Rarely do studies compare spatially-explicit with spatially-neutral results, and those that have done so suggest that the two approaches can lead to different results (Shulz and Joyce 1992, Wilson *et al. in press*). Such studies have provided 'snapshots' of spatial effects at one or a few spatial scales, and hence, the general applicability of the results are unknown. To fully understand the effects of spatial variables, we need to

establish relationships between habitat use and availability data that account for spatial characteristics across a continuum of scales. Only then can we anticipate the effects of spatial variables on our study designs, analyses, and conclusions.

My objective is to determine the mechanistic relationship between measures of habitat use by animals and the spatial characteristics of landscapes. Specifically, I use simulations of animal movements through landscapes to generate distributions of expected habitat use under a null model of no habitat selection. Because simulations are insensitive to the underlying distribution of habitats, I expect the variances, but not the means, associated with habitat use to differ among the simulations. Turner *et al.* (1989a) suggested that, in landscape ecology problems, examining variance may be more useful than considering means.

I address the following questions: 1) how does expected habitat use under the null hypothesis differ between spatially-explicit and spatially-neutral models?; 2) how does expected habitat use under the null hypothesis differ across spatial scales?; and 3) how is the relationship between expected habitat use under the null hypothesis and spatial scale affected by landscape characteristics?

Establishing these general relationships will help us to understand the potential effects of spatial characteristics on habitat use analyses, and guide managers in making decisions that are ecologically sound.

## Methods

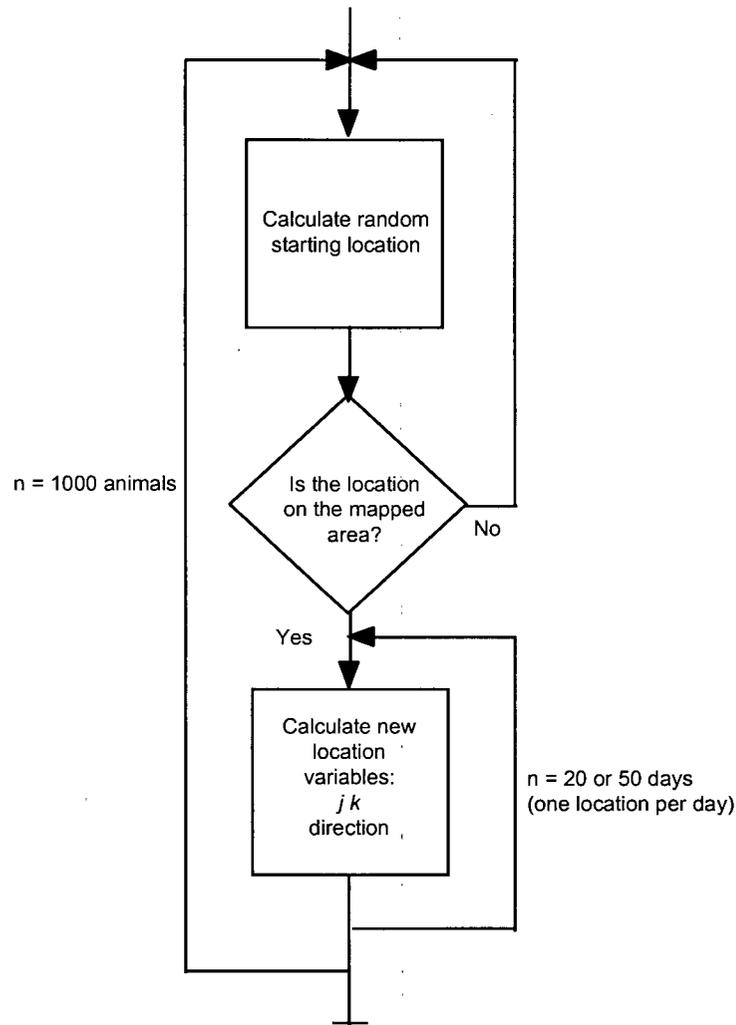
I used a correlated random walk model (see Chapter 1) that was insensitive to the underlying distribution of habitats to generate expected patterns of habitat use. Changing the number and distribution of daily movement distances, and the spatial distribution of starting points, provided the variation in scale and pattern of movements relative to specific habitat maps.

Different habitat maps provided the variation in landscape characteristics. Models were written in the REXX scripting language (International Business Machines, Hursley, UK; Appendix II).

Each model run consisted of 1000 simulations, each representing the movements of one animal over either 20 or 50 days. Animals were located once per day (Figure 2). Simulations were started at random points on habitat maps. I also ran simulations where starting points were restricted to a smaller area on the landscape (representing about 13% of the mapped area in the south-central portion of the map) to test the effects of sampling animals that were not distributed randomly across the landscape.

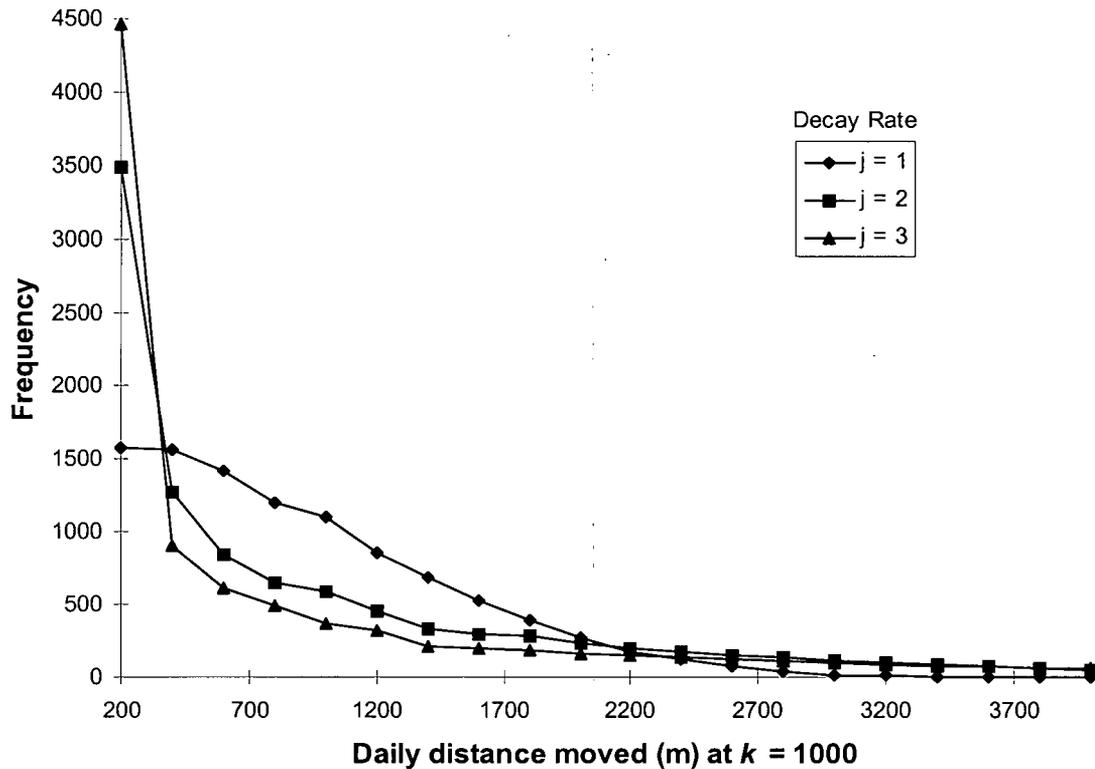
Changes in an animal's direction between subsequent locations were correlated by summing two random numbers between 0 and 360 degrees drawn from a uniform distribution, and dividing by two. The result of this calculation was to bias the next direction of travel opposite to the previous direction. This was done to generate more realistic home ranges; uncorrelated movements produced very large home ranges. However, the bias did not produce a central tendency to movements. Increasing the number of locations in a simulation always increased home range size.

Daily movement distances were drawn from a decay distribution. The shape and size of this distribution was varied in different model runs, to test the effects of movement characteristics. Movement distances were based on a draw of random numbers ( $x$ ) from a normal distribution ( $\bar{x} = 0; s^2 = 1$ ). The draws were transformed by the equation:  $y = abs(x)^j \cdot k$ ; where  $y$  represented the transformed variate,  $j$  was the rate of decay (varied between 1 and 3; Figure 3), and  $k$  was a multiplier (varied between 10 m and 10 000 m) that determined the spatial scale of the daily distances moved. Changes in  $j$  altered the variance of daily movement distances, while changes in  $k$  affected the scale of the movements.



**Figure 2.** Structure of the habitat-insensitive, spatially-explicit movement model. Variables  $j$  and  $k$  controlled the shape and size of the distribution regulating daily movement distances. The structure of the spatially-neutral model was the same, except that subsequent locations were drawn randomly rather than being determined by a movement distance.

Data from each model run of 1000 simulations were compiled by calculating the proportion of locations from each simulation that fell in each of the four habitat types. To be included in further analyses,  $>9$  locations had to be located on the mapped area of the landscape. The proportions of locations in each habitat were arcsine square-root transformed to compensate for the truncated distribution of proportions (Sokal and Rohlf 1981).



**Figure 3.** Distributions of daily distances moved ( $y$ ) for habitat-insensitive simulations. Decay functions illustrated were calculated with  $k = 1000$  and  $j = 1, 2,$  or  $3$  for the equation  $y = abs(x)^j \cdot k$ .

I generated simulations at different spatial scales by systematically changing  $k$ , producing changes in home range sizes among model runs. If there were effects due to spatial variables, I predicted that variance associated with the use of each habitat type would decrease as spatial scale (*i.e.* home range size) increased, because simulated animals within a model run would be more likely to use habitats differently if their mobility was restricted on the landscape. I also expected this effect to lead to different variances among maps with similar habitat proportions but different habitat arrangements.

To illustrate the relationship between variance in habitat use and spatial scale under a null model, I plotted the variance of habitat use for each of the habitat types against the average

home range size for each set of 1000 simulations. Fifty-seven sets of simulated movements at distinct spatial scales were plotted.

To clarify the role of landscape pattern in generating the patterns of variance in habitat use, I plotted the coefficient of variation (CV) of habitat use at each scale for each habitat, for the fall and 'random a' maps, against the ratio of average home range size to median patch size. CV controlled for the correlation between variance in habitat use and the proportions of different habitat types. The transformation on the x-axis to the ratio of average home range size to median patch size made the comparison of landscapes easier to interpret by partially controlling for differences in patch size distributions among maps. I used the median patch size rather than the average because size distributions were strongly skewed towards small patches, and the shapes of the distributions differed between the two landscapes. I used the median patch size for the entire landscape, rather than the medians for individual habitat types. Using either the overall median, or individual medians for different habitat types, produced curves of the same shape, although using different medians for each habitat shifted the curves slightly along the horizontal axis. Larger median patch sizes shifted curves to the left along the x-axis.

I also examined the relationship between variance in habitat use and the proportions of different habitats among all landscapes by plotting a scaling dimension ( $1 - D$ ; Gardner *et al.* 1989, Sugihara and May 1990), against the proportions of habitats, where  $D$  was equal to the slope of the double-log plot of variance in habitat use versus the ratio of average home range size to median patch size. To avoid distortions caused by the tails of the variance distributions, I restricted the plots to x-axis values between 0.02 and 50 (these values were the ratio of average home range size to median patch size).

$D$  is the fractal dimension and is commonly used to characterise how a measured quantity changes as the scale of observation changes (Sugihara and May 1990). In this case, it measured

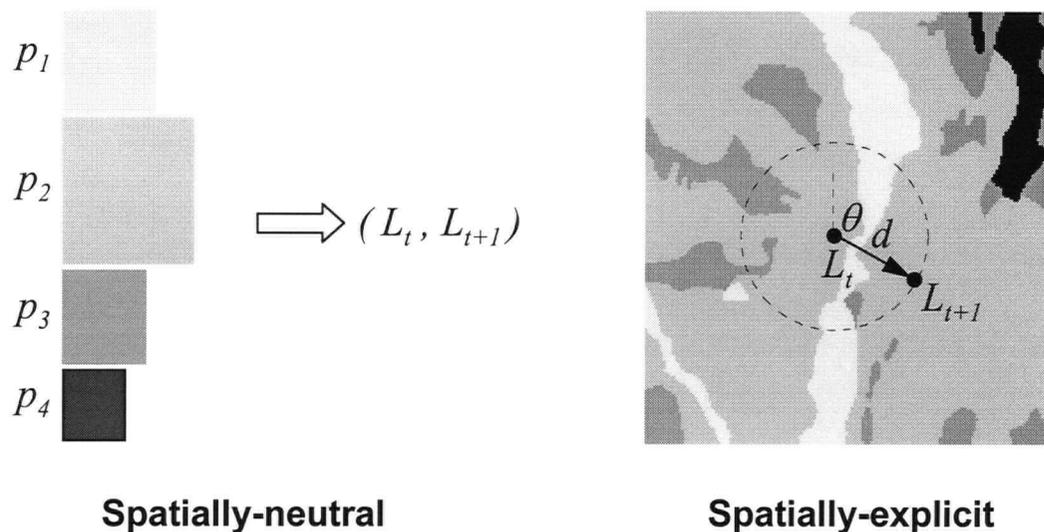
the rate of change in variance in habitat use with changes in spatial scale. Habitat types that differed in their sensitivity to scale with respect to variance in habitat use had different values of  $D$ . A high value of  $1 - D$  suggested that the distribution and abundance of a habitat type generated large changes in variance in habitat use as the scale of animal movements changed. This plot summarised the relationship among the slopes of the variance in habitat use - spatial scale curves in a manner similar to other studies examining issues of scaling in ecology (Sugihara and May 1990).

I ran parallel simulations with a spatially-neutral model to generate distributions of variance in habitat use that would be expected under a spatially-neutral null hypothesis. This model followed the structure of the spatially-explicit model and was also insensitive to the underlying distribution of habitats (Figure 2), but each new location was randomly assigned a habitat type solely on the basis of that habitat type's proportion on the landscape, rather than on the basis of a spatially-referenced movement on the landscape. As a result, no movement or landscape characteristics were considered in the spatially-neutral model, and hence there were no spatial effects by definition (Figure 4). The same results could have been derived analytically, but I used this model to parallel the construction of the spatially-explicit model.

I calculated home ranges by the fixed kernel technique (Worton 1987) with the *Kernelhr* home range program (D. E. Seaman and R. A. Powell, North Carolina State University, Raleigh, NC). Mean home ranges were calculated from the first 100 simulations of each model run because of practical computational limitations.

## Results

Both the spatially-explicit and spatially-neutral simulations produced mean proportions of habitat use that were equal to the proportions of habitat types on the landscapes. However,

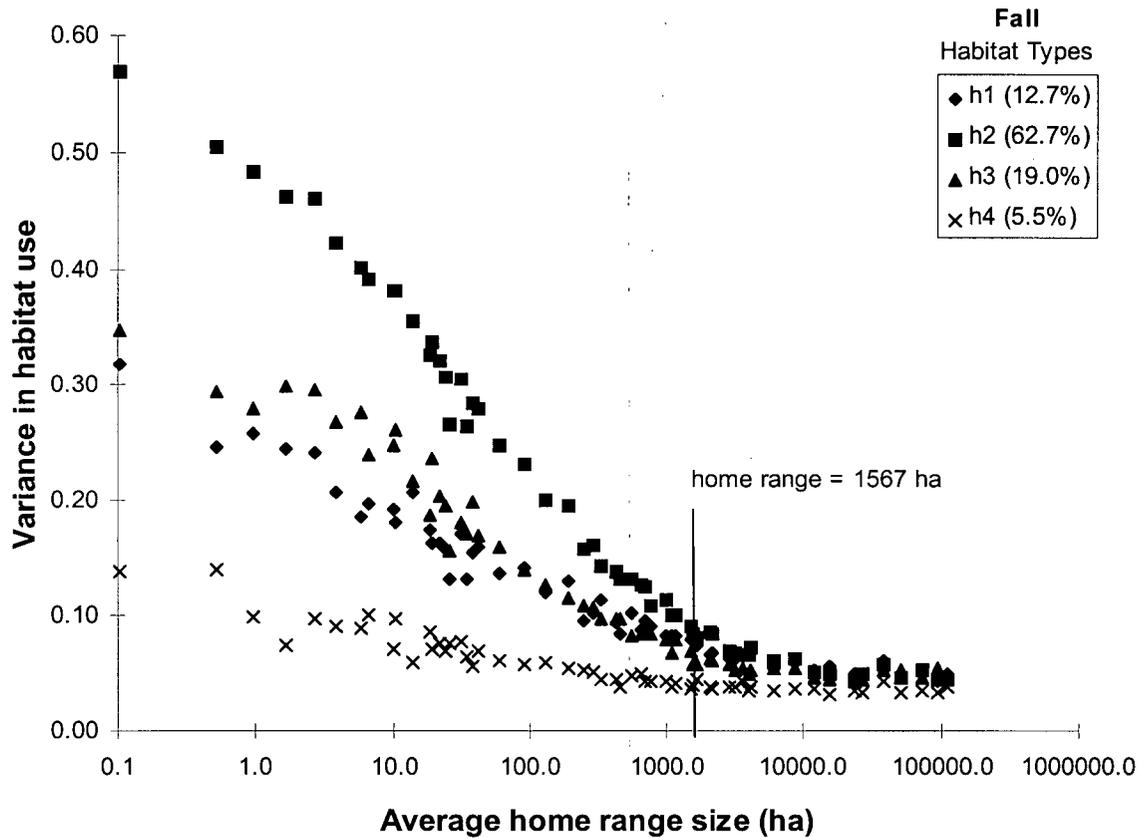


**Figure 4.** A comparison of spatially-neutral and spatially-explicit methods. In spatially-neutral simulations, locations ( $L$ ) at time  $t$  were drawn independently from habitats according to their proportions on the landscape ( $p$ ). In spatially-explicit simulations, habitat use at  $t + 1$  was a function of the initial location ( $L_t$ ), the direction of movement ( $\theta$ ), and the distance travelled ( $d$ ).

variance in habitat use differed between the two models. Variances associated with the spatially-explicit null model changed with spatial scale and were at least an order of magnitude greater than those associated with the spatially-neutral model. Variances associated with the spatially-neutral model did not differ across spatial scales (by definition). The following results refer to the distributions generated by the spatially-explicit null model simulations.

Variance in habitat use differed among habitats and landscapes, and differed among sets of animal movements with different characteristics. Variance was highest at small home range sizes and for the most common habitats in a landscape. Differences in variance in habitat use among habitats disappeared at larger home range sizes. This produced an inverse-logistic distribution of variances when plotted against home range size (log-transformed; Figure 5). I defined the ‘intersection point’ of the curves as the minimum home range size where the greatest difference among variances was <10% of the maximum variance on the graph.

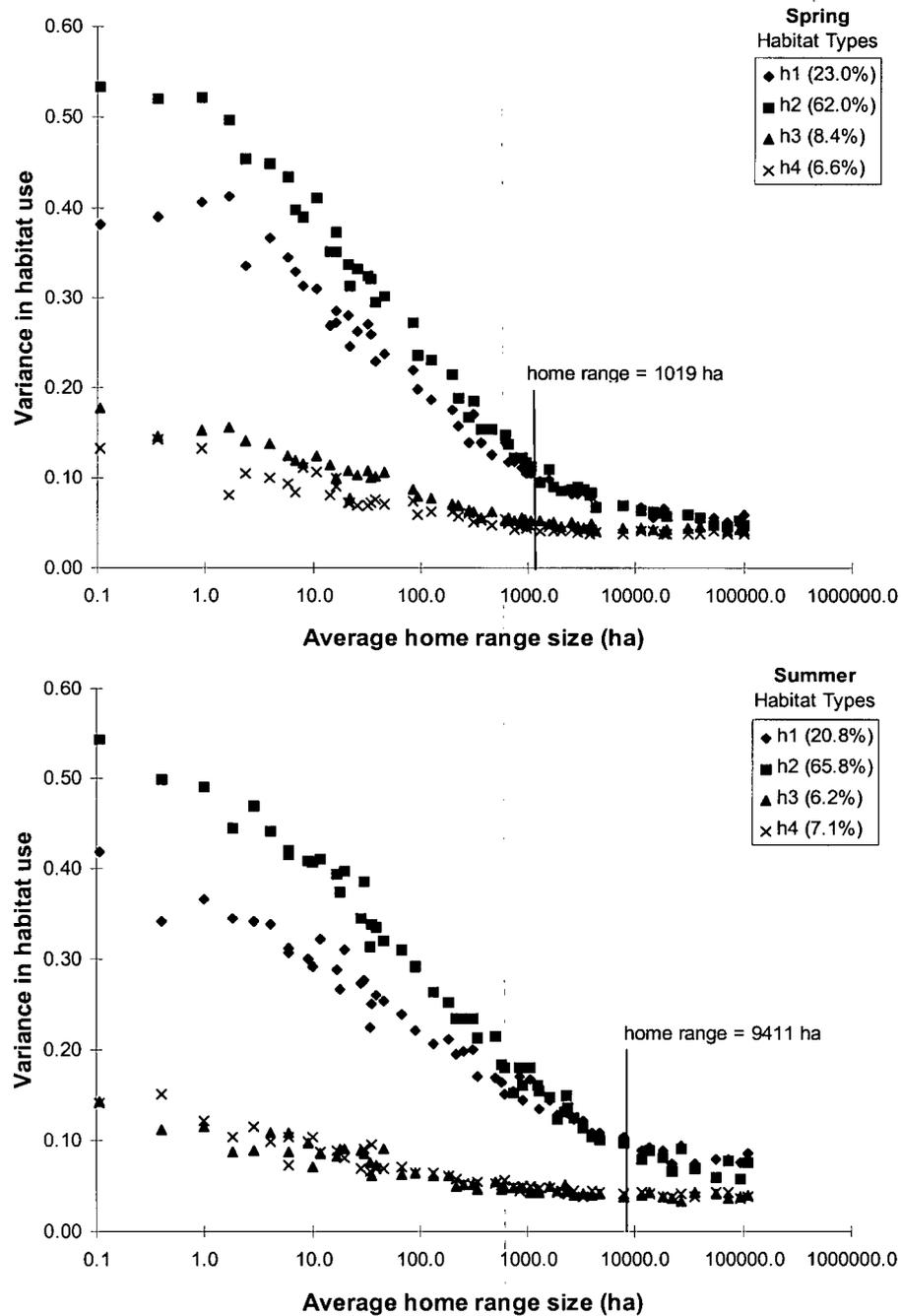
The three seasonal maps, and the 3-habitat fall map (not illustrated) produced similar plots; however, the shapes of the curves for each habitat type were related to the proportions of



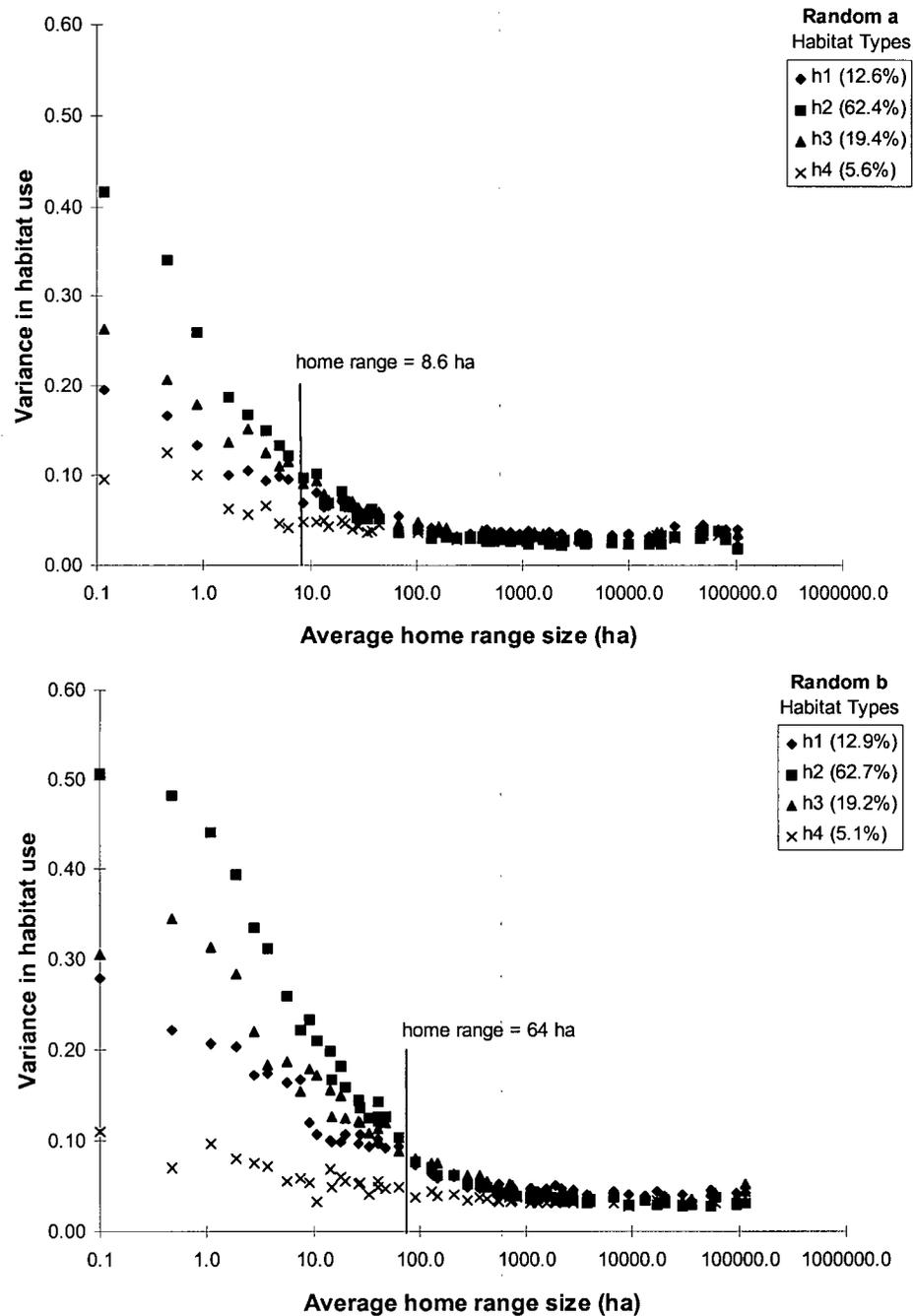
**Figure 5.** Relationship between average home range size (log-transformed) and variance in proportional use of the four habitat types. Movements were simulated on the fall map. Habitat use proportions were square-root arcsine transformed. Each point represents the mean of 1000 simulations. The vertical line marks the smallest home range size where the greatest difference among the variances was <10% of the maximum variance on the graph.

habitats on the landscapes; variances were higher at small home range sizes for more abundant habitat types (Figures 5, 6). The intersection point differed on each map in its position along the x-axis. The general shapes of the curves generated from the seasonal and random landscapes were similar, but the intersection points differed (Figure 7).

Increasing the sample size of locations from 20 to 50 points had no effect on results. Home ranges based on 50 points were larger than those based on 20 points, but the variance in habitat use associated with a given home range size, regardless of whether it was generated from 20 or 50 points, was the same. Because simulated animal movements were habitat insensitive, this



**Figure 6.** Relationship between average home range size (log-transformed) and variance in proportional use of the four habitat types. Movements were simulated on the spring (top) and summer (bottom) maps. Habitat use proportions were square-root arcsine transformed. Each point represents the mean of 1000 simulations. The vertical line mark the smallest home range sizes where the greatest difference among the variances was <10% of the maximum variance on the graphs.

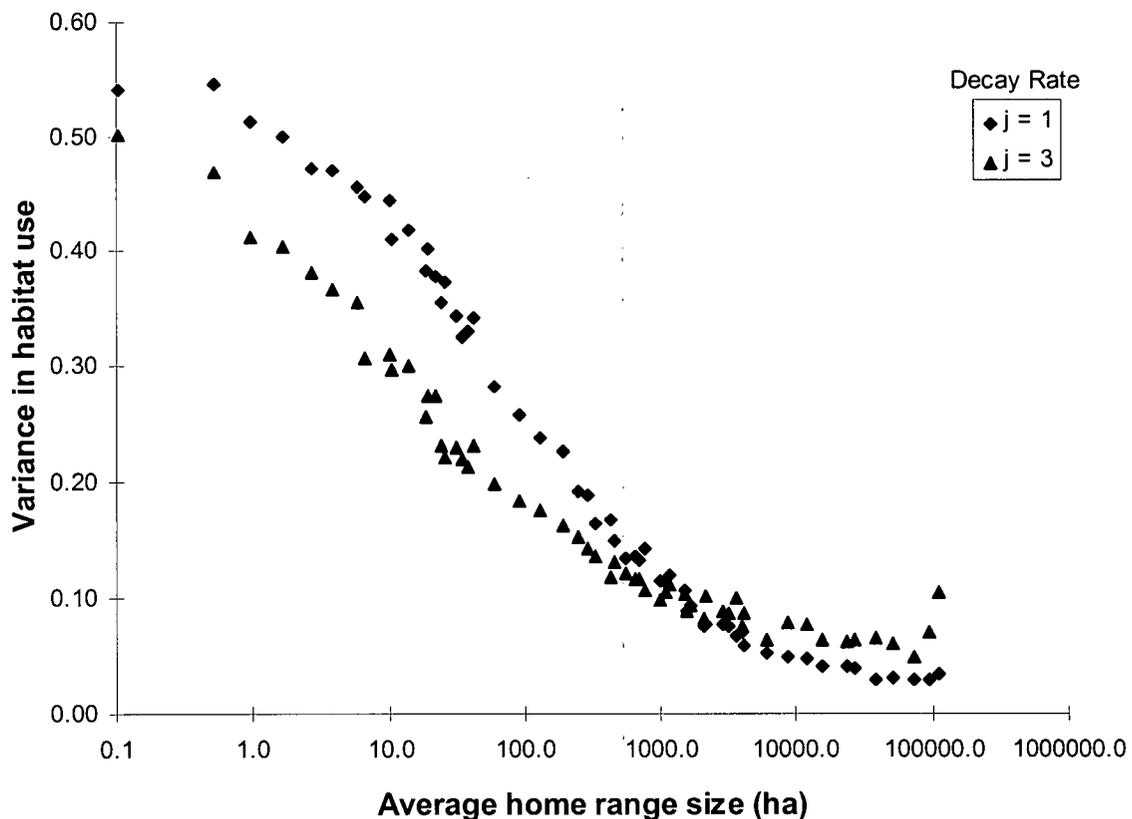


**Figure 7.** Relationship between average home range size (log-transformed) and variance in proportional use of the four habitat types. Movements were simulated on the 'random a' and 'random b' maps. Habitat use proportions were square-root arcsine transformed. Each point represents the mean of 1000 simulations. The verticals line mark the smallest home range sizes where the greatest difference among the variances was <10% of the maximum variance on the graphs.

result did not differ among different landscapes.

Restricting starting points to an area smaller than the entire landscape ('biased simulations') affected the shape of the variance curves for simulations based on the fall map, but not for simulations based on the 'random a' map (not illustrated). Variance curves for the biased simulations based on the fall map were shallower than those based on unbiased simulations, although the shapes were very similar.

The shapes of the distributions of daily distances moved affected the variance-home range plots. Distributions based on higher values of  $j$  (producing long, flat tails in the frequency distributions; Figure 3) flattened the variance curves (Figure 8). Increasing the value of  $j$



**Figure 8.** Effect of varying the shape of the distribution of daily distances moved on the variance in habitat use across home range sizes. Habitat type h2 is illustrated. Curves for  $j = 1$  and  $j = 3$  in the equation:  $y = abs(x)^j \cdot k$  are illustrated. The shapes of the distributions are illustrated in Figure 3. More skewed distributions flattened the curves.

increased the coefficient of variation (CV) in home range size among simulations. CV for  $j = 1$  averaged 61%, while for  $j = 3$ , CV averaged 121%. A more skewed distribution of daily movement distances generated more variable home range sizes.

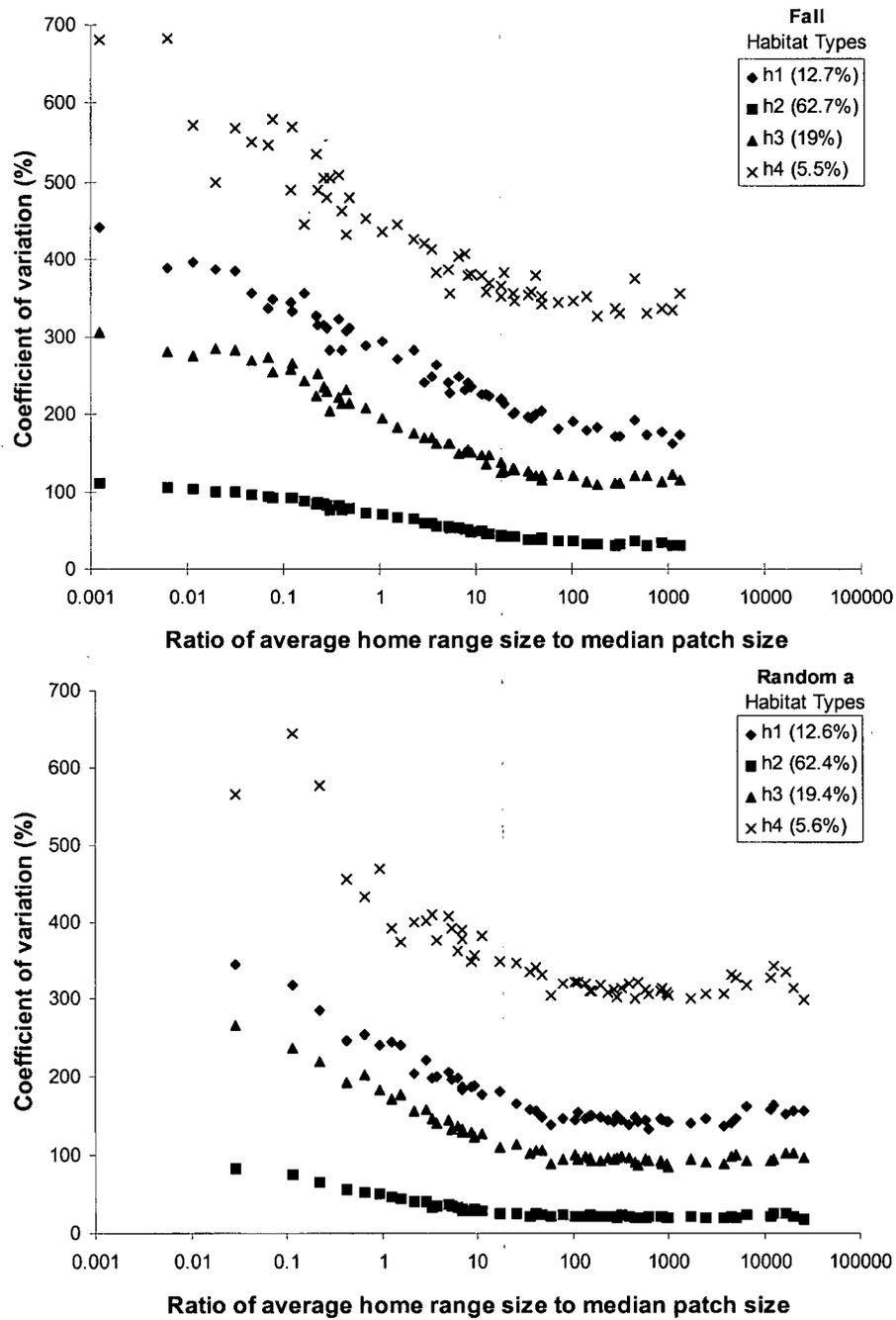
Plotting CV in habitat use against the ratio of home range size to median patch size (of all habitat types combined) controlled for the correlation between habitat quantity and variance in habitat use, and allowed the direct comparison of landscapes with different patch sizes (Figure 9). The differences among the slopes were much smaller on these plots when compared to Figures 5, 6 and 7. In addition, the rank order of the habitat types from highest to lowest variance were the reverse of those on the variance home range plots.

The reason for the reversal was likely related to the small denominator used to calculate CV for rare habitat types. Within regions of relatively constant slope, the slopes were steeper on the random map than on the fall map (Figure 9).

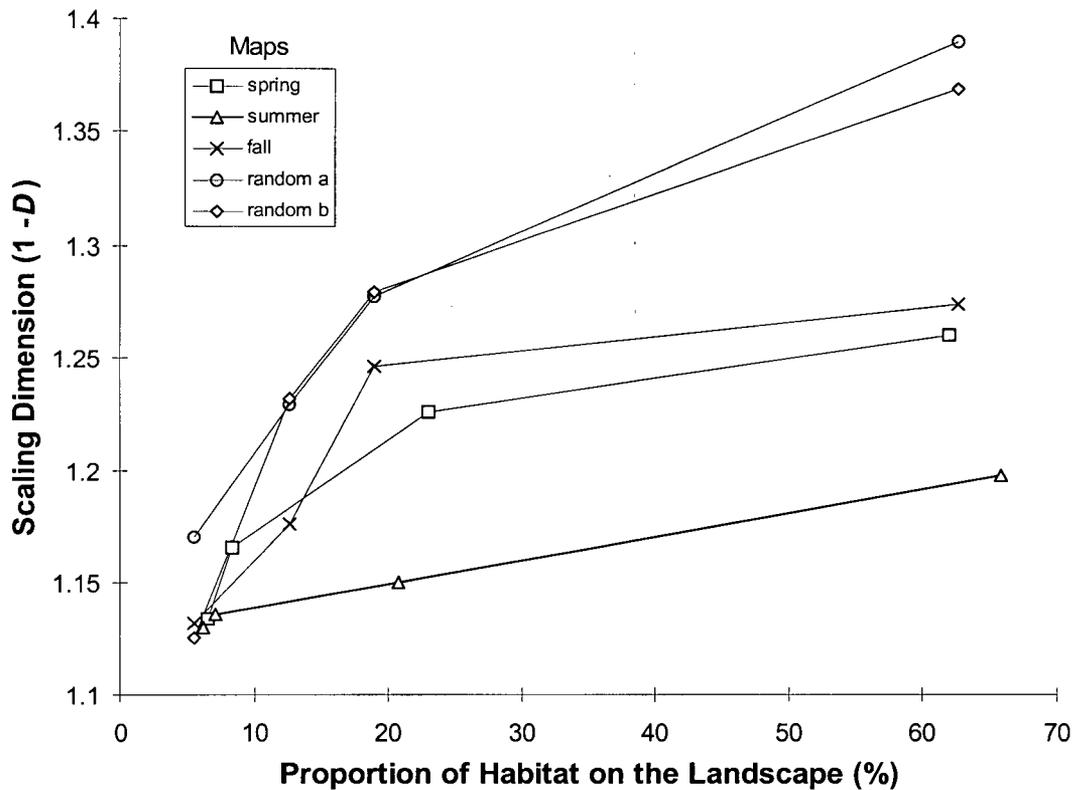
Variances in use of more common habitats were generally more affected by changes in the scale of animal movements (Figure 10). Across maps, the magnitude of the scaling dimension was also weakly related to contagion; variance in habitat use was more strongly affected by scale on maps with lower contagion values.

## Discussion

Habitat use analyses usually test a null hypothesis which asks whether animals use habitats in proportion to their availability. The results from the simulations in this chapter suggest that the variances associated with the use of habitats expected under the null hypothesis, differ between spatially-explicit and spatially-neutral hypotheses, and in the spatially-explicit case, also differ across spatial scales. That is, the predictions of a spatially-neutral null model will not reflect expected habitat use when there are significant spatial effects. The patterns of variance in



**Figure 9.** Relationship between the ratio of average home range size to median patch size (log-transformed) and coefficient of variation in habitat use. Model parameters were the same as those in Figures 5, 6, and 7.



**Figure 10.** Relationship between scaling dimension ( $1 - D$ ) and the proportions of habitat types for all the maps with four habitats (see Table 1). Scaling dimension is simply one minus the slope of the log-log plot of the variables plotted in Figure 9. Only average home range size to median patch size ratios between 0.02 and 50 were considered.

habitat use for the spatially-explicit simulations suggest the circumstances for which spatial effects can be expected to influence the results of habitat use analyses.

#### *Understanding Patterns of Variance in Habitat Use in the Spatially-explicit Model*

The relationship between variance in habitat use and average home range size that was generated by the spatially-explicit model was similar among all the landscapes that I analysed. All of the variance curves had the characteristic inverse-logarithmic shape, with apparent asymptotes at very small and very large home range sizes on most maps. This shape described the general relationship between variance in habitat use and spatial scale for the spatially-explicit model.

Other theoretical studies have demonstrated the existence of critical thresholds in spatial patterns which identify changes in important variables above and below critical scaling limits (in double-log plots; Turner *et al.* 1989a). In my analysis, there were no such sharp discontinuities, but there were three different phases to the curves for each habitat type in each simulation. These areas of relatively constant change in variance with changes in home range size, indicated the existence of 'domains of scale' (Wiens 1989). The asymptotes at very small and at very large home range sizes indicated the scaling limits imposed by the characteristics of the maps. At these asymptotes, variance ceased to be a useful measure for describing the scaling properties of the interaction between animal movements and landscape pattern. For example, the variance in habitat use of the habitat types on the fall map (Figure 5) were almost the same for home ranges >5000 ha. For animals with home ranges of this size and larger, habitat use inferences could be made with little regard for the spatial characteristics of the fall landscape.

The distinctiveness of the three phases of the variance curves was most evident for the most common habitat types. One of the principal reasons for this was that the more common types could comprise more variable proportions of each home range. For instance, a rare and widely scattered habitat type could never comprise a large portion of an animal's home range. However, a common habitat type could completely fill a home range or be completely absent, depending on the location of the home range on the landscape, and on the size and distribution of habitat patches. In effect, variance in habitat use was positively correlated with the proportions of habitats on the landscape. Correlations of this kind are a well known statistical property, but their potential effects have not been considered in habitat use analyses. My analyses suggest that their importance will depend on the relative spatial scale of investigation.

Theoretically, a curve should have reached an asymptote at a point where entire home ranges fell completely within a single pixel. Variance is maximised at this point because proportional

use of habitat can be only 0 or 100%. Therefore, the grain of the map (pixel size) sets the point at which variance in habitat use is maximised. In practice, results at this resolution are trivial; if animals are to use different resources, their home ranges should never fall within a single pixel. If they do, the habitat has been mapped at an inappropriate scale to identify the differential use of resources by animals (Kotliar and Wiens 1990).

Beyond the absolute limit of resolution governed by a map's pixel size, patch size also imposes a practical limit. Below a particular size, home ranges can fit completely within a single patch. At this point, the variance is also maximised, for the same reasons given above. However, this home range size will vary for each habitat type, because habitat types differ in average patch size. In general, the most common habitat has the largest patches, and larger home ranges can fit entirely within these patches than within the patches of rare habitats. This suggests that the variance curves should reach asymptotes at different home range sizes, with the curve for the most common habitat type flattening at the largest home range. However, the variance curves are not independent; the amount of the most common habitat type constrains the variance of the other habitat types and affects the shapes of their curves. Also, when variance in habitat use of the most common habitat is small, then variances associated with other habitat types must also be small.

Variance in habitat use decreased as home range size increased. Although the curves changed at different rates, the slope was greatest for the most common habitat type. At large home range sizes the different variance curves converged. The intersection point was where most home ranges contained a proportion of each habitat type similar to the habitat's proportion on the landscape. Because simulated animals had no habitat preferences, the sets of simulations with large home range sizes most closely reflected the predictions of the spatially-neutral null model; that is, spatial effects were minimised at large home ranges where variances were low and

curves flat. However, variances were still an order of magnitude larger than those generated by the spatially-neutral simulations.

Variance in home ranges size affected the shapes of the variance curves. Where home range size was more variable (higher values of  $j$ ), variance in habitat use curves tended to be flatter. Normally of course, home ranges vary in size within species, although the differences between home range sizes may be correlated with important variables that should not be pooled (age, sex, reproductive, season, etc.; e.g. Schooley 1994).

### ***Landscape Pattern***

Fahrig (1997) suggested that, in some landscape ecology studies, the effects of absolute amounts of habitats may have been understated and the effects of spatial pattern may have been overstated because the variables are rarely varied independently. In my study, the proportions of different habitat types (and the resulting correlation with variance in habitat use) were the most important variables affecting the shapes of the variance-home range curves, although the distribution of patch sizes and their arrangement also affected results. The size and spatial distribution of patches are related characteristics; when patches are smaller, different habitat types can be more interspersed. Variables that measure spatial distribution of habitat types such as contagion (based on pixel adjacencies) and *Fragstat's* interspersion/juxtaposition index (based on patch adjacencies) tend to vary with changes in patch size distributions.

The effect of patch size and distribution was clear from comparisons of curves for different maps. For example, the upper curves for the fall and summer maps ( $h_2$ ; Figures 5, 6) were generated from similar habitat proportions, but the summer curve was considerably flatter, probably reflecting its higher average patch size (Table 1).

Combining two rare habitat types on the fall map (3-habitat fall map, Table 1) did not influence the shapes of the remaining variance curves. This may at first appear at odds with the fact that the curves were not independent; however, the lack of independence was due to the unit-sum constraint of habitat proportions (Aebischer *et al.* 1993). Simply summing two proportions did not influence the proportional use of the other two habitat types. Conversely, the effect of increasing the number of habitats by classifying one of the four habitats into additional types would have resulted in flatter curves for the resulting subdivided habitat types, with no effect on the curves for the other habitats.

The role patch size and distribution played in defining the variance curves was also clear in the results for the random landscapes, dominated as they were by small and evenly distributed patches. Small patches pushed the intersection of the variance curves to the left along the x-axis. That is, even small home ranges on the random landscape consisted of representative proportions of the habitat types (Figure 7).

When I controlled for the differences among maps in the ratio of home range size to median patch size, and for differences caused by the correlation of variance in habitat use with proportion, the resulting curves still had a characteristic shape. These differences were primarily the result of the different spatial arrangement of habitat patches on the maps, independent of differences in median patch size. Variance in habitat use was scale dependent over a smaller range of animal movement scales on maps with more evenly distributed habitat types (low contagion; *e.g.* 'random a' map), than on maps with more clumped distributions (higher contagion). An additional effect of an even distribution of habitat types was to maintain low, stable variances at smaller home range sizes (relative to patch size).

The influence of landscape pattern was not always clear from the model simulations. This was probably due to the large number of simulations run on each landscape, and to the starting

points being completely random. This generated large, unbiased but area-restricted sampling of the landscape. Simulations with restricted starting points generated different variance curves than simulations with random starting points, although the effects were relatively minor. Curves of variance in habitat use were similar in shape, although variances tended to be lower at smaller home range sizes than in unbiased simulations. Because simulations were started on a smaller area of the landscape (smaller map extent), there was less overall variation in habitat composition among home ranges.

The interaction between map extent and patchiness, and its effect on habitat use analyses, was first suggested by Porter and Church (1987). They noted that changing the boundaries of a map (the extent) could affect the measurement of habitat selection, particularly if the landscape was composed of a few, large patches. This is the effect that I detected when comparing unbiased simulations to simulations with biased starting points. Reducing the area on which the simulations were started, effectively reduced the extent of the sampling area, which in turn reduced the variation in the habitat composition of home ranges. However, the effect on curves of variance in habitat use was only obvious on the seasonal maps, which were dominated by fewer, larger, less evenly distributed patches than were the random maps. Therefore, contagion was a useful measure for distinguishing trends in variance in habitat use.

Map extent has attracted attention in the habitat use literature (*e.g.* Porter and Church 1987), although the language has often been different than that used here. Defining habitat available to animals is largely an issue of defining an appropriate mapping extent. By dividing selection analyses into different orders, Johnson (1980) was effectively determining habitat availability within different mapping extents. Many subsequent studies have followed Johnson's suggestion and analysed habitat use at more than one scale, although many researchers have used the same location and/or mapping data to test selection within a study area and within home ranges (*e.g.*

Aebischer *et al.* 1993, Mauser *et al.* 1994, Carroll *et al.* 1995). This erroneously treats the two selection events as independent, although the same location data are tested twice, and the selection behaviour at larger scales constrains selection at the smaller scales.

### ***Summary of Spatial Effects***

How do these results suggest better study designs? Measuring habitat at scales relevant to the study animal reduces the errors that occur with the arbitrary imposition of mapping scale (Burrough 1981, Addicott *et al.* 1987, Wiens and Milne 1989). Using simulations to generate expected patterns of habitat use under a spatially-explicit null hypothesis can help to identify appropriate scales, and also illustrate the consequences of choosing an inappropriate scale.

The ratio of home range size to median patch size can serve as a rough indicator of the potential for spatial effects. In my simulations, variance in habitat use began to increase when home ranges were less than about ten times the median patch size. This effect is independent of the number of habitat types. The more habitat types on the landscapes, the smaller the median patch size, and the smaller the effect of spatial variables at a given home range size. The ratio of home range to patch size would be a simple statistic to include in published studies of habitat use. Although researchers often report home range sizes, they rarely include patch size characteristics with descriptions of study areas (Wilson, *in prep.*).

I emphasise that the ratio of average home range to median patch size is only a rough estimation of the probability of spatial effects. The median patch size that generates adequately low variances in habitat use will differ for each research circumstance, depending on several different variables, including those which I examined in this chapter (*i.e.* characteristics of daily movement distances, spatial distribution of starting points, various landscape characteristics).

The relationship between spatial scale and variance in habitat use also suggests that the power of statistical tests to examine habitat use will change with scale. Where home ranges are small in relation to average patch size, more animals will be required to detect a given effect size than where home ranges are large.

Researchers should also consider the possible effects on analyses of the correlation between variance in habitat use and habitat proportions. The effects can be significant where home ranges are small relative to the size of habitat patches.

Beyond the methodological issues for researchers, land managers should exercise caution when basing management decisions on the results of habitat use studies. For example, high variances in use of certain habitats by sampled animals may be an artefact of spatial variables, rather than an indication of differences in individual behaviour. Common habitat types, or habitats that consist of large patches relative to the mobility of animals, are particularly vulnerable to this effect.

The results of the simulations in this chapter generate a number of interesting questions that could be tested in field studies. Examples include: 1) does reclassifying several habitat types into one make null hypotheses about habitat selection more difficult to reject?; 2) within a study, is there a correlation between the size of home ranges and the likelihood of detecting habitat selection?; and 3) is the failure to reject the null hypothesis of no selection due to the use of a habitat type in equal proportion to its availability, or due to high variance in use among individuals? Examining questions such as these in the context of field studies could provide evidence for the relationships I have described in simulated data.

## Chapter 4. Effects of Habitat Affinity on Habitat Use

### Introduction

In Chapter 3, I examined the effect of spatial variables on habitat use across a variety of scales, using simulated animal movements insensitive to the quality of different habitat types. Of course real animals are not expected to use habitats in proportion to their availability. They are sensitive to different habitats in their environment, and their use of habitats is expected to differ from that predicted by a null model.

Examining how animals differentially use habitats in space and time is the purpose of most telemetry studies (Stoms *et al.* 1992, Arthur *et al.* 1996). Differential habitat use is usually reported as selection or preference index values, where selection is defined as the use of habitats disproportionately from their availability, and preference as the likelihood that a habitat would be chosen if offered on an equal basis with others (Johnson 1980). Habitat use studies usually test a simple hypothesis: whether habitats are used in proportion to their availability (Alldredge and Ratti 1986). In practise, this hypothesis is usually rejected in published studies; a failure to reject this null would suggest that habitats had been categorised or mapped incorrectly for the species in question.

The spatial dimension of use-availability data is not considered in analyses of selection and preference, except where the analysis is repeated at different 'levels of selection' (Johnson 1980). However, this only captures the spatial effects of different mapping extents, it does not address the possible effects of other variables, such as the characteristics of animal movements or the arrangement of habitat patches (*c.f.* Porter and Church 1987, Otis 1997). Hence, the role of spatial variables in determining the preference of animals for different habitats is largely unknown.

A central difficulty in studying the effects of spatial variables on habitat use in the field is that the true behaviour of animals is unknown. Therefore, the problem lends itself well to modelling where behaviour can be defined by specific rules and sampled without error. However, a complication arises when modelling differential habitat use because there are few studies that have addressed how animals should move among habitats to maximise fitness (Milne 1988, Lima and Zollner 1996). The issue has been studied in the context of optimal foraging (*e.g.* Pyke 1978), but the design and purpose of habitat use studies do not immediately suggest a simple currency to maximise, because habitat use is assumed to be correlated with a host of life history requisites.

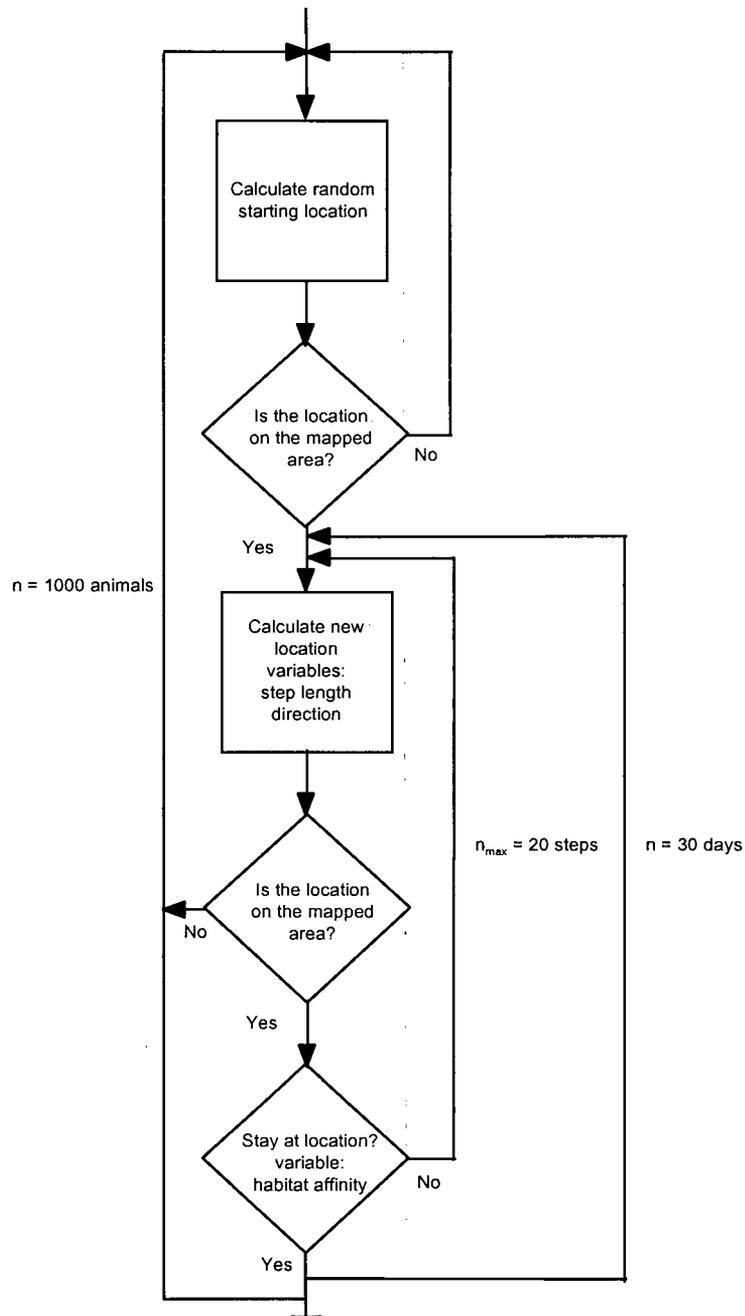
In this chapter, I examine the effects of spatial variables on habitat use by first introducing a currency of value called 'habitat affinity', which is simply the likelihood that an animal will remain in a patch for the rest of the day. I present this currency as a simple behaviour rule to serve as a starting point to examine the optimal movements of animals in the context of habitat use studies. In addition to a currency of habitat value, habitat-sensitive modelling requires a rule to define the information available to simulated animals about their habitats. I use an 'information-free' approach (Lima and Zollner 1996) in which animals have no information about habitats before they arrive, either from prior experience, or from environmental cues about distant habitats. Although they have no information about surrounding habitats, they know the value of the patch in which they are located. I use this rule to minimise assumptions, and also to provide a contrast with the omniscience assumption of use-availability analyses. The approach that better approximates the behaviour of animals is unknown, but the different assumptions affect the inferences we make about the relationships between wildlife and their habitats.

Using habitat affinity as the basis for making my models habitat-sensitive, I then develop spatially-neutral and spatially-explicit models to examine how habitat affinity, landscape pattern, and the scale of animal movements interact to generate habitat selection. Specifically, I pose the following questions: 1) does habitat affinity affect measures of habitat preference differently for spatially-explicit and spatially-neutral models?; 2) how do habitat affinity and landscape characteristics interact to influence measures of habitat preference?; and 3) how well do different measures of habitat preference reflect habitat affinity, given the influence of spatial variables?

### Methods

The spatially-explicit model used to generate simulations in this chapter was based on the correlated random walk model used in Chapter 3, but modified to make animal movements sensitive to the underlying habitat. The model was written in *Borland C++ 1.0* (Borland International, Inc., Scotts Valley, CA; Appendix III). Modifying the model to make it habitat-sensitive required a number of changes (Figure 11). First, modelled animals made at least one or several small steps of equal length per day, as opposed to the one step of variable length per day used in the Chapter 3 model. This introduced two new variables: step length and the number of steps per day.

In addition, 'habitat affinity' provided the sensitivity of modelled animals to the underlying habitats. Habitat affinity was the probability that an animal would remain at a location for the rest of the day. This was the currency of value that I defined for habitats. It was meant to represent a composite rating of all the characteristics that contribute to the life history requirements of simulated animals on a daily basis. Habitat affinity values were defined for



**Figure 11.** Structure of the habitat-sensitive, spatially-explicit model. Simulated animals moved at least one step per day. Step-length was varied from 1 to 20 map pixels in different simulations. The structure of the spatially-neutral model was the same, except that subsequent locations were drawn randomly rather than being determined by a movement distance.

each of the habitat types, and remained constant through the sampling period. Note that habitat affinities were absolute values and did not depend on the relative affinities of other habitats.

In reality, the value of habitats reflects a mix of depletable or seasonal and non-depletable resources, and some real habitats contain only a single resource used by animals (*e.g.* mineral licks, water holes, dens). I used the simple concept of habitat affinity to minimise assumptions.

Model runs consisted of 1000 simulations of 30 days each. Each simulated day consisted of up to 20 steps. Step length was varied between 1 and 20 map pixels for different model runs. Each map pixel was 50 m x 50 m, and this unit set the lower limit of the scale for modelled movements. Step lengths were measured in pixels rather than in metres because pixel-to-pixel distances were slightly longer if movements occurred along the four diagonal directions than along the four cardinal directions. Changing step lengths among simulations allowed me to vary the scale of animal movements, and hence, the size of home ranges. As with the model used in Chapter 3, correlated animal movements reduced the size of home ranges compared to an uncorrelated model, but the home ranges had no central tendency. Hence, increasing the step length always increased home range size. A consequence of this was that there was no difference between varying step length and changing the sampling frequency of animals. Therefore, I held sampling frequency constant at one location per day and varied step length only.

Habitat affinities were varied between 10% and 100% for one habitat type at a time. Other habitat affinities were held constant at 0%. To test the effects of moderate 'background' affinities, I also ran simulations where affinities were increased from 0% to 20%. As a result, I only modelled two different habitat affinities at a time among four habitat types (see Chapter 5 for an example for modelling four different affinities simultaneously). Because affinities

affected daily movement distances, they also affected home range sizes; higher habitat affinities resulted in smaller home ranges.

I used the fall and 'random b' maps for the simulations (Table 1, Figure 1). These maps had identical habitat proportions but differed in the size and distribution of habitat patches (Chapter 2). I restricted simulations to these maps to simplify the interpretation of results. I used the 'random b' rather than the 'random a' map because of the larger patches on the 'random b' map; the lower limit of movements for the habitat-sensitive model were still several times the average  $x$  or  $y$  dimension of most patches on the 'random a' map.

I also ran parallel simulations with a spatially-neutral model to distinguish trends in preference analyses resulting from spatially-neutral effects. Because preference is a relative measure of habitat value and habitat affinity is absolute, I predicted that the two measures would not always correspond, regardless of the effects of spatial pattern. The spatially-neutral model followed the structure of the spatially-explicit model (Figure 11), except that each new position was randomly assigned a habitat type solely on the basis of that type's proportion, rather than on the basis of a spatially-referenced movement (Figure 4). As a result, there was no step length. This procedure was similar to one used by Alldredge and Ratti (1986, 1992) to examine rates of type I and type II error among four habitat use analysis methods. However, they determined habitat use on the basis of random draws from *a priori* 'used' habitat proportions, rather than using the concepts of steps and habitat affinity that I used.

The random starting points of simulated animals may produce a spatial effect, and to examine the effect of this model parameter, I also ran simulations that did not begin to record the locations of simulated animals until they had already made 30 daily movements.

I used three indices to examine results: one based on differences between use and availability, one based on ratios, and one based on ranks (Appendix IV). The difference method I used was

Strauss' Linear Index ('SLI'; Strauss 1979). SLI has a number of properties that make it ideal for analysing these types of simulations (Lechowicz 1982). The index varies linearly from -1 to 1, allowing the use of inferential statistics. This was particularly important because I calculated means and dispersions across the 1000 simulations of each model run. The primary drawback of the index is that values cannot be compared across maps with different proportions of habitat. This is important for researchers who make inferences across several, diverse sites (Lechowicz 1982). However, the proportions of different habitats on the maps that I used for simulations did not differ.

For comparison purposes I also analysed simulations with Chesson's (1983) index. 'Chesson's alpha' is essentially a normalised forage ratio, and is unaffected by different habitat proportions, unlike SLI. However, it is a non-linear index, so changes in used or available habitat proportions do not produce consistent changes in alpha across all values of use and availability (Lechowicz 1982). This hampers statistical analysis and reported means and measures of dispersion should be interpreted with caution. The index varies from 0 to 1, with 'preference' indicated by values greater than  $1/n$ , where  $n$  is the number of habitats (in this case, four).

Both SLI and Chesson's alpha are affected by the unit-sum constraint of proportions (Aebischer *et al.* 1993). To address this problem, I also analysed simulations with Johnson's (1980) method. This method is similar to SLI in that it calculates a difference between use and availability, but uses relative ranks of both the use and availability of different habitats. The resulting 'Johnson ranks' are averaged among animals. The ranks are normally distributed and can be used in parametric statistical tests (Johnson 1980). Alldredge and Ratti (1986, 1992) discuss the advantages and disadvantages of this method.

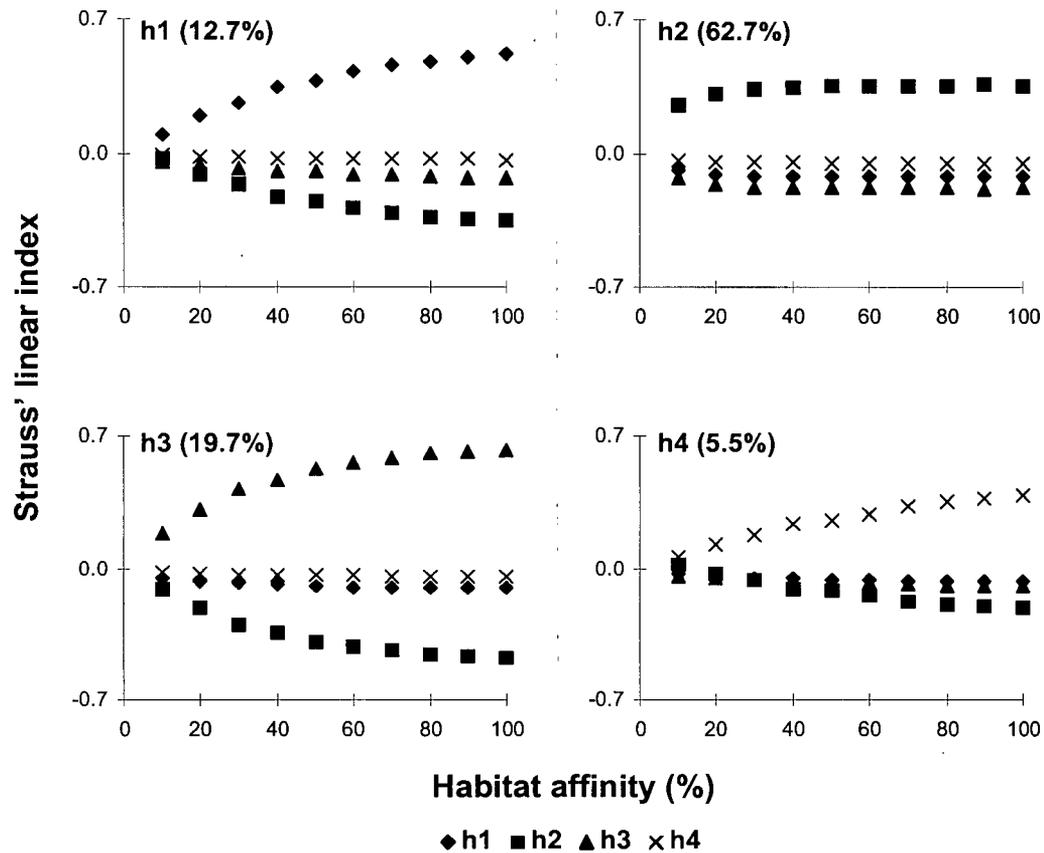
SLI and Johnson ranks are selection indices, while Chesson's alpha is a preference index because habitat availability is normalised (Johnson 1980, Chesson 1983). However, Johnson (1980) refers to differences in selection indices as indicating preference, and I use this convention in reporting results from all three indices.

I chose these three methods for their relative simplicity and applicability to use-availability problems. Logistic or other regression methods appear in the literature, however, they have been used to compare used and unused sites, or to generate statistical models of habitat preference across a number of variables or map layers (*e.g.* Pereira and Itami 1991, Manly *et al.* 1993, Mladenoff *et al.* 1995), rather than the more common approach of determining habitat availability based on map coverages. Other methods were unsuitable for this study because they were based simply on confidence intervals (Neu *et al.* 1974).

Sample sizes were large enough that confidence intervals ( $\pm 2$  SE) for mean index values were very small (typically two orders of magnitude smaller than means); hence, error bars were omitted from graphs for legibility.

## Results

Habitat affinity values had a strong effect on the SLI analysis for both the spatially-explicit and the spatially-neutral models, although the relationship was not linear. In other words, the measured preference of animals for different habitat types was related to the habitats' perceived value (*i.e.* affinity), but other variables affected the correspondence between the two measures, producing curves that approaches asymptotes at higher affinity values (Figure 12). The relationship between habitat affinity and SLI values depended on the proportions of different habitat types on the landscapes. SLI values were higher for more common habitats at a given affinity. The only exception to this was h2, the most abundant type. The curve defining the



**Figure 12.** Relationship between Strauss' linear index (SLI) and actual habitat affinity for simulations on the fall map. Each point represents 1000 simulations. Each simulation modelled movements for 30 days, with 20 movements (each of 5 pixels) per day. Affinity values were varied for one habitat type at a time and are graphed separately (h1 - h4; proportions for the fall map are in parentheses). Habitat affinity was held at 0% for the other three habitat types in each graph.

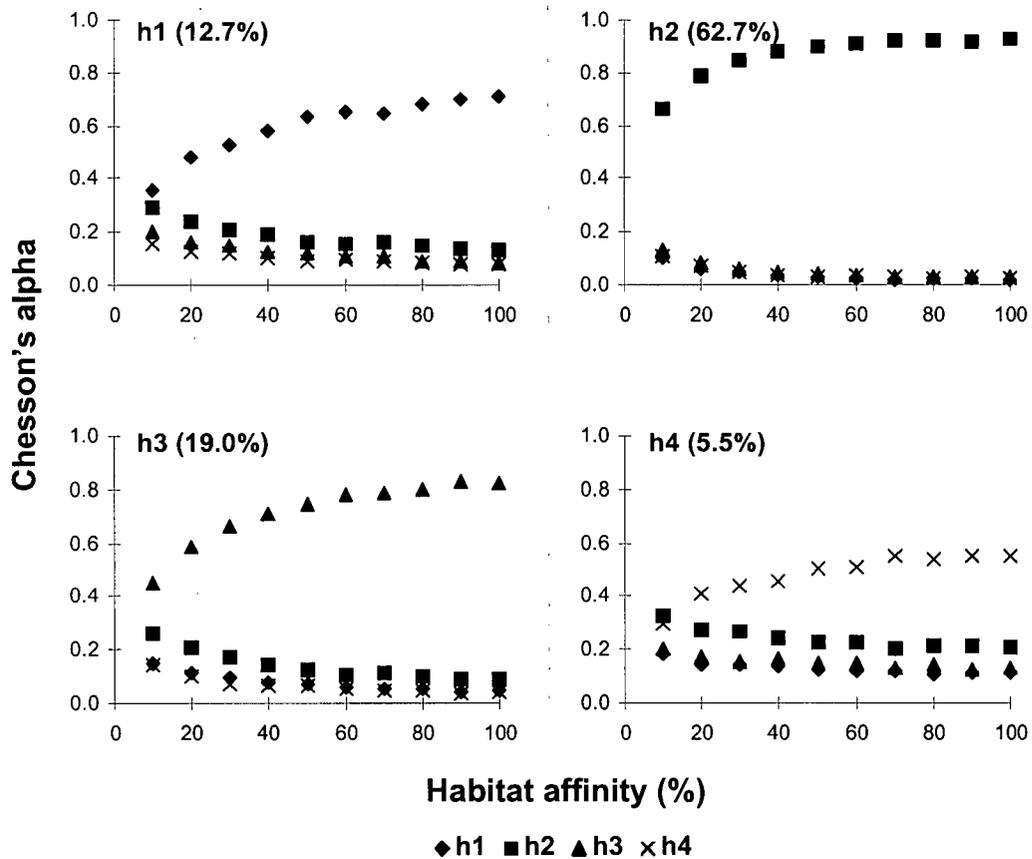
relationship between affinity and selection for this habitat reached an asymptote near its highest theoretical SLI value ( $1 - p$ ; Figure 12).

There was only one case among all simulations where there was ambiguity in the habitat preference results. That was in the case of h4, the rarest habitat type, where an affinity of 10% produced an SLI that was only slightly greater than the SLI of the most common habitat type, h2, even though the affinity of h2 was 0%.

SLI values for different habitat types on the same landscape were not independent. Hence, when affinities were held constant for all but one habitat type, the habitats assigned affinities of

0% almost always had negative SLI values. The magnitude of these three values varied directly with their own proportion on the map, and inversely with the proportion, and directly with the affinity, of the other habitat type (Figure 12). For example, h2 had the most negative SLI values when a habitat affinity >0% was assigned to any one of the other three habitats (Figure 12).

I reanalysed the same simulations using Chesson's alpha (Figure 13). Curves for habitat types with >0% affinity were similar to the results of the SLI analysis, with magnitudes of alpha still sensitive to the amount of the habitat. For habitat affinities of 0%, Chesson's alpha was more effective than SLI at controlling the impact of different habitat proportions, although

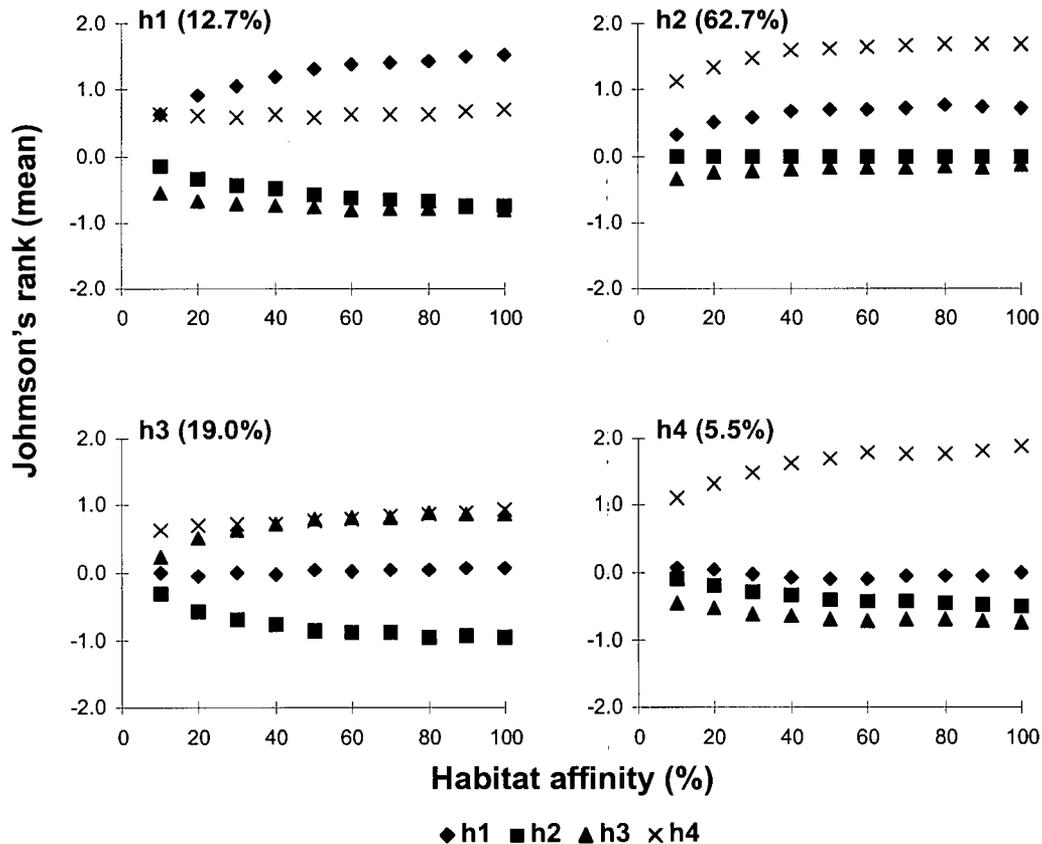


**Figure 13.** Relationship between Chesson's alpha and actual habitat affinity for simulations on the fall map. Each point represents 1000 simulations. Each simulation modelled movements for 30 days, with 20 movements (each of 5 pixels) per day. Affinity values were varied for one habitat type at a time and are graphed separately (h1 - h4; proportions for the fall map are in parentheses). Habitat affinity was held at 0% for the other three habitat types in each graph.

proportions still affected alpha values.

For example, h2 had alpha values greater than 0.25 (*i.e.*  $>1/n$ , therefore indicating preference, although the actual habitat affinity was zero) when rare habitat types had affinities of 10-20%. The rank order of preference for h2 was greater than h1 or h3 across all simulations where the affinity for all three habitat types was held at 0%.

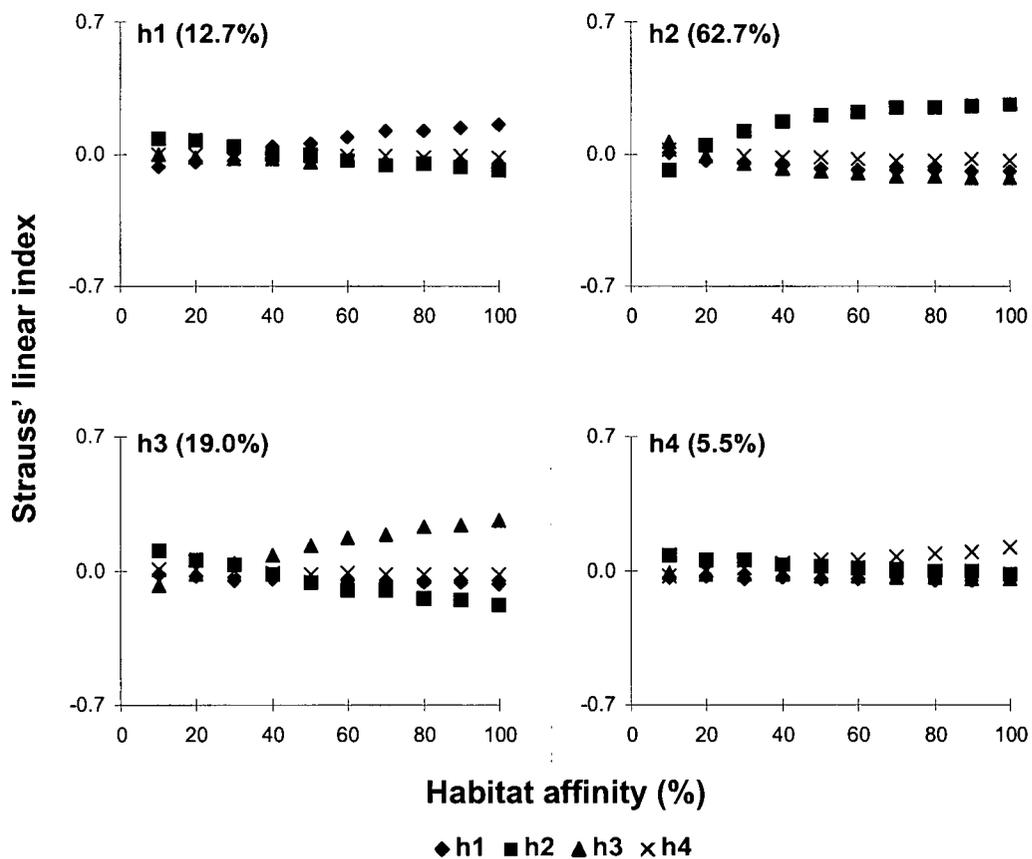
Johnson's (1980) ranking method misidentified preference for the rarest habitat type (h4) in all simulations where its affinity was held constant at 0% (Figure 14). The magnitude of the preference was related to the amount of habitat with an affinity  $>0\%$ . For instance, where



**Figure 14.** Relationship between Johnson's rank and actual habitat affinity for simulations on the fall map. Each point represents 1000 simulations. Each simulation modelled movements for 30 days, with 20 movements (each of 5 pixels) per day. Affinity values were varied for one habitat type at a time and are graphed separately (h1 - h4; proportions for the fall map are in parentheses). Habitat affinity was held at 0% for the other three habitat types in each graph. Plotted ranks have the opposite sign of the actual Johnson's ranks to allow comparison with other results.

affinity for h2 was varied between 10% and 100%, preference was highest for h4, and the index for h2 was about 0 across all habitat affinities. Preference was correctly identified for h1 and h3 over most affinities, but preference was still higher for h4 than would be expected for a habitat type with an affinity of 0%.

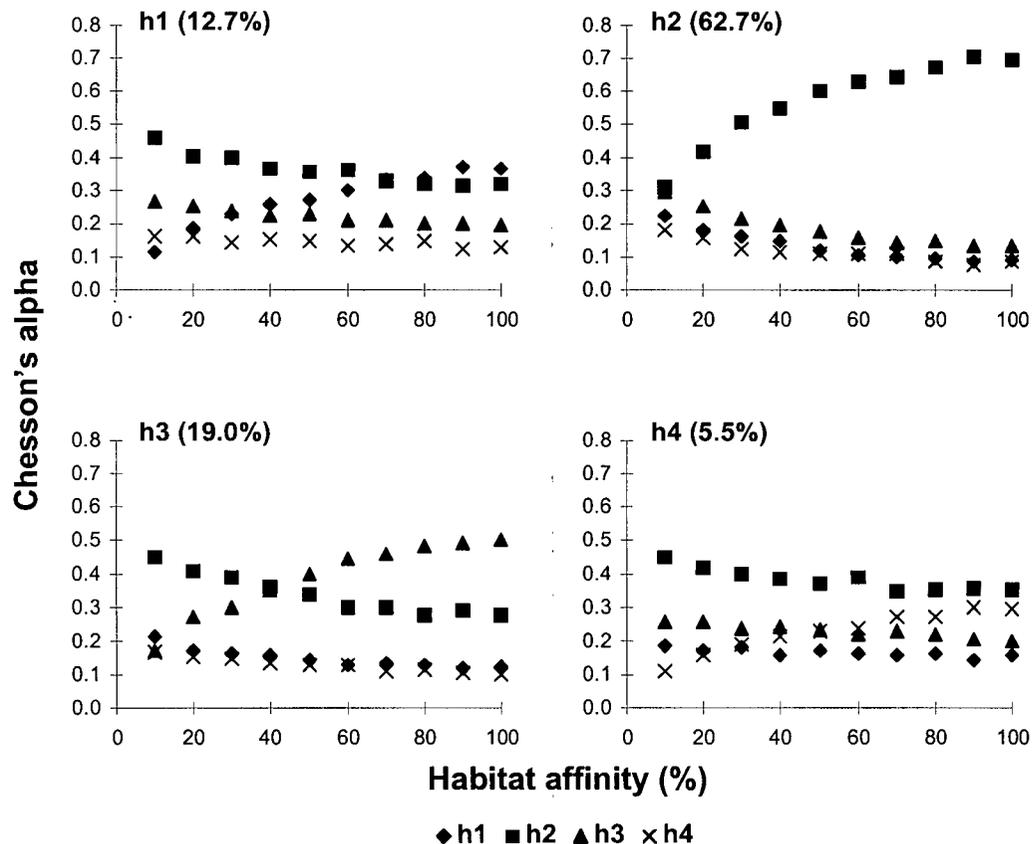
Holding the affinity values of three habitats at 20% while varying those of the fourth habitat, produced a different pattern of SLI values to those in Figure 12 (Figure 15). SLI values were smaller and less variable than the corresponding values in Figure 12. Also, the lowest affinity at which a habitat type was distinguishable from the other three, varied according to its proportion



**Figure 15.** Relationship between Strauss' linear index (SLI) and actual habitat affinity for simulations on the fall map. Each point represents 1000 simulations. Each simulation modelled movements for 30 days, with 20 movements (each of 5 pixels) per day. Affinity values were varied for one habitat type at a time and are graphed separately (h1 - h4; proportions for the fall map are in parentheses). Habitat affinity was held at 20% for the other three habitat types in each graph.

on the landscape. For instance, preference for h2 was obvious at an affinity value of 30%, just above the 20% affinity for the other habitat types. However, for h3, preference was only distinguishable for affinity values  $\geq 40\%$ . Preference for rarer types was even more difficult to distinguish (Figure 15).

Analysis of the same data with Chesson's alpha produced a similar pattern, although preference for habitat types was only evident at higher affinities than in the SLI analysis (Figure 16). In fact, the rarest type was never the most preferred, even at an affinity of 100%. The most abundant habitat had a strong effect on relative preferences. Johnson's rank analysis produced



**Figure 16.** Relationship between Chesson's alpha and actual habitat affinity for simulations on the fall map. Each point represents 1000 simulations. Each simulation modelled movements for 30 days, with 20 movements (each of 5 pixels) per day. Affinity values were varied for one habitat type at a time and are graphed separately (h1 - h4; proportions for the fall map are in parentheses). Habitat affinity was held at 20% for the other three habitat types in each graph. Note the different y-axis scale than the Chesson's alpha results in Figure 13.

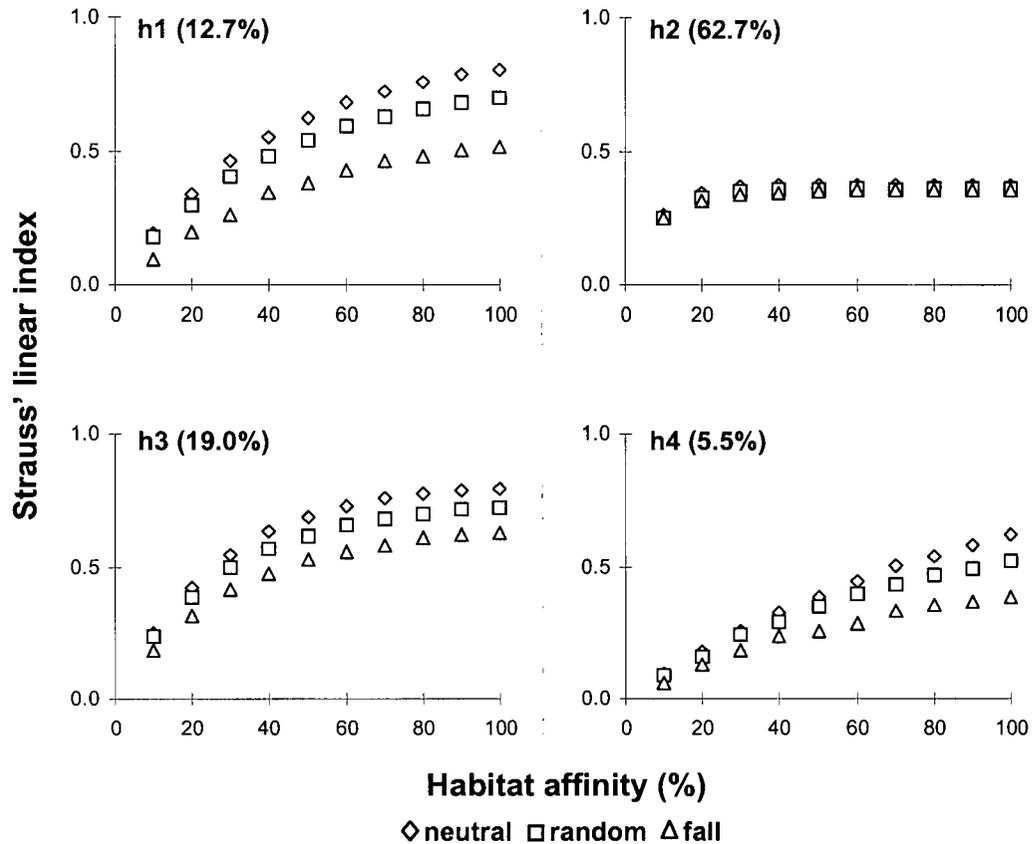
the opposite result; the rarest habitat type (h4) was preferred among all simulations (not illustrated).

All of the trends described so far were the result of a single characteristic scale of animal movements on the same map (fall), so the resulting patterns were not strictly the result of movement scale and/or landscape pattern. The same general patterns appeared when the same parameters were used to model movements with the spatially-neutral model. However, the spatial dimension of the data did have an effect. This is illustrated by plotting the SLI results for simulations on the fall and 'random b' maps, as well as for the spatially-neutral model (Figure 17).

Across all habitat types, the spatially-neutral model produced the highest SLI values, followed by simulations on the 'random b' map, with the lowest values on the fall map. Home ranges were the same for simulations on the two seasonal maps, although the ratio of average home range size to median patch size was higher for the 'random b' map due to the smaller relative patch size on the random map. Because Figure 17 shows results across models but within habitat types, other analysis methods would produce the same patterns and I did not plot results for Chesson's alpha and Johnson's rank results.

Random starting points for animals had little effect on the preference analysis. SLI results were nearly identical to the plots in Figure 12. Maximum SLI values were between 3% and 14% higher for simulations where animals were left for 30 daily movements before being recorded. The greatest effect was on preference for the rarest habitat.

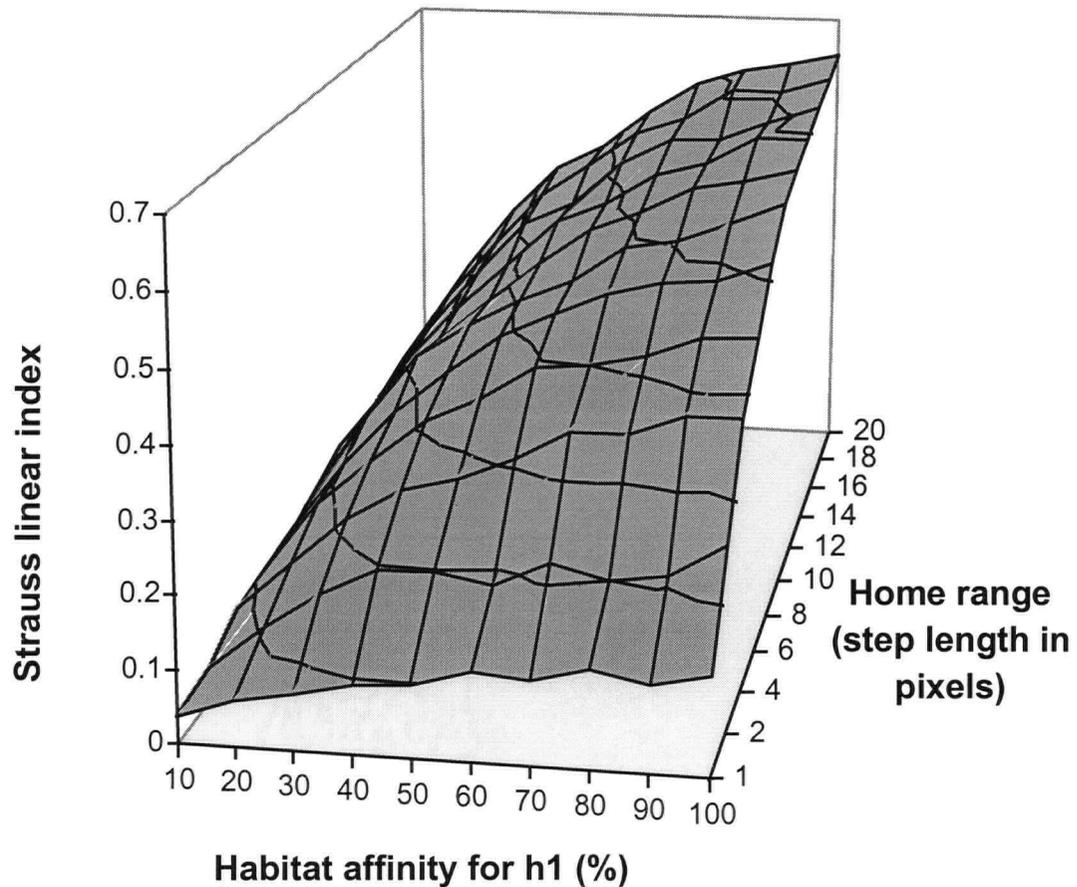
Varying step lengths gave rise to different home range sizes, and home range size affected SLI values. The magnitude of the effect of home range size varied across different habitat affinities (Figure 18). SLI differed little across affinities for small step lengths, but were more



**Figure 17.** Relationship between Strauss' linear index and habitat affinity for the spatially-neutral model and the spatially-explicit model when simulated on the 'random b' and fall maps. Each point represents 1000 simulations. Each simulation modelled movements for 30 days, with 20 movements (each of 5 pixels) per day. Affinity values were varied for one habitat type at a time and are graphed separately (h1 - h4; proportions for the fall map are in parentheses). Habitat affinity was held at 0% for the other three habitat types (not illustrated).

obvious at longer step lengths. That is, habitat affinity had the least influence on preference when home ranges were small.

Although I used step length in Figure 18 to represent differences in home range sizes, the relationship was more complicated. Larger step lengths produced larger home ranges when affinity values were held constant, but higher affinity values produced smaller home ranges when step length was held constant. When affinity values were higher, simulated animals were more likely to remain in the same location for longer periods of time, thus leading to smaller



**Figure 18.** Relationship between Strauss' linear index, habitat affinity, and home range size, as represented by step length. Simulations were conducted on the fall map. Only the h1 habitat type is illustrated. Each point on the surface grid represents 1000 simulations. Each simulation modelled movements for 30 days, with 20 movements per day.

home range sizes. However, step length had a greater effect on home range size than did habitat affinity, although the effect of affinity on home range size was greatest for long step lengths.

The net result of the interaction between step length and habitat affinity was that the relationship between habitat affinity and SLI was flatter than if home range size been kept constant, because home ranges actually decreased in size along the x-axis in Figure 18. Home range sizes varied between  $152 \pm 113$  ha for the shortest step length and the highest affinity, to  $4.5 \pm 2.0$  km<sup>2</sup> for the longest step length and lowest affinity. In general, higher affinities produced smaller home ranges, particularly for abundant habitat types.

## Discussion

As in Chapter 3, results differed between spatially-neutral and spatially-explicit simulations, although the general trends in preference results were similar for both models. The magnitudes of preferences for different habitats were influenced by affinities, landscape pattern, and the scale of animal movements.

### *Effects of Habitat Affinity on Preference Analyses*

In the case of strong selection for, or preference of, one habitat type, the other types are necessarily measured as *avoided*, or at least *less preferred*. This will always be true because of the unit-sum constraint of proportions (Aebischer *et al.* 1993), and is one of the basic problems of preference analyses. It gave rise to the curious situation in my analyses where habitats with affinities of 0% often had different preference ranks, although simulated animals were essentially indifferent to these habitats.

Chesson's (1983) method claimed to calculate an index that is independent of relative proportions (Lechowicz 1982); however, this independence only applies to situations where behaviour with respect to different 'components' (in my case, habitats) is the same (Chesson 1983). Hence, the three habitats with 0% affinity in Figure 13, had similar alpha values despite differences in proportions, because an animal's behaviour associated with the habitats (*i.e.* affinity) was the same. But the magnitude of these alpha values was still dependent on the amount of habitat and habitat affinity for the type assigned an affinity >0%.

Aebischer *et al.* (1993) cited Johnson's (1980) method as one which is unaffected by the unit-sum constraint, however, in my study it generated a number of misleading results, due to the ranking method used to classify use and availability. Both Johnson's ranks and SLI were very sensitive to relative habitat proportions, but had the advantage of being readily analysed with

conventional statistics. Calculating means and dispersions for preference values is important in light of Aebischer's *et al.* (1993) warning about the correct assignment of experimental units to animals rather than to location points.

The affinity for habitat types, as well as their proportions on the landscape, had strong effects on preference indices, regardless of the method of analysis. As expected, higher affinities produced higher preference values, but the magnitudes were affected by the proportions of habitat types. The effect of habitat proportions on model results differed among analysis methods. For SLI, the most common habitat (h2) had the lowest theoretical SLI value ( $1 - p$ ), which led to asymptotes at a lower SLI than some less abundant habitats (h1 and h3). Chesson's alphas for h2 also reached an asymptote, but at a preference value higher than all the less abundant habitats. Johnson's method failed to identify preference for h2, because the rarity of the h4 habitat type ensured a high preference ranking among all simulations, even when its affinity was held at 0%.

At high affinities for h2, simulated animals essentially stayed in h2 patches for most of the sampling period. Because starting points were random, animals began proportionally in all four habitat types, but upon entering an h2 habitat, were unlikely to leave. Because animals also started in other habitats, the asymptote was slightly lower than the theoretical maximum preference values.

There were less obvious asymptotes in simulations that tested affinity for other habitat types, when analysed by Strauss' (1979) method. These habitats had higher theoretical SLI values because they were less abundant. However, the maxima were not realised because habitats were too rare on the landscape to be exploited to the extent suggested by their habitat affinities. This arose for at least two reasons. First, simulated animals began at random locations such that at least the distribution of first locations were in proportion to the proportions of habitats on the

landscape. Reducing this bias by allowing simulated animals to move across landscapes before recording their habitat use increased the preference for habitats with  $>0\%$  affinity 3% to 14%. Second, animals were forced to move at least once per day. As a result, the rarest habitat (h4) was never highly preferred, simply because simulated animals encountered it so rarely.

Authors have expressed concern about the difficulties of measuring preference or selection for rare habitat types (Johnson 1980, Lechowicz 1982, Chesson 1983). These concerns are based on the effects of low sampling frequencies, or few 'use' observations for habitats with low proportions. Preference values for rare types can be spurious because just one observation can have a major impact on preference results. My results were free of such sampling concerns due to the large sample sizes used, but they did point to another potential problem: even where sampling is adequate, preference indices may still underestimate affinity for a habitat because animals are unable to fully exploit it due to low encounter rates. This will hold for animals that rely primarily on searching for suitable habitats, rather than for animals that return to sites based on prior experience.

Moderate habitat affinities (20%) for the three habitats held constant in simulations generally made preference for the fourth habitat more difficult to distinguish. Chesson's alpha values were similar among habitats with 0% affinity, but differed considerably among habitats with 20% affinity (except where affinity for h2 was varied between 10% and 100%). Again, the differences were related to the proportions of the habitat types. Preference for h2 at 20% affinity was higher than preference for less abundant habitats with 20% affinity.

### *Effects of Landscape pattern on Preference Analyses*

Preference results differed between landscapes with the same habitat proportions but different arrangements, and differed from the spatially-neutral model results generated by the same

habitat proportions. The spatially-neutral simulations produced the highest SLI values, and the landscape with the largest and most poorly interspersed habitat patches produced the lowest SLI values, for a given habitat affinity. This pattern held for all but the most common habitat type, for which SLI values were the same across the range of affinities. This occurred because large and poorly interspersed habitat patches, relative to the mobility of the study animal, generally reduced the likelihood that different habitats would be encountered in direct proportion to their availability. In fact, the rare habitats were consistently encountered less often than predicted by their availability by animals with small home ranges.

The h1 habitat type serves as an example of how the patchiness of landscapes affected the results of preference analyses. This habitat type comprised about 13% of the landscape. In the spatially-neutral model, each movement that began from an h1 patch had a 13% chance of encountering another patch of h1. On the 'random b' and fall maps, h1 patches were small and surrounded by other habitat types. Therefore, for spatially-explicit simulations on these maps, the probability that an animal which began in an h1 patch would move into another h1 patch was actually less than 13%. The larger and more poorly interspersed the habitat patches on the map, the stronger the effect.

This example demonstrates one way in which the coincidence of habitats affected preference results. The use of habitats was a function of both their abundance and of how patches were arranged with respect to each other on the landscape. In this case, the arrangement of h1 patches resulted in less use by simulated animals in the spatially-explicit simulations than in simulations based on the spatially-neutral model. Conversely, habitat types consistently associated with h1 patches would be used more than predicted by a spatially-neutral analyses, particularly when habitat affinity for the h1 type is high.

### *Effects of Movement Scale on Preference Analyses*

Home range size affected the magnitude of preference values in the simulations. Small home ranges produced low preference values, even at high habitat affinities. This was a function of the frequency with which habitats were encountered. Animals with small home ranges were able to exploit only a small number of patches and were less likely to fully exploit habitats with high affinities. In contrast, simulated animals that ranged widely were more likely to exploit all available habitats because they were more likely to encounter all habitat types in proportion to their availability. This led to the interesting and important conclusion that preference was scale-dependent. The scale dependency of predictions is an important area of interest in landscape ecology (Milne *et al.* 1989, Turner *et al.* 1989a, Keitt *et al.* 1997). My results here underline the importance of mapping habitat at the proper scale for animal movements, as explained in Chapter 3.

The emergence of a discrepancy between what animals wanted (habitat affinity) and what they were able to exploit (measured habitat preference) was an important result of my simulations. Some differences were expected, because preference is a relative measure that depends on other available habitats, while habitat affinity is absolute. However, what was unexpected was that the spatial characteristics of habitats interacting with the scale of animal movements also influenced the magnitude of the discrepancy between preference and affinity. Isolated but suitable habitat patches may not be used by animals due to the scale of their movements (Milne *et al.* 1989).

My results suggest that rare, but high quality habitat patches will be under-utilised, regardless of their location on the landscape, and the degree of this under-utilisation will be related to the pattern and size of habitat patches, and on the movement rules of animals. This result depended on the 'information-free' nature of the simulations. Spatial learning and memory will reduce, or

even reverse this effect. Where resources are predictable in space and/or time, learning and memory, rather than random encounter rates, are more likely to explain the use of rare, high quality patches.

### *Applicability of the Model*

The model presented in this chapter is only one of many models that could be used to describe the movements of animals through landscapes. However, as an early attempt for this type of modelling, it provides a basis against which to examine the movement behaviour of animals in the field. Prior to this work, animal movements had been modelled as diffusion processes through landscapes consisting of a grid of habitat and non-habitat pixels (Gardner *et al.* 1989, Turner *et al.* 1993, Boone and Hunter 1996). I have extend these methods in several novel ways.

First, I considered the effects of modelling more than two habitats. Many published models consider only suitable and unsuitable habitats (Milne *et al.* 1992, Wiens *et al.* 1997). Second, all the habitat types in my landscapes were 'permeable.' That is, all could be traversed, albeit at different rates. This is in contrast with the permeable/impermeable scenario used in percolation modelling (Gardner *et al.* 1989, O'Neill *et al.* 1988b, Turner *et al.* 1989b, *c.f.* Turner *et al.* 1994), and in studies of spatially-explicit population dynamics (Wiens *et al.* 1997). Finally, rather than examining movements through a simple grid with randomly arranged pixels (*e.g.* Gardner *et al.* 1989), I used both random maps and actual landscapes (Milne *et al.* 1992, Turner *et al.* 1994, Boone and Hunter 1996, also used real landscapes). Although more sophisticated, the model was not necessarily a better predictor of the optimal movements of animals through landscapes, but it provides a predictive basis against which the movements of animals sampled in the field can be compared.

I modelled movements in a relatively 'information-free' manner (Lima and Zollner 1996), which limited the behaviour of simulated animals to rudimentary responses to different habitats. Habitat sensitivity in the model was restricted to influencing the time that an animal remained in a patch. This is only one potential response of animals to habitat cues. For instance, animals with distinct home ranges may exhibit habitat sensitivity by returning often to high quality habitats, rather than simply staying longer when they enter them. They may also periodically move away from high quality habitats to avoid predators, or to move into habitats that contain different habitat attributes. Although learning, perception, and other behaviours may be incorporated into movement models (Saarenmaa *et al.* 1988, Turner *et al.* 1994), they add several untested, and perhaps untestable variables to the equation (Boone and Hunter 1996). I followed the logic of Starfield (1997), who argued that we should build small, pragmatic models that focus on particular problems rather than attempting to model reality with complex models.

Finally, I also extended the method to consider the differential use of habitats defined by differences in overall 'value' (*i.e.* affinity). Defining habitats as patches of different overall 'value' to animals is common in habitat capability and suitability modelling (Laymon and Barrett 1986). With the proliferation of these models and their application in wildlife management, I believe it is important to understand the variables affecting the performance of such models.

In my model, I affected the amount of time that animals spent in patches by changing habitat affinity. Increasing habitat affinity decreased the average size of home ranges. Other researchers have theorised that animals exploiting sparse resources may do so over larger scales than when resources are abundant (O'Neill *et al.* 1988b). The foraging theory equivalent is the question of whether optimal territory size should decrease with increasing with food density. This is only

roughly equivalent because territory implies an exclusive area rather than a nonexclusive home range. The theoretical literature suggests that territory size may either increase or decrease with increasing food density, depending on the currency animals are trying to maximise, and on trade-offs with intruder pressure (Schoener 1983).

An unavoidable consequence of making the model habitat-sensitive was that unlike the simulations in Chapter 3, movements reported in this chapter were not independent of the map's scale. That is, movements from patch to patch were influenced by the size and arrangement of the patches themselves. If I had used a more general map that had been produced at a smaller scale (larger and fewer patches), the simulated movements would have been different. I restricted simulations to just two maps to minimise this scaling effect. In reality, we face many decisions when mapping habitat, and animals may move independently of some of the features we choose to map. Animals also make decisions simultaneously at a number of different spatial and temporal scales (Johnson 1980, Addicott *et al.* 1987), responding to environmental features that also exist at a variety of scales (Kotliar and Wiens 1990). We may or may not be capturing these features in our single-scale habitat mapping (Addicott *et al.* 1987, Morris 1987). My model was restricted to examining habitat selection at a single scale, where scale was ultimately determined by the size and arrangement of the habitat patches. I know of no way around this problem because of the necessity to establish a 'true' habitat for simulated animals to sample.

Decisions about currency, and issues surrounding the dependence of modelled movements on mapping scale, obviously affect the applicability of my model; however, we need more empirical evidence before deciding if these assumptions are any more or less realistic than those of spatially-neutral habitat use studies, in which animals have information about all habitats, and can move among them with little or no cost. Incorporating these rules into my movement

model would have produced simulations in which animals would have moved only once to a single, high-quality patch, and stayed there for the remainder of simulation period.

The information-free aspect of my model was the reason simulated animals moved, but there is an obvious middle ground between the information-free and perfect information extremes. Animals should move among patches when the quality of patches changes with time, and if sampling habitats is the primary means of assessing patch quality. Quality changes with forage growth and with depletion by foragers. Foraging studies have provided some evidence that animals react in a way that maximises net energy gain in a fluctuating environment; that is, they use all foraging choices, good and bad, according to their value, rather than simply staying in the best patch (*e.g.* Smith and Dawkins 1971, Pyke *et al.* 1977). Studies of wildlife habitat use usually ignore the dynamic nature of patch quality (other than gross seasonal stratification, *e.g.* Fuhr and Demarchi 1990). The landscapes I used were also static with respect to patch quality, and animals were aware of the value of patches without sampling. Modelling habitat affinity as I did in this chapter produced a pattern of habitat use similar to that which might have been expected in a foraging model that considered varying patch qualities.

### *Summary of spatial effects*

My concept of separating habitat affinity and habitat preference revealed a number of potential problems with employing preference analyses to assess the value of habitats to animals. An important result of my simulations was that the magnitude of preference index values depended on the proportions of different habitat types and their arrangement on the landscape. Traditional use-availability studies of wildlife have not considered the constraints imposed by the spatial dimension of landscapes and the potential effect of these constraints on preference analyses.

Rare habitat types were less likely to be identified as preferred, particularly if they were distributed in a few, widely dispersed patches. This occurred even if animals had high affinities for those habitats. This result was dependent of the 'information free' nature of the simulations. Nominal affinities for common habitat types distorted the rank order of preference for different habitats. Generating preferences that reflected habitat affinity was more difficult for landscapes that were dominated by large, poorly interspersed patches. Researchers should be cautious when making inferences about the value of rare habitats based on the results of habitat preference analyses.

The unit-sum constraint, and constraints imposed by the spatial dimension of the landscapes, produced measures of habitat preference that were inconsistent with actual habitat affinity. The proportions of different habitat types, their patch size and arrangement on the landscape, and the relative magnitudes of habitat affinities all influenced the contrast between habitat preference and habitat affinity. A useful technique may be to iterate the absolute affinities for habitats based on preference analyses. This idea is explored in the next chapter.

Finally, different measures of habitat preference differed in their ability to reflect habitat affinities. Johnson's (1980) method performed poorly, particularly when identifying the affinities for rare habitats. SLI's weakness was the different rank order of preference reported for habitats with identical affinities. Chesson's alpha controlled this problem, but the non-linear nature of the index could result in misleading results if the preferences of animals with different selection behaviours were combined in a single analysis. None of these problems were unique to the spatially-explicit model; including the spatial dimension of the data primarily influenced the magnitude of preference values. Understanding the performance of the various indices is critical to applying the methods and interpreting results.

These conclusions raise a number of issues for land managers. First, rare habitat types that are important for wildlife may not be revealed through studies of habitat use. The values of rare but high quality habitats may be discounted as a result of low encounter rates by animals. This effect will be magnified when patches are widely dispersed across the landscape (*i.e.* more fragmented) and contain ephemeral resources.

Second, the nature of rare habitat types may not be captured by preference analyses. Small, high quality patches may contain important life history requisites (*e.g.* dens) that are used by animals over broader temporal scales than day-to-day movements. Analyses based on counts of locations may not capture these important habitats. In addition, the behaviour rules governing the use of these habitats may be different than those for more common habitat types. Dens, water holes, etc. are more permanent and their use will depend more on learning and memory than on encounter rates.

Understanding the relationships between animals and rare and/or fragmented habitats is a significant challenge to researchers, and the reduction and further fragmentation of these habitats through landscape change make the relationships even more difficult to infer.

These conclusions generate several questions that could be examined in field studies. For example, is there a negative correlation between habitat patch size and preference (within a habitat type)? Or, can habitat preferences be altered by manipulating the size and arrangement of patches, while keeping overall habitat proportions the same? Much of this chapter deals with the perception of habitats by animals, and in moving from simulations to field studies, we are restricted to measuring correlates of animals' perceptions. The actual relationship between a perception like habitat affinity, and measured habitat preference, is unknowable. However, the simulations in this chapter have suggested that different methods of measuring preference vary

in their ability to detect true habitat affinities (where such affinities are known). These results can lead to better designs, even if actual affinities remain unknown.

## Chapter 5. A Spatially-explicit Examination of Grizzly Bear Telemetry Data

### Introduction

Habitat-use studies have been the traditional method used to assess habitat for grizzly bears in specific areas of British Columbia (Hamilton 1987, Simpson 1987, McLellan 1989, MacHutchon *et al.* 1993); however, Fuhr and Demarchi (1990) developed a method of assessing grizzly bear habitat in BC at mapping scales of 1:50 000 and 1:250 000 (hereafter referred to as 'the F-D models') without the use of radio telemetry data. The 1:50 000 model was intended to evaluate habitat at the operational level (the scale at which most decisions are made about habitat modifications), while the 1:250 000 model was intended to be used at the planning scale. The F-D models are best described as 'capability' rather than 'suitability' models, although the terms are not consistent in the literature (*e.g.* Laymon and Barrett 1986, Suring *et al.* 1988). That is, they attempt to assess the ability of habitats to provide the life history requisites of grizzly bears based on the overall characteristics of habitat types under optimal conditions. The currency of the models is carrying capacity, measured in grizzly bears per 100 km<sup>2</sup>. Carrying capacity is used because the goal of the models is to predict the potential size of grizzly bear populations. This goal is in contrast with habitat suitability index (HSI) modelling, which commonly refers to models that generate a suitability index based on the interaction of a number of relationships between elements of the habitat, and their importance to a species (Laymon and Barrett 1986, Suring *et al.* 1988, Pereira and Itami 1991, Mladenoff *et al.* 1995).

One of the principal reasons the F-D models were developed for the Flathead Valley, BC is that a long-term study of grizzly bear ecology has been conducted there since 1978 (McLellan 1989, F. Hovey, pers. comm.). As a result, a large sample of telemetry locations are available to

validate the models. A thorough test of the F-D models is beyond the scope of this chapter; however, the data and habitat capability maps provide an opportunity to examine differences between the patterns of habitat use generated by real and simulated data, and to examine the role of spatial variables.

In this chapter, I examine overall patterns of habitat use by grizzly bears among the F-D capability classes, and compare them to patterns generated with the results of simulated animal movements on the F-D 1:50,000 scale capability map. The fit of the data to the F-D model is unimportant for the interpretation of the comparison, only the actual association between locations and the capability map is relevant. The purpose of the comparison is to determine the relative roles of spatial variables, habitat affinities, and analysis methods, on the inferences made about broad-scale patterns of habitat use.

Following the results of the last two chapters, I pose two main questions: 1) could the spatial dimension of habitat data an important factor in generating the observed pattern of habitat preference?; and 2) how well do measures of habitat preference reflect the habitat affinities suggested by the model?

### Methods

I assumed: 1) that the sampling intensity of individual bears did not affect measures of habitat use, and; 2) that relative differences in location density reflected differences in habitat use. Error due to the violation of this second assumption may occur if a population is not near carrying capacity (Hobbs and Hanley 1990), or if locations are strongly affected by social behaviour (Van Horne 1983, *c.f.* Fagen 1988). McLellan and Hovey (1995) provide evidence that the Flathead population is close to carrying capacity.

Maps derived from the F-D model contained patches consisting of one or more biophysical habitat units. I pro-rated the value of each patch based the relative proportions of different habitat types within each patch. After this adjustment, patches were classified into *nil*, *low*, *medium*, and *high* categories by using Fuhr's and Demarchi's (1990) carrying capacity estimates as the upper boundary of each rank category.

Because telemetry data do not directly estimate carrying capacity, I assumed the model predicted that habitat use by bears would be proportional to the carrying capacity estimates of patches. The F-D model is based on the premise that habitats with higher predicted carrying capacities should exhibit higher use by bears. This use should be reflected in the telemetry data collected in the Flathead Valley. Regionally, the F-D model is supposed to be adjusted for current conditions through the application of 'step-downs' (Manning *et al.* 1994). There are adjustments in carrying capacity estimates that account for modifications to the habitat such as roads. Fuhr and Demarchi (1990) suggested the use of such adjustments, but no standard guidelines are available (Manning *et al.* 1994) and I do not consider them here. Because they apply regionally, they should not affect the relative qualities of habitats among capability classes.

I calculated habitat preference for grizzly bears during the summer season to compare against simulated data. The summer data were most appropriate for this analysis because they provided a large sample of bear-years ( $n = 78$  individuals with  $>9$  locations) and an initial analysis indicated a significant pattern of preference among habitat classes. The spring sample consisted of few bear-years with  $>9$  locations ( $n = 9$ ), while in the fall sample use did not differ significantly among habitat classes (unpubl. data). I needed  $>9$  locations for each bear for comparison with results from my movement model, which required that  $>9$  locations be located

on the mapped landscape to be included in the analysis. The same bears in different years were treated as independent samples, and data were pooled across age and sex classes.

I compared the preference results for the summer grizzly bears to simulated results based on the spatially-neutral and spatially-explicit models used in Chapter 4, using Strauss' Linear Index (SLI; Strauss 1979), and the methods of Johnson (1980) and Chesson (1983). For the simulations, I generated results at a scale similar to the grizzly bear data by using step lengths that resulted in home ranges that were similar in size to the seasonal bear home ranges (using the fixed kernel technique; Worton 1987). In practise, the simulated home ranges varied considerably due to the relationship between habitat affinity and home range size in the model. I generated parameters for the model based on home range data, rather than on the characteristics of bear movements, because of the variable 'step lengths' of the field data. That is, the time between bear relocations was variable, and therefore an analysis of turning radii and movement distances would have been inappropriate.

For both the spatially-neutral and spatially-explicit models, I generated model runs of 1000 simulations for each of two different sets of habitat affinities. I used a null model set (no affinity for any of the habitat classes), and a set of affinities based on the qualitative habitat ranks outlined by the F-D model. The affinity values I used were: *nil* 0%; *low* 11%; *medium* 34%; and *high* 100%. This was only one of many sets of affinities that could have been used, based on the interpretation of carrying capacity estimates from the F-D model. I ran simulations where starting points were randomly located throughout the study area, and where they were restricted to the centre portion of the landscape, as in Chapter 3. This was to reflect a bias in the actual bear data; most bears were captured in the south-central portion of the study area.

I also determined the set of affinities that would produce the same pattern of habitat preference in simulations as that observed in the grizzly bear data. I systematically varied

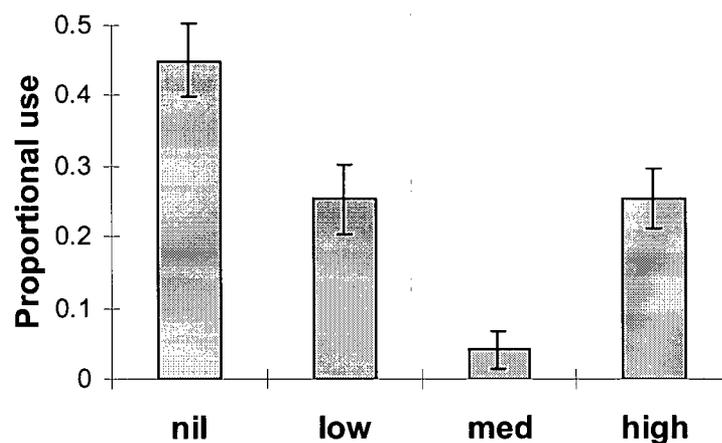
affinities for the habitat classes between 0 and 90%, in 30% intervals (due to practical computational limitations). I then determined the set of affinities that produced the best fit to the observed grizzly bear data.

I compared mean SLI values between ranks with two-tailed t-tests with an adjusted alpha of 0.008 to compensate for the non-independence of comparisons (Sokal and Rohlf 1981).

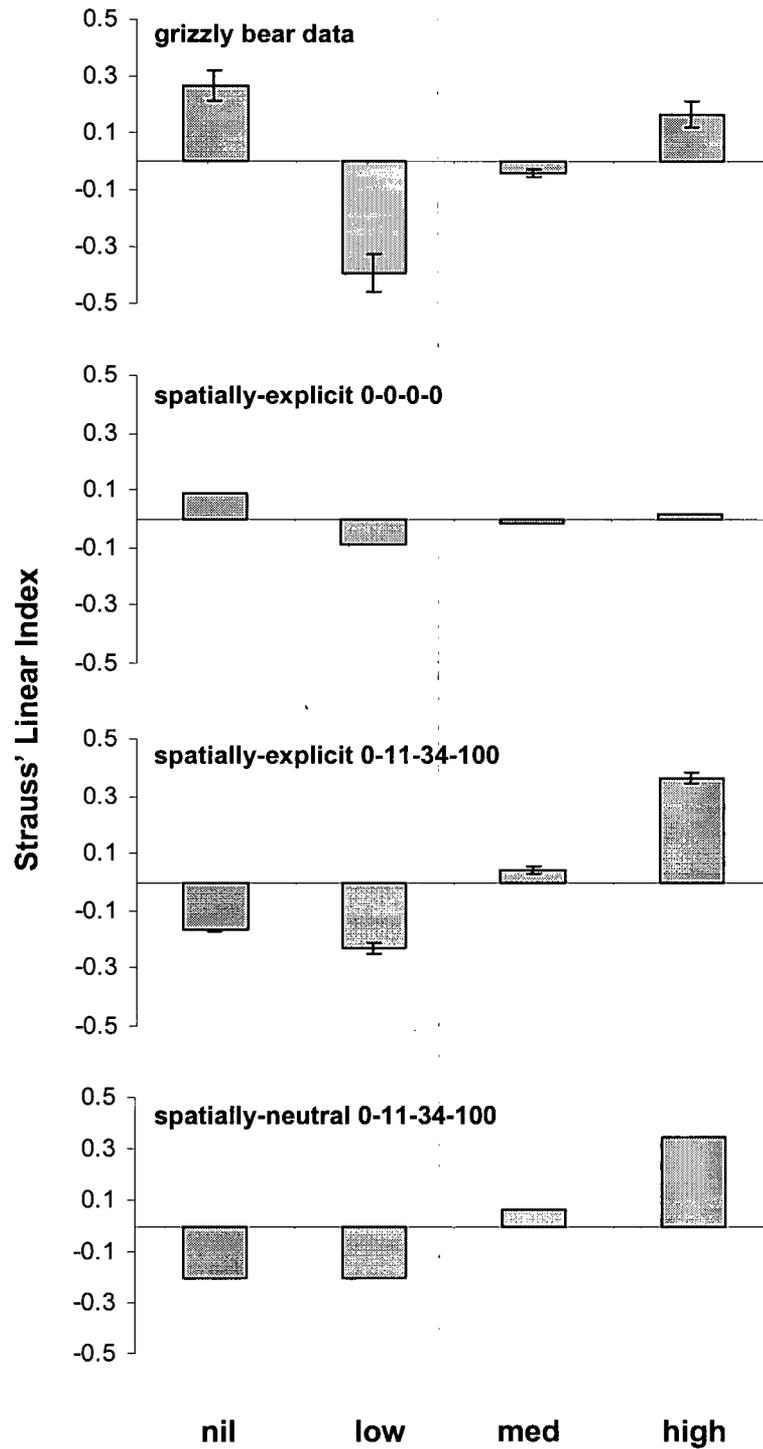
### Results

Summer bear home ranges averaged  $84 \pm 61 \text{ km}^2$  ( $n = 59$  bear-years; home ranges were calculated for bears with  $>19$  locations). For the actual grizzly bear data, *nil* habitats were used most frequently and *medium* habitats the least, according to gross proportions of locations (Figure 19). SLI values among the four habitat classes were significantly different from each other, and followed the expected rank order for all except the *nil* class (Figure 20). Simulations based on starting points restricted to the south-central portion of the study area did not change the rank order of habitat use, nor significantly the magnitude of preference values.

The spatially-neutral model produced expected results when run with all habitat affinities



**Figure 19.** Proportional use of the four habitat classes by grizzly bears ( $n = 78$ ) in the Flathead Valley, BC. Error bars are  $\pm 2$  standard errors and are based on non-transformed data. They are provided for descriptive purposes.



**Figure 20.** Comparison between summer grizzly bear data and several simulations. All pairwise comparisons were significant ( $P < 0.001$ ) except comparisons between *nil* and *high* habitat capability classes for the bear data, and between *nil* and *low* habitat capability classes for the spatially-neutral model results. The four numbers following the model descriptions are the habitat affinities assigned to the *nil* - *high* habitat capability classes. Error bars are  $\pm 2$  standard errors.

equal to zero; preference among the four habitat classes did not differ from each other and were all very close to zero (not illustrated in Figure 20).

For the spatially-explicit model, the same habitat affinities produced significantly different preferences among the four rank classes, and the rank order was the same as that for the grizzly bear data, except that the *nil* class was preferred over the *high* category (Figure 20). Home ranges for the simulated data ranged between  $32 \pm 26 \text{ km}^2$  for simulations with high affinities, to  $179 \pm 59 \text{ km}^2$  for simulations with affinities of zero.

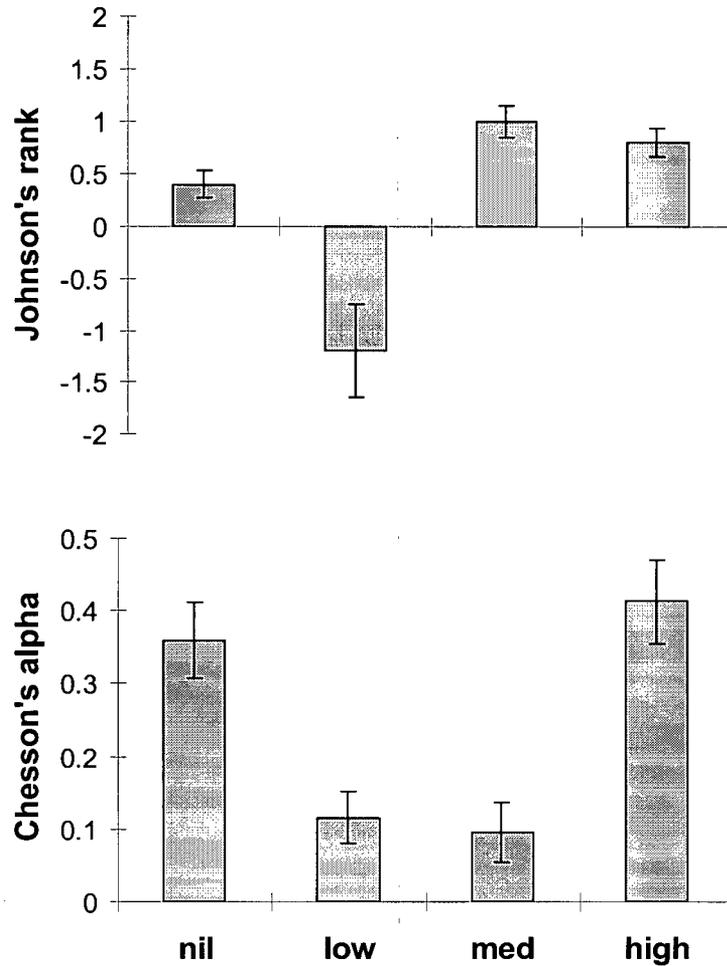
Using estimated habitat affinities to correspond to the four rank classes of the F-D model further altered the habitat preference results of the simulations. The spatially-neutral and spatially-explicit models generated similar preferences, with the exception again of the *nil* class, which was not preferred over the *low* class in the spatially-neutral simulations as it was in the spatially-explicit results (Figure 20).

Not surprisingly, analysis of the bear data with Johnson's ranks and Chesson's alpha produced different patterns (Figure 21). Johnson's ranks are distributed normally, but Chesson's alpha values are not. Therefore, measures of dispersion for Chesson's alpha should be interpreted with caution.

The habitat affinities that best fit the observed pattern of habitat preference for the summer bear data were: *nil* 30%; *low* 0%, *medium* 0%; and *high* 60%. This pattern was best reflected in Chesson's alpha results (although not the same), but could not have been predicted by SLI or Johnson's ranks. In fact, multiple optima were predicted by iterations based on Johnson's ranks.

## Discussion

Despite the potential problems of the F-D 1:50,000 model, and the problems with evaluating these types of models in general (Manning *et al.* 1994, Rickers *et al.* 1995), the summer data fit



**Figure 21.** Johnson's rank and Chesson's alpha analysis of the summer grizzly bear data. For the Johnson's rank results, all pairwise comparisons were significant ( $P < 0.001$ ) except comparisons between *medium* and *high* habitat capability classes. Chesson's alphas are not normally distributed and error bars should be interpreted with caution.

the expected rank order of preference for three of the four habitat classes. The exception was the *nil* class, which was one of the most preferred. This identifies a weakness in the F-D model.

### *The Role of Spatial Variables*

Landscape characteristics consist of two categories of variables: the spatially-neutral proportions of habitats, and the spatially-explicit arrangement of habitats. Previous chapters have demonstrated the effects of different habitat proportions, and of habitat arrangement on

measures of habitat use and preference. The results of simulations in this chapter suggest that the pattern of habitat preference observed in grizzly bear data could be at least partly explained by the spatially-explicit arrangement of habitats. In simulations with 0% affinity across all habitat classes, the rank order of preference in the spatially-explicit simulated data was essentially the same as that in the grizzly bear data. That is, animals with no affinity for the different habitat classes produced the same pattern of preference. This pattern was not evident in the spatially-neutral results, suggesting the pattern of preference was the result of the arrangement of habitats, rather than of the spatially-neutral habitat proportions. The only substantial difference between the spatially-explicit simulation results and the bear data results was the greater magnitudes of preference calculated for the bear data. Unfortunately, the relative roles of habitat arrangement and of habitat affinity in generating these higher magnitudes are difficult to separate.

The habitat preferences calculated for simulations with habitat affinities of 0% appear to contradict the results of Chapter 3, where habitat-insensitive simulations at different scales led to variance differences in habitat use, but did not generally change the means. The reason for this discrepancy lies in the different movement rules of the models used in Chapters 3 and 4. Because the model in Chapter 3 was completely insensitive to the underlying habitat map, simulated animals were allowed to wander back and forth across the landscape boundary. In contrast, the Chapter 4 model, also used in this Chapter, truncated the movements of simulated animals once they left the landscape. The reason for this was that there was no way to assign movement rules to animals that were not located on mapped patches. This may seem like a minor difference, but it introduced a bias with respect to which animals were included in the analysis. Because  $>9$  locations had to be available for an animal to be included, there was a natural tendency for the simulated home ranges to be centred closer to the interior of the map

than if the simulations had followed the rules of the model used in Chapter 3. The distribution of the *nil* class of habitats, which were found primarily in the valley, resulted in the pattern seen in Figure 20; habitats classified as *nil* value were one of the two most preferred classes.

The rule for including simulated animals on the edge of the map was largely responsible for producing a pattern of habitat use similar to that observed in the grizzly bears data. Only bear-years that included >9 locations on the mapped area were included in the analysis, which biased bear locations towards the centre of the valley. Of course the bias may not have been entirely methodological. The Flathead map is flanked on the east and west by rugged mountains that may influence the movements of both grizzly bears and grizzly bear researchers, leading to a greater number of locations in and near the valley.

#### ***Habitat Affinities Predicted by the Model***

Simulations based on habitat affinities derived from the F-D model produced a different pattern of preference than that observed in the bear data. The *nil* habitat category was less preferred, but the magnitude was smaller than in the spatially-explicit simulations than in the spatially-neutral results, where the *nil* class had SLI values that did not differ from those of the *low* class. In the spatially-neutral results, the rarity of the *nil* category was countered by its lower affinity to produce a preference similar to the *low* class. In the spatially-explicit results, the *nil* class was preferred over the *low* class, even though the assigned affinities suggested the opposite. A conclusion of Chapter 4 holds here – preference is not necessarily an accurate predictor of habitat affinity, and whether it is will be influenced by the proportions of different habitats and their spatial characteristics. Once again, only habitat proportions are usually considered in traditional studies of wildlife habitat use.

### ***Habitat Affinities Suggested by the Grizzly Bear Data***

The results of the SLI preference analysis of the grizzly bear data suggested that bears preferred habitats classified as *nil* and *high*, strongly avoided *low* habitats, and were essentially indifferent towards *medium* habitats. The affinities that provided the best fit to this pattern of preference were quite different, suggesting no discrimination between *low* and *medium* habitats, and a greater affinity for *high* than *nil* habitats. Analysis of the bear data with Chesson's alpha produced a pattern that was close to that which would be expected based on the modelled habitat affinities. Johnson's ranks produced yet another pattern in the bear data that did not resemble the modelled habitat affinities. My analysis suggests that Chesson's alpha may provide the best method for generating a correspondence between preference and actual habitat affinities.

### ***Patterns of Habitat Use and Constraints of Landscapes***

Returning to my original hypothesis, the pattern of habitat preference observed in the summer grizzly bear data was at least partly caused by the spatial characteristics of the landscape. The rank order of preference could be explained by the spatially-explicit arrangement of habitats, without reference to the affinity of bears for different habitats, but the magnitudes of the preferences were influenced by unknown habitat affinities.

Grizzly bears respond to environmental patterns at several scales (Johnson 1980, Addicott *et al.* 1987). As a result, their movement behaviour represents an integration of information across both temporal and spatial scales. The transfer of information across scales reduces the sharpness of scale boundaries, making inferences about scale effects more difficult (Wiens 1989).

Simulated movements in this chapter were sensitive to environmental pattern at only one scale, but still produced a broad-scale pattern of habitat preference that resembled that shown in the

grizzly bear data. Thus the complex behaviour of grizzly bears at small scales did not appear to obscure the broader-scale pattern of habitat preference.

## Chapter 6. Conclusions

A common theme throughout this study has been the notion that scale and pattern affect our ability to make inferences about ecological processes. To understand mechanisms that produce patterns of habitat use, we need to understand how the patterns of points that we use to represent animal behaviour, interact with the patterns of habitat patches we use to represent animal environments. The scales of both can be at least partly controlled by data collection methods. We can change the representation of an animal's use of habitat by relocating the individual more or less frequently. Also, we can change the representation of an animal's habitat by measuring different environmental variables, or by choosing different limits along environmental gradients to delimit habitats. The results of my study suggest that these scaling decisions can affect our ability to make inferences about the process of habitat selection. Decisions about scale affect the expected pattern of habitat use under a null model of no habitat selection (Chapter 3), the measurement of habitat preference (Chapter 4), and can produce significant habitat preferences in the absence of a mechanism of habitat selection (Chapters 3 and 5).

A reductionist approach to examining habitat use might call for the measurement of animal behaviour and of habitats at the finest possible scales, to build the dynamics of the system from the 'ground-up'. Doing so may leave us vulnerable to becoming lost in endless detail, with few rules for separating the trivial from the non-trivial. We would also run the risk of being misled by local idiosyncrasies. An alternative, but complementary approach for complex systems, is to recognise the scale-dependency of their processes, and to look for broader-scale, robust patterns that emerge above the intractable detail.

As ecologists, we rarely use the language of systems theory, although we exercise some of its concepts (Allen and Starr 1982). The process of ecological modelling involves making decisions about scale; the variables that we include in a model are related to the scale of the process we are trying to capture. These decisions are often intuitive, particularly for species such as grizzly bears that range at very human scales. Hence, there was little evidence in the grizzly bear data that I examined, to suggest the Flathead mapping was conducted at an inappropriate scale. However, the appropriate scale for modelling the habitat use behaviour of other species may not be as obvious. For example, wolverines (*Gulo luscus*) are relatively small animals that have very large home ranges (Hornocker and Hash 1981). This species suggests scales of perception that are both larger and smaller than human scales. Our perceptions may affect our characterisations of habitat for animals with very different perceptions. I have shown that the scale consequences of these perceptions can affect the inferences we make about habitat use.

I investigated the consequences of the scales that we impose on studies of wildlife habitat use, and attempted to generate some system-independent guidelines for anticipating these consequences when designing and analysing habitat use data. As with the approaches of most researchers in this area, my results arose primarily from simulated data. However, my system was generally more complex than other attempts at modelling animal movements and habitat use. The introduction of habitat affinities, four different habitat types, and variation in movement behaviour, were important steps in generating more realistic models. In some ways, these variables tended to blur the effects of scale and pattern, but a number of important relationships emerged.

I have shown that the proportions of different habitat types had the greatest influence on measures of habitat use and preference. Common habitats provided the clearest evidence for the

existence of domains of scale, but were also responsible for distorting preference analyses and misrepresenting the true affinities of animals for habitats. On the other hand, rare habitat types often produced no discernible patterns of preference at all, regardless of their affinity values. It was also clear from my simulations that the arrangement of habitats influenced habitat use, and its effects were greatest when animal movements were small in relation to habitat patch size. However, habitat arrangement was also sufficient to produce significant patterns in habitat preference, even without a mechanism for animals to differentially select habitats.

The effects of landscape pattern were not only restricted to the measurement of habitat use and preference. The amount and arrangement of habitats constrained the ability of animals to exploit habitats according to their affinities. Hence, rare habitat types with high affinities were never highly preferred, because they were encountered so rarely by animals. This produced preferences that were scale dependent, such that the response of animals to the quality of habitats depended on the scale of their movements across the landscape.

Perhaps the most striking conclusion of my study was the inter-dependency of nearly all the variables that I examined. Measures of the proportion, arrangement, use, and preference of one habitat type, were dependent on the same measures of all other habitat types. The scale-dependency of preference meant not only that the magnitude of preference for a habitat type depended on the scale of animal movements, but that it also depended on the size of the habitat patches. This in turn influenced the interspersion and juxtaposition of habitat types, and this then influenced movements by altering the time animals spent in patches. Understanding the nature of these interdependencies is important if we are to exploit the information provided by the spatial dimension of habitat use and availability data.

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## Appendix I

Definitions of landscape indices (McGarigal and Marks 1995).

Interspersion/Juxtaposition index (*IJI*):

$$IJI = \frac{-\sum_{i=1}^{m'} \sum_{k=i+1}^{m'} \left[ \left( \frac{e_{ik}}{E} \right) \ln \left( \frac{e_{ik}}{E} \right) \right]}{\ln \left( \frac{1}{2} [m' (m' - 1)] \right)} \quad (100)$$

Contagion index (*CONTAG*):

$$CONTAG = \left[ 1 + \frac{\sum_{i=1}^m \sum_{k=1}^m \left[ \left( P_i \right) \left( \frac{g_{ik}}{\sum_{k=1}^m g_{ik}} \right) \right] \cdot \left[ \ln \left( P_i \right) \left( \frac{g_{ik}}{\sum_{k=1}^m g_{ik}} \right) \right]}{2 \ln(m)} \right] \quad (100)$$

Variables:

<i>i</i>	1, ... , <i>m</i> or <i>m'</i> patch types
<i>k</i>	1, ... , <i>m</i> or <i>m'</i> patch types
<i>m</i>	number of patch types, excluding landscape border
<i>m'</i>	number of patch types, including landscape border
<i>e<sub>ik</sub></i>	total length (m) of edge in landscape between patch types <i>i</i> and <i>k</i> ; includes boundary and background edge segments involving patch type <i>i</i>
<i>E</i>	total length (m) of edge in landscape
<i>P<sub>i</sub></i>	proportion of landscape occupied by patch type <i>i</i>
<i>g<sub>ik</sub></i>	number of adjacencies between pixels of patch types <i>i</i> and <i>k</i>

## Appendix II

The REXX script used in the habitat-insensitive simulations. Additional scripts to summarise output are not included.

```

/* This is the habitat-insensitive movement REXX script */

ECHO OFF
call RxFuncAdd 'MathLoadFuncs', 'REXXMATH', 'MathLoadFuncs' /* load REXXMATH functions */
call RxFuncAdd 'Rexxbase_init', 'REXXBASE', 'Rexxbase_init' /* load REXXBASE functions */

call MathLoadFuncs
call Rexxbase_init

/* data entry */

SAY
SAY
SAY "Insensitive movement model v5.6"
SAY "Number of animals?"
num_animals=linein(input.txt)
SAY num_animals
SAY "Locations per animal?"
num_loc=linein(input.txt)
SAY num_loc
SAY "Decay power? (between 1 and 3)"
power=linein(input.txt)
SAY power
SAY "Distance multiplier?"
multiplier=linein(input.txt)
SAY multiplier
SAY "map file"
mapfile=linein(input.txt)
SAY mapfile

error=rexxbase_opendbf('mapfile')

/* main program loop, repeated for each animal and simulation */

theta=0

DO i=1 TO num_animals
  SAY i
  x=RANDOM(680000, 695000) /* sets limits of starting positions */

  y=RANDOM(5428900, 5444000)
  CALL Calculate
  DO j=2 TO num_loc
    CALL Distance /* calculates distance */
    CALL Direction /* calculates new direction */
    x=x+sin(theta)*d /* new x,y position */
    y=y+cos(theta)*d
    CALL Calculate
  END
END

error=rexxbase_closedbf('mapfile') /* closes map file */
error=stream('\output\output.txt', command, close)
error=stream('\output\hrinput.txt', command, close)
EXIT

/* function to calculate new row/column position, and write the values to the output files */

Calculate:
  x1 = TRUNC((x - 661000)/50)
  y1 = TRUNC((5459150 - y)/50)
  IF x1>=1 & x1<=1141 & y1>=1 & y1<=604 THEN /* checks to make sure location is on map */
    DO

```

```

        record=(y1-1)*1141+x1          /* calculates record number and queries dbf file */
        error=rexxbase_gotorecord('mapfile', record)
        z=mapfile.habitat
    END
    ELSE z=-1
    error=LINEOUT('.\output\output.txt', i x y z)          /* general output file */
    if i<101 then error=LINEOUT('.\output\hrinput.txt', i x y)
                                                              /* file for kernelhr, first 100 hr's */
RETURN

/* Calculates distance */
Distance:
    d=0

    DO k=1 TO 12          /* 12 numbers are summed to produce one random number */
        c=RANDOM(10000)/10000 /* adjusted for the whole numbers drawn by RANDOM */
        d=d+c
    END

    d=d-6                /* adjustment to mean 0 and variance 1 */
    d=pow(ABS(d),power)*multiplier /* controls decay distribution */
RETURN

/* Biased direction calculation */
Direction:
    theta_old=theta          /* remembers previous direction */
    theta=0
    DO k=1 TO 2
        theta=theta+RANDOM(360)
    END
    theta=theta/2
    theta=theta/360*2*3.141593 /* converts theta to radians */

    theta=theta_old+theta
                                /* adds old and new radian values for new direction, relative to north */

    IF theta>6.283185          /* checks to see if the sum of the directions exceeds 360 degrees */
        THEN theta=theta-6.283185
RETURN

```

## Appendix III

The C++ script used in the habitat-sensitive simulations. Additional scripts to summarize output are not included.

```
// sensitive.cpp: this is the habitat sensitive movement script

#include <stdio.h>
#include <conio.h> //for clrscr
#include <math.h> //for trig functions
#include <stdlib.h> //string conversion functions
#include <time.h> //for time functions

void map_load(); //user functions
void start();
void map_query();
void direction();
void step();
void stay_go();

int mapfile[700000]; //global declarations
char *mapname;
int pixel_value, column, row, i, num_animals, x1, y1, z, num_locations, num_steps, j, k, m,
multiplier, theta, n, go;
long x, y;
int pr_z[5];
time_t t;

main(int argc, char *argv[])
{
    FILE *stream2, *stream3; //main function variable declarations

    if (argc != 10)
    {
        printf("\nnot enough command line paramters were entered\n\n");
        exit(1);
    }

    //read command line parameters into variables
    mapname = argv[1]; //sets mapfile to first command line argument
    num_animals = atoi(argv[2]); //takes number of animals from the command line
    num_locations = atoi(argv[3]); //number of locations per animal
    num_steps = atoi(argv[4]); //number of steps per day
    multiplier = atoi(argv[5]); //step distance
    pr_z[1] = atoi(argv[6]); //stay probability for habitat 1
    pr_z[2] = atoi(argv[7]); //stay probability for habitat 2
    pr_z[3] = atoi(argv[8]); //stay probability for habitat 3
    pr_z[4] = atoi(argv[9]); //stay probability for habitat 4

    //prints parameters
    printf("\n\nmap file: %s", mapname);
    printf("\n\nnumber of animals: %i", num_animals);
    printf("\n\nnumber of locations: %i", num_locations);
    printf("\n\nnumber of steps: %i", num_steps);
    printf("\n\nmultiplier: %i", multiplier);
    printf("\n\nprob. h1: %i", pr_z[1]);
    printf("\n\nprob. h2: %i", pr_z[2]);
    printf("\n\nprob. h3: %i", pr_z[3]);
    printf("\n\nprob. h4: %i", pr_z[4]);

    map_load(); //loads map into RAM
    srand((unsigned) time(&t)); //reinitializes random number generator

    stream2 = fopen("./output\\output.txt", "w"); //file for general output
    stream3 = fopen("./output\\hrinput.txt", "w"); //for kernelhr
}
```

```

//main program loop

theta = 0; //necessary, don't ask..

for (i = 1; i < (num_animals+1); i++) //repeats for each animal
{
    printf("\n%i", i);
    do //ensures starting position on non-zero pixel
    {
        start();
        map_query();
    }
    while(z < 1);
    fprintf(stream2, "%i %i %i %i\n", i, x, y, z); //writes output file
    fprintf(stream3, "%i %i %i\n", i, x, y);
    //writes output from the first 100 animals for kernelhr

    for (j = 2; j < (num_locations+1); j++)
    {
        for (k = 1; k < (num_steps+1); k++)
        {
            direction();
            step();
            map_query();
            if (z < 1) //if animal wanders off map, stop and go to next animal
                break;

            stay_go();
            if (go == 0) //decision to stay on pixel or move on
                break;
        }
        if (z < 1) //needed to drop out of current animal
            break;
        else
        {
            fprintf(stream2, "%i %i %i %i\n", i, x, y, z); //writes output file
            fprintf(stream3, "%i %i %i\n", i, x, y);
            //writes output from the first 100 animals for kernelhr
        }
    }
}

fclose(stream2);
fclose(stream3);

return 0;
}

//this code loads the file into RAM

void map_load()
{
    FILE *stream1;

    printf("\n\nloading map...");
    stream1 = fopen(mapname, "r"); //opens map file for input

    column = 1; //ignore that C arrays start with location 0
    row = 1;

    do //loads map 1 row at a time
    {
        do
        {
            fscanf(stream1, "%i", &pixel_value); //reads from input map file, writes to array
            mapfile[(row - 1)* 1141 + column] = pixel_value;
            ++column;
        }
        while(column < 1142);
        column = 1;
    }
}

```

```

    ++row;
  }
  while(row < 605);

  fclose(stream1);
}

//calculates starting position

void start()
{
  x = 661050 + (rand() % 57001);           //random function picks integer >=0
  y = 5428900 + (rand() % 30151);
  x1 = int((x - 661000) / 50);
  y1 = int((5459100 - y) / 50);
}

//queries map and returns value

void map_query()
{
  if(x1 >= 1 && x1 <= 1141 && y1 >= 1 && y1 <= 604) //ensures location is on map
    z = mapfile[(y1 - 1) * 1141 + x1];
  else
    z = -1;
}

//calculates new direction

void direction()
{
  int theta_old;
  theta = 1 + (rand() % 8);
  if (theta > 8)
  {
    //checks to see if the sum of the directions exceeds 360 degrees
    theta = theta - 8;
  }
  //brackets required due to consecutive if statements
  if (theta < 1)
    theta = theta + 8; //same but opposite to above
}

//increments pixel on map

void step()
{
  switch (theta)
  {
    case (1): //N
      y1 = y1 - multiplier;
      break;

    case (2): //NE
      y1 = y1 - multiplier;
      x1 = x1 + multiplier;
      break;

    case (3): //E
      x1 = x1 + multiplier;
      break;

    case (4): //SE
      y1 = y1 + multiplier;
      x1 = x1 + multiplier;
      break;

    case (5): //S
      y1 = y1 + multiplier;
      break;

    case (6): //SW
      y1 = y1 + multiplier;
      x1 = x1 - multiplier;
      break;
  }
}

```

```
case (7):                //W
    x1 = x1 - multiplier;
    break;

case (8):                //NW
    y1 = y1 - multiplier;
    x1 = x1 - multiplier;
    break;

default:
    printf("\ninvalid");
}

x = x1 * 50 + 661000;    //sets next x and y location
y = 5459100 - y1 * 50;
}

//decision to stay on pixel or leave
void stay_go()
{
    int prob;
    prob = (rand() % 1001);
    if (prob > (pr_z[z] * 10)) //choose probability between 0 and 1
        go = 1;                //returns 1 to move, 0 to stay
    else
        go = 0;
}
```

## Appendix IV

Calculation of indices use to measure habitat preference among simulated animals.

Strauss' Linear Index (Strauss 1979):

$$SLI = r_i - p_i$$

Chesson's alpha (Chesson 1983):

$$\alpha_i = \frac{\frac{r_i}{p_i}}{\sum_i \frac{r_i}{p_i}}$$

where  $r_i$  is the proportional use of the  $i$ th habitat type, and  $p_i$  is its proportional availability

Johnson's ranks (Johnson 1980):

$$\bar{t}_i = J^{-1} \sum_{j=1}^J (r_{ij} - s_{ij})$$

where  $r_{ij}$  is the rank of the usage of habitat  $i$  by animal  $j$ ,  $s_{ij}$  is the rank of the availability of habitat  $i$  for animal  $j$ , and  $\bar{t}_i$  is the preference for habitat  $i$  averaged among all animals ( $J$ )