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**WILDLIFE MOVEMENT IN FRAGMENTED HABITATS:
THE INFLUENCE OF LANDSCAPE COMPLEXITY**

by

Darren J. Bender

A thesis submitted to
the Faculty of Graduate Studies and Research
in partial fulfilment of
the requirements for the degree of

Doctor of Philosophy

Carleton University
Ottawa, Ontario

15 December 2000

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The undersigned hereby recommend to
the Faculty of Graduate Studies and Research
acceptance of the thesis,

“Wildlife Movement in Fragmented Habitats:
The Influence of Landscape Complexity”

submitted by
Darren J. Bender

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ABSTRACT

Most wildlife populations exist in heterogeneous landscapes where the distribution of habitat is spatially-subdivided, and consequently, its abundance and distribution is heterogeneous. Two influential theories predict the distribution of organisms in spatially-structured environments: island biogeography and metapopulation theory. Despite the wide acceptance of these theories, they are inconsistent at explaining the distributions of terrestrial species, perhaps because both theories are patch-based and do not consider heterogeneity that occurs within the matrix (i.e., non-habitat). The goal of this dissertation was to examine whether the patch-based approach is appropriate for predicting the movement and distribution of wildlife in mosaic landscapes where the matrix is heterogeneous.

I constructed a spatially-explicit computer simulation model to investigate how landscape pattern affected the movement of animals among patches of habitat. I assessed the association between patch attributes (e.g., size, shape, and isolation) and immigration success, and then examined how heterogeneity in the matrix influenced the ability to predict immigration from a patch attributes. I found that in landscapes with homogeneous matrices, most of the variation in patch immigration rate (about 85%) could be explained by patch attributes. However, the relationship declined sharply when heterogeneity in the matrix was introduced. These results indicate that patch-based models, such as those based on island biogeography or metapopulation theory, may not adequately predict the movement and distribution of wildlife in landscapes where landscape composition and pattern are complex.

In a field study that tested the modelling results, I observed the abundance and movement behaviour of white-footed mice (*Peromyscus leucopus*) and Eastern chipmunks (*Tamias*

striatus) in agricultural landscapes. I paired 10 agricultural landscapes that had relatively homogeneous matrix compositions with 10 heterogeneous landscapes to examine whether the abundance or movement of mice and chipmunks could be equally predicted in both types of landscapes using a patch-based model. Although abundance was not predictable, the movement of experimentally relocated animals was associated with patch attributes, but movement was less predictable in heterogeneous landscapes. These results provide further evidence that matrix heterogeneity can influence wildlife movement, and such information may be a missing factor in patch-based models like those based on island biogeography or metapopulation theory.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 INVESTIGATING SPATIALLY-SUBDIVIDED POPULATIONS

Most wildlife populations exist in heterogeneous landscapes where the distribution of habitat is spatially-subdivided, and therefore, the abundance and distribution of a species is normally not homogeneous (Wiens 1976). Two very influential theories have arisen to explain the distribution of organisms in spatially-structured environments: the theory of island biogeography (MacArthur & Wilson 1967) and metapopulation theory (Levins 1970, Hanski & Gilpin 1991). The central tenet for both of these theories is that local populations exist in islands or patches of habitat, and the abundance and distribution of a species can be predicted by the spatially-dependent rates of extinction and colonization. Generally speaking, the predicted colonization rate for an island or habitat patch declines as the distance to the source of colonizers increases, and extinction rate increases for an island or patch that is small and/or isolated. These two theories follow a patch-based approach which considers only the distribution of habitat in the landscape, and assumes that the intervening area (called the *matrix*) is homogeneous.

These theories have been applied to terrestrial landscapes, particularly where the effects of habitat loss and fragmentation are a concern (e.g., see reviews by Opdam 1991, Hanski 1994, Hanski & Ovaskainen 2000). However, both theories assume that pieces of habitat are separated by a homogeneously inhospitable matrix, which may not be a realistic assumption in terrestrial systems where there is usually a diverse composition and heterogeneous distribution of many landscape elements (Harrison and Taylor 1997). Thus,

island biogeography theory and metapopulation theory view landscapes as a system of spatially-subdivided patches of habitat, which is an oversimplification of real terrestrial landscapes which can be viewed more appropriately as a mosaic of many landscape types. The goal of my dissertation was to investigate how well the patch-based approach could be applied to complex landscapes that might be better represented as mosaics. To achieve this goal, I examined animal movement in different types of landscapes using both computer simulated data and data collected from small mammal populations in agricultural landscapes near Ottawa, Ontario. The details of this work, my interpretation of its outcome and the conclusions I arrived at are detailed in subsequent chapters.

1.2 STRUCTURE OF DISSERTATION

My dissertation is arranged in a logical structure that has two main approaches (see Figure 1.1). The first approach is a theoretical investigation of the effects of landscape pattern and landscape complexity on animal movement. I used computer simulation modelling as a tool to make predictions about the influence of patch characteristics and matrix heterogeneity on animal movement. The second approach is an empirical investigation that complements the theoretical work. I observed the distribution and movement behaviour of white-footed mice (*Peromyscus leucopus*) and Eastern chipmunks (*Tamias striatus*) in agricultural landscapes, and statistically modelled the effects of landscape pattern on these animals to look for agreement between my model predictions and actual relations in nature.

The theoretical investigation comprised the bulk of my dissertation research, and accordingly, I have broken it down into three separate chapters. The first of these chapters (Chapter 2) provides a detailed description of the modelling approach I used to simulate data regarding the movement of animals in heterogeneous landscapes. I built this model using an

approach called object-oriented model design, and I describe the advantages of using this paradigm in simulation modelling. I also describe in detail the components, structure and function of my model. Such description is necessary for the reader to fully evaluate my simulation methods, including the strengths and limitations of my approach which influence the interpretation of data and conclusions.

Chapter 3 examines the relationship between patch characteristics (patch size, shape, and isolation) and animal movement. A key component to nearly all current patch-based population approaches (e.g., island biogeography, metapopulations) is that movement into a patch is predictable from patch characteristics, namely size and isolation. The influence of patch area has been well studied (see reviews by Andrén 1994, Bender et al. 1998), particularly because patch area can be measured with little ambiguity. However, the influence of isolation is less apparent (Andrén 1994, Andrén 1996). There are a number of ways to measure isolation, and each may reflect different characteristics of a patch. In Chapter 3, I review the use of patch isolation metrics as predictors of patch immigration rate. I also conduct an overall evaluation of how well patch size, shape, and isolation are able to predict immigration rate on a patch-by-patch basis in binary (habitat/non-habitat) landscape maps.

Terrestrial landscapes in reality do not look like binary maps of habitat and non-habitat because the matrix is almost always heterogeneous. Chapter 4 elaborates on the previous chapter: I examine how adding complexity in the form of a heterogeneous matrix affects animal movement. Specifically, I investigate how well patch-based models of immigration are able to predict immigration in landscapes with homogeneous matrices vs. in landscapes with heterogeneous matrices. I also examine how increasing the complexity of the matrix (with respect to composition and configuration of the pattern of matrix heterogeneity) affects predictable movement. The implication of this work is that patch-based models may make

reasonable predictions of immigration rate in non-complex landscapes, and therefore, they adequately reflect the major process shaping the distribution of animals and the dynamics of the population. Yet in complex landscapes, patch-based models may not reasonably predict animal movement, meaning that island biogeography or metapopulation approaches may not be appropriate for complex, terrestrial landscapes. Chapter 4 directly tests this uncertainty by evaluating the performance of a patch-based model in both binary and complex landscapes.

1.3 DIATRIBE: WHY THEORETICAL AND EMPIRICAL INVESTIGATIONS MUST GO HAND IN HAND

Theoretical investigations, particularly theoretical models, are very powerful from the perspective that one can perfectly manipulate every factor of interest and control for any potentially confounding effects within a rigorous experimental design. Such rigor, replication, and strict use of controls is generally impossible in field studies, particularly in the field of landscape ecology where the broad scale of research puts considerable logistic constraints on the design and collection of ecological data. Modelling is an attractive approach for this reason. However, theoretical models suffer from one very considerable constraint: the congruence between modelling results and natural phenomena is usually unobtainable directly. That is, empirical observations cannot be collected in nature to replicate the modelling investigation. (If they could in practice, there would be little reason to produce the model!). Therefore, this constraint imposes a serious limitation on the interpretation of the outcome of a model: one cannot immediately determine the validity or generality of a model. Depending on how reasonable the modelling assumptions were, a model may accurately or poorly reflect natural phenomena. For this reason, it is my personal belief that models cannot be used to make definitive statements about natural patterns or processes in ecology.

Having said this, however, models *do* serve at least two very useful purposes: First, they can generate well-reasoned predictions that *can* be tested using observations from nature. From this perspective, modelling is a powerful heuristic tool that can sort through complexity and distinguish important patterns or processes for further investigation. Given the costs associated with field research (logistics, money, time), it makes sense to narrow-down the set of ecological questions that we attempt to answer. Second, models can be demonstrative, illustrating potential mechanisms that could shape the phenomena we observe in nature. A powerful example is the simple Lotka-Volterra cyclic population model (Opdam 1991) that demonstrated that the most basic predator-prey interactions could produce dynamic patterns in population size. Demonstrative models should not be interpreted as *the* mechanism, but rather as a possible mechanism, identifying an interesting hypothesis for future research. In either case, models can be used to accelerate the research process by stimulating research interest in important directions. It is in this spirit that I applied my modelling and directed my empirical work.

Finally, I need to state that a major goal of my graduate work was to better my knowledge of theoretical approaches in ecology, and more importantly, to learn how theoretical and empirical approaches can be integrated. Such interplay is necessary for the continued advancement of the science, and one has only to look at the leaders of our field to see that this is true. Pioneering work by scientists such as David Tilman, Robert May, Simon Levin, Buzz Holling, James Brown and others, demonstrates that pursuing a research career that integrates theoretical and empirical pursuits can yield incredible insights into ecological systems.

Figure 1.1: Conceptual structure of the dissertation.

CHAPTER 2

DESCRIPTION OF THE SIMULATION MODEL

2.1 INTRODUCTION

The simulation model described in this chapter is a generic, flexible piece of software that I constructed and used for the simulation studies presented in this dissertation. The purpose of this chapter is to (1) describe the modelling approach I adopted when designing my simulation model, and (2) provide a thorough description of the computer simulation software I created. There are many possible modelling approaches and many programming languages and paradigms, each of which have advantages and disadvantages for computer simulation modelling. In this chapter, I provide an explanation of the approach I adopted, which was to use object-oriented program design to construct my software. I also contrast this approach to procedural programming, which historically has been the standard approach for scientific computing, and I explain the advantages of object-oriented design over the procedural approach. In the second section of this chapter, I discuss the biological components I was interested in modelling. I detail the rationale and framework of the abstract model I used to simulate components of an ecological system, namely a spatially sub-divided animal population. In the last section of the chapter, I explain how I took this abstract model and implemented its design into a computer simulation model. I provide model flow diagrams and component descriptions for the generic simulation model I constructed so that the reader can understand my approach and evaluate the assumptions and constraints of my software.

I feel such elaborate explanation is necessary because any model, *by definition*, is only a limited abstraction of reality, and therefore, can *never* be interpreted without considering the

fundamental assumptions it relies upon. Although any author of a model would normally just state these assumptions, the process of translating an abstract model into an actual piece of computer software creates constraints which introduce “hidden” assumptions that are not always made apparent. Modelling is a tricky business and every reader should be careful to understand the limitations imposed by the design and recognize what constraints this places on interpretation and application to real-world biological situations.

2.2 APPROACHES FOR CREATING SIMULATION SOFTWARE

As in the investigation of complex ecological systems, there are at least two contrasting approaches for developing simulation routines. The first is the ‘top-down’ approach, where one begins programming routines to carry out the most general operations in a simulation (e.g., population growth over discrete time for x number of runs). As the programmer proceeds, he/she incorporates finer levels of detail to the simulation (e.g., population-level characters such as density dependence mechanisms, then age-structured population growth mechanisms, then individual-level stochastic elements for demographic parameters). In this approach, one fashions the ‘procedures’ of the simulation routines first, and incorporates the finer levels of detail around the more general procedures. Finer details/procedures are nested within more general ones within the conceptual and programmatic structure of the model. This programming paradigm is termed the procedural approach, and it has dominated scientific computing for its ease of computing and natural language structure. Languages such as Fortran and Pascal are good examples of procedural-based languages that have been widely used and have been immensely popular for scientific programming.

The second approach is to do the opposite, and start by fashioning the most basic elements of the simulation routines first. In this ‘bottom-up’ approach, one starts by defining

the most primitive elements or objects that are important to the model. For example, if we follow the biological population example above, the first thing a programmer might define would be an individual organism. But if genetic processes were the focus of the model, one might start at a finer level of biological organization and begin with a genome or even a chromosome. Once the most primitive levels are defined, one 'builds-up' by defining elements at higher positions in the hierarchy. For example, a fixed number of unique pairs of chromosomes compose an element called a genome, or many similarly-aged individuals compose an element called a population cohort. If spatial aspects are important in a model, another example is that one might define territories which can then be aggregated into patches, and many patches constitute a landscape element. In this approach, the model is completed by defining how the different elements in the model interact with one another: e.g., male and female individuals can reproduce (if they are the same species and in the same location), or individuals perceive the boundary of a habitat patch they occupy and are unlikely to move beyond it. There are only practical limits to how many levels of aggregation or hierarchy exist in the model. Also, the relationships among objects are defined completely independently of the design of the object, making object implementation an adaptable and dynamic process that facilitates incredible design flexibility. This programming paradigm is termed object-oriented design (Meyer 1988).

Object-oriented programming is based on the idea that programs should represent the interactions between real objects rather than the linear sequence of calculations commonly associated with procedural programming (Chapman 1931). Object-oriented design allows a modular approach to constructing computer simulation models. Modularity allows the programmer to define elements that are generally not interdependent upon one another, allowing models to be updated with greater flexibility than those designed with traditional

modelling approaches (He et al. 1999). Object-oriented design is attractive for ecological models, particularly individual-based population simulations because an object-based model can be designed to parallel the structure of an ecological system. The flexibility and modularity of the approach makes it easy to modify model assumptions and simulation/run specifications (He et al. 1999).

For these reasons, I adopted the object-oriented approach when I constructed my simulation routines despite the fact that object-oriented simulation models were rare in the ecological literature. However, since I have begun this work, applications of object-oriented modelling have started to become more commonplace (Sequeira et al. 1997). Applications come from many areas of biological sciences, including ecosystem modelling (Chapman 1931, Reynolds & Acock 1997), population modelling (Tischendorf 1997, Congelton et al. 1997), crop and plant models (Lemmon & Chuk 1997, Acock & Reddy 1997), and forest landscape modelling (Mladenoff and He 1999, Gardner et al. 1999). A number of programming languages permit object-oriented design, and I chose the popular C++ language. C++ is very portable, meaning that programs written in C++ can be compiled and executed on many different computer platforms (e.g., UNIX, Windows, DOS, Mac O/S, etc.) with little or no modification. This was an attractive feature because it allowed me to run simulations on whatever computers were available at the time. Most of my simulations were performed on SUN UNIX workstations maintained by L. Fahrig, Communications and Computing Services, and the College of Natural Sciences, Carleton University. Some early simulations were also performed on Windows-based Pentium computers maintained by the Department of Biology, Carleton University.

2.3 MODEL ELEMENTS

My model is implemented as an individual-based, spatially-explicit simulation. It is individual-based because the basic operations, and most importantly the stochastic elements, operate at the level of the individual organism. The model is spatially-explicit because every simulated animal has a virtual spatial location associated with it, and each animal has the capability to move through space. Space is modelled as a two-dimensional grid of cells (hereafter referred to as the *landscape*). The landscape is the fundamental spatial element in the model. The model has the capability to input landscape maps from a geographical information system (GIS), which allows it to incorporate nearly any type of landscape composition and pattern that an animal might encounter in the real world.

The following sub-sections elaborate on the representation of landscape patterns, the animal movement routines, and the routines that link movement and landscape pattern, as well as the simulation framework. A generalized conceptual representation of the model is shown in Figure 2.1, and the elements are discussed in detail below. A generalized universal modelling language (UML) diagram is provided as Figure 2.2 to illustrate the structure of the model, and details regarding class variables and functions are presented in Table 2.1.

To avoid confusion in terminology, please note that in object-oriented design terminology a *class* refers to the actual section of computer code that defines a set of methods, properties and data that are conceptually related, whereas an *object* is what is created by the software when a class is implemented. This distinction is a fine one, however, and I use these terms somewhat interchangeably. In either case, I use the SMALL CAPITALS font-type to designate these classes/objects.

2.3.1 Landscape Class

One goal for my modelling work was to incorporate a high degree of realism in the representation of landscape structure. Many spatially-explicit models, particularly the cellular automata models, use stochastic routines to simulate landscape patterns. Yet, these artificial landscapes often bear little resemblance to actual landscape patterns because (1) artificially generated landscapes often have very poor spatial resolution (often 100 x 100 raster cells per landscape or less) yielding a distinctly “blocky” appearance, and (2) patch size, shape and degree of clumping is more consistent than would be found in real landscapes (Krummel et al. 1987), although stochastically-generated fractal patterns may be an exception to this, (Mandelbrot 1982, Milne 1988, With & King 1999). A limitation of using unrealistic landscape pattern is that one cannot know if the modelling results obtained can be extrapolated to real landscape patterns that are generally much more complex (With & King 1997, see reviews by With 1997).

One method for incorporating realistic landscape pattern in a spatially-explicit model is to use GIS maps of actual landscape patterns. This technique was reviewed by Tischendorf (Tischendorf 1997) and he found that despite the wide availability of GIS software and data, there were very few examples of spatially-explicit models in ecology that utilized this technology, probably because computational costs were high and software integration was difficult. However, in recent years computing power has greatly increased, and GIS software manufacturers have made their data storage formats more accessible, meaning that it was practical for me to construct routines to incorporate high-resolution GIS maps directly into my simulation software. My model has the ability to use native IDRISI for Windows 2.0 GIS binary format or ArcView 3.2 GIS binary export format maps of any size and resolution, given enough computing power. I chose to use landscapes of 512 x 512 cells in size which captures

a fine degree of detail in landscape pattern (see Figure 2.3) yet the computational costs associated with movement simulation at such fine resolution are not excessive.

For the purposes of simulation, input landscape maps must be categorized and patch-based. A patch is defined as any contiguous (orthogonal or diagonal), homogeneous collection of cells. Landscape maps can be either binary (i.e., 2 landscape types: habitat and non-habitat; Figure 2.4a) or mosaic (i.e., >2 landscape types; Figure 2.4b) representations. In my model, the LANDSCAPE object actually has two member classes or “sub-classes” within it: (1) the GRID class, which stores the raster map(s) inputted from the GIS in the computer memory, and (2) the PATCH class which stores topological and statistical information (e.g., patch area, number of territories, number of current occupants) for every patch in the landscape. There is always at least one GRID object in every landscape, and this is the binary representation of breeding habitat. The habitat grid can be overlaid onto a second GRID if a heterogeneous matrix is required. This grid maps the different types of matrix that occur based on their perceived inhospitability to the animals. Keeping the maps of habitat and matrix separate facilitates simulation runs where one is varying matrix heterogeneity while keeping the pattern of habitat consistent. The PATCH class is used mainly for accounting purposes to keep track of the number and density of organisms within each patch of habitat in the landscape. Most importantly, it keeps a running tally of the number of new immigrants to enter the patch (i.e., patch immigration rate), which is the fundamental “output” of this simulation model.

2.3.2 Individual Animal Class

Individual animals are represented as non-sexual organisms with no age-specific traits (i.e., there is no sex- or age-structure in the model). All animals have a very simple life history that begins with a dispersal phase immediately after birth, during which the organism attempts to locate unoccupied habitat. If unoccupied habitat is located, the organism will reproduce

once producing a single offspring and then die. There is no other source of mortality in the model, which simplifies the demographics greatly ensuring that the net rate of reproduction is always zero. Similarly, animals that emigrate off the landscape are immediately replaced by a new immigrant that appears at a random location on the boundary of the landscape. Therefore, the population's size is always consistent, and fluctuations in population size are never a factor that can influence the outcome of this model. This is desirable because the focus of my investigation is on animal movement and not population dynamics, *per se*. The effect of landscape structure on dispersal mortality and population dynamics is a related but independent investigation that would make a logical "next-step" to my work. I chose to focus on movement because it is the fundamental process that links spatial pattern of a landscape to the regional population dynamics in all spatially-structured population models. Specifically, immigration is a key process in the patch-based models, particularly island biogeography and metapopulation models, and immigration rates need to be predictable from the spatial pattern of the landscape for these models to predict population dynamics.

A fundamental property of every ANIMAL object is its ability to interact with the structure of the landscape and use this information to move. These features are implemented in a separate MOVEMENT class (described below). The basic properties of an ANIMAL are its ability to recognize unoccupied habitat, reproduce itself, and remember where it has been in the landscape. These properties are also used by POPULATION class (described below).

2.3.3 Movement Class

If one can liken my LANDSCAPE class to a chessboard and the ANIMALS to pawns, then the MOVEMENT class is an unseen hand that moves the chess pieces about the board. The MOVEMENT class serves two purposes: (1) it manages the transitions in location that occur for all moving animals at each time step of the model, and (2) it simulates the decision process (if

any occurs) that an animal might go through while moving among patches in a heterogeneous landscape. This class is unique in that it is the only class to have a stochastic element to it, and therefore, all variability among replicate runs (i.e., same parameter values) is a consequence of the random elements associated with the MOVEMENT class.

Animal movement from place to place occurs as a function of two parameters: stepping distance and direction of movement. The stepping distance is a parameter that reflects the maximum dispersal potential of an organism within each time step. To ensure that an animal could move freely, but without making unrealistically large “leaps” across the landscape, I arbitrarily set the stepping distance per time step at approximately 1% of the landscape size (5 pixels). If this parameter is increased significantly, there is very little response of the animal to landscape structure because it becomes much easier for an animal to “leap” from one place to any other place in the landscape in a single time step, or the animal simply moves off the landscape too easily. If stepping distance is much smaller, the potential number of adjacent cells that can be visited becomes very limited, reducing it to the unrealistic lateral- or diagonal-only movement of a cellular automata model. At reasonable stepping distances (5 cells and greater) it is possible to model a near-continuous distribution of possible directions of movement. Two types of movement were defined based on the way direction was determined: (1) *random movement* occurred when the direction of movement was drawn randomly from a uniform distribution of turning angles, and (2) *directed movement* occurred when the direction of movement was based on the previous step’s direction plus some angle drawn at random from an approximately normal distribution (with a mean of zero and a standard deviation of $\pi/2$) using the polar form of the Box-Muller transformation (Box & Muller 1958). For case (1), this translates to movement steps that are uncorrelated to previous steps, whereas in case (2) there is a strong correlation in movement direction from step to step,

and case (2) is often called a correlated-random walk for this reason (Kareiva & Shigesada 1983).

The MOVEMENT class also simulates a decision process that an animal might go through when it encounters a boundary between two different types of land cover. In the model, habitat patch boundaries are semi-permeable, meaning that animals will always move into habitat when they are in the matrix, but a decision must be made to exit habitat. The decision is modelled as a simple probability based directly on the level of hospitability that is assigned to the matrix. If the matrix is heterogeneous, animals may also have to make decisions when moving between different types of matrix. The difference in hospitability values between two adjacent matrix patches determines the probability of crossing their boundary: if the new patch is only slightly less hospitable than the current patch, there is a greater probability of crossing than if the new patch is much less hospitable; if the new patch is more hospitable, then the probability of crossing equals one. Note that the MOVEMENT class for simulations using a heterogeneous matrix (i.e., implemented as a matrix GRID) is actually a derived form of the generic MOVEMENT class called HMOVEMENT (see Figure 2.2).

HMOVEMENT has all the same functionality as MOVEMENT, but also incorporates additional features for interpreting heterogeneous matrix pattern and hospitability, as well as boundary-crossing decision routines for movement in the matrix.

2.3.4 Population Class

The POPULATION class manages all the animals present in a simulation. It interfaces the MOVEMENT class with every animal, and provides accounting features, such as balancing immigrants and emigrants and balancing births and deaths. This class was designed so that it could be revised in the future if more complex population dynamics (e.g., age structure) were to be included in the model. Currently, such features are not implemented.

2.3.5 Parameters Class

The PARAMETERS class is a static object in the model that can be accessed by every other class during a simulation. It stores parameters for the number of runs per simulation, population size, movement type (random or directed), dispersal ability (stepping distance) of the animals, and hostility of the matrix (if homogeneous), as well as the memory locations of the landscape and population objects. These parameters must be defined by the user at the beginning of the simulation run, along with the filenames of the habitat map and matrix map (if used). Parameter values are passed to the software as command-line arguments to the program for each set of runs. A range of parameter values are processed in batch jobs where the program is run over and over using unique parameter combinations. Generally speaking, only the pattern of the landscape varied from run to run.

2.3.6 Utility Classes

There are numerous utility classes and subroutines present in the model that do not appear in Figures 2.1 and 2.2. Generally speaking, these classes are implemented only to provide necessary but mundane operations such as conversion of GIS file formats into GRIDS, dynamic memory management, and the storage of Cartesian (x, y) coordinates as a single attribute. Additionally, a “container” object is implemented in the model to manage replicate simulation runs (i.e., repetitions on one set of parameters). The code facilitates the creation of multiple “container” objects, meaning that one could specify a range of parameter values and iterations in one large process, instead of having to process them one at a time (i.e., batch processing). However, I usually ran my simulations on multiple computers, and it was simply easier to manage the many runs using batch processing. This method was also advantageous if there was a hardware failure or the model crashed (for external reasons) because one could simply restart the batch process at the exact point it left off.

2.4 MODEL OUTPUT

The model has the capability of outputting various patch-level statistics for each run, including total number of immigrants, total number of emigrants, average patch occupancy, and average number of occupied territories. Because I was most interested in patch immigration, I chose to examine only the total number of immigrants to a patch for each run. The model directly output information in the form of a comma-delimited spreadsheet giving the run number, landscape ID, patch ID, and total immigration rate. Multiple runs of each parameter combination were performed for all types of simulations, so it was necessary to summarize this. I constructed a program that read the output of each run of the model and summarized immigration rate as the mean and standard deviation of the numbers of immigrants by landscape ID and patch ID for every possible combination of parameters. Additionally, an import script automated the conversion of this spreadsheet data directly into a Microsoft Access database. The use of a database management system greatly facilitated the maintenance and retrieval of data, which is an issue in modelling studies where the amount of information collected becomes very large and difficult to manage (over two million records and two gigabytes of information were produced in my simulations).

2.5 SUMMARY

In this chapter, I have provided a detailed description of the modelling techniques and the modelling software I used to generate all the simulated data presented in this dissertation. The model I constructed is a generic piece of software that is capable of incorporating many types of landscapes, including landscapes with complex matrix composition. The real power of this model is its ability to simulate animal movement under nearly any landscape pattern scenario. I made use of this power by simulating animal movement under a wide range of

different types of landscapes (simulated and realistic) to see how landscape pattern and complexity affects animal movement. In the next two chapters, I report how this model was used to examine two questions: how habitat patch attributes can be used to predict animal movement, and how complexity of the matrix can influence this predictive ability.

Table 2.1: Description of class functions and variables from Figure 2.2. Note that class declarations (i.e., constructor and destructor functions) are not listed because they occur for every class and their implementation is relatively trivial.

Class Name	Member	Type	Description
LANDSCAPE	inImg	pointer to GRID	memory location of GIS raster image object (GRID)
	numPatches	integer	number of habitat patches in landscape
	params	pointer to PARAMETER	memory location to access simulation parameters
	patches	array of PATCH's	an array of PATCH objects which store patch-level information (e.g., number of immigrants or territories)
	pnfFile	pointer to stored patch information	pointer to file containing the patch-level information to be read into patches array
	pnfFileName	string	path name to the pnfFile
	addImmigrant	function	populate landscape with one new animal
	confirmPNF	function	detect if a pnfFile already exists
	createPNF	function	analyze landscape structure and store patch-level information in a new pnfFile
	readPNF	function	read patch-level information (e.g., size and location of a patch, number of territories within a patch)
	showImmigrants	function	return the number of new immigrants that have visited each patch

Class Name	Member	Type	Description
GRID	imgArr	array of integers	memory array that stores information about every cell present in the GIS raster image
	inFile	pointer to GIS coverage	pointer to IDRISI GIS file
	numPatches	integer	maximum patch ID value in GIS file
	params	pointer to PARAMETER	memory location to access simulation parameters
	startPatch	integer	minimum patch ID value (if greater than one)
	countPatches	function	determine and store actual number of unique patches
	getNumPatches	function	returns number of patches
	getStartPatch	function	returns minimum patch ID value
PATCH	area	integer	patch area in pixels
	maxHomes	integer	number of territories in the patch (function of area)
	numHomes	integer	current number of unoccupied territories
	numEmigrants	integer	number of animals to emigrate from patch
	numImmigrants	integer	number of new animals to immigrate to patch
	patchID	byte	unique patch ID value
	xmax	integer	maximum horizontal extent of patch

Class Name	Member	Type	Description
	xmin	integer	minimum horizontal extent of patch
	ymax	integer	maximum vertical extent of patch
	ymin	integer	minimum vertical extent of patch
	addImmigrant	function	increment numImmigrants counter by one
	addEmigrant	function	increment numEmigrants counter by one
	setID	function	assign unique patch ID from GIS coverage
	setMaxHomes	function	assign maxHomes from area of patch
	showID	function	return patchID value
	showEmigrants	function	return numEmigrants
	showImmigrants	function	return numImmigrants
	showMaxHomes	function	return maxHomes
	showOccupied	function	return maxHomes – numHomes
POPULATION	animals	array of ANIMAL's	an array of ANIMAL objects (i.e., the population of animals)
	inImg	pointer to GRID	memory location of GIS raster image object (GRID)
	inLand	Pointer to LANDSCAPE	memory location of complete LANDSCAPE object

Class Name	Member	Type	Description
ANIMAL	params	pointer to PARAMETER	memory location to access simulation parameters
	popnSize	function	return number of animals in landscape
	badSearches	integer	number of failed attempts at finding unoccupied habitat
	curPatch	integer	patch ID value for current location (> 0 if in habitat)
	curPosn	POSITION object	Cartesian (x,y) coordinates of current location in landscape
	ID	integer	unique ID value
	inImg	pointer to GRID	memory location of GIS raster image object (GRID)
	inPatches	integer	number of patches the animal has visited
	lastDir	double float	last movement direction, in radians
	lastPatch	integer	patch ID value of last patch visited
MOVEMENT	lastPosn	POSITION object	Cartesian (x,y) coordinates of previous location in landscape
	params	pointer to PARAMETER	memory location to access simulation parameters
	startPatch	integer	patch ID value of "birth" patch of animal
	curAnim	pointer to ANIMAL	current ANIMAL object to be moved
	current	POSITION object	animal's current location in landscape

Class Name	Member	Type	Description
	dist	integer	stepping distance at each time step
	inImg	pointer to GRID	memory location of GIS raster image object (GRID)
	inLand	Pointer to LANDSCAPE	memory location of complete LANDSCAPE object
	params	pointer to PARAMETER	memory location to access simulation parameters
	target	POSITION object	animal's target location for next movement step
	detect	function	determine what type of habitat (if any) occurs at a given location
	directedMove	function	determine next position using direction-correlated movement
	direction	function	return direction (in radians) between to POSITION objects
	distance	function	return distance (in pixels) between to POSITION objects
	move	function	assess projected trajectory for habitat patch boundaries, and if encountered, decide whether to cross
	project	function	determine movement path along a trajectory from current location to target location
	randomMove	function	determine next position using random movement
	reset1	function	remove an individual from the landscape and create a new individual at a random position on the landscape boundary
	reset2	function	remove an individual from the landscape and create a new individual in a randomly-selected habitat patch

Class Name	Member	Type	Description
HMOVEMENT	inImg	pointer to GRID	individual in a randomly-selected habitat patch
	inLand	Pointer to LANDSCAPE	memory location of complete LANDSCAPE object
	matrixImg	pointer to GRID	memory location of GIS raster image object (GRID) of matrix
	detect	function	determine what type of habitat/matrix occurs at a given location
	direction	function	return direction (in radians) between to POSITION objects
	hDetect	function	determine what type of habitat and matrix occurs at a given location
	hProject	function	determine movement path along a trajectory from current location to target location (matrix aware version)
	move	function	assess projected trajectory for matrix and/or habitat boundaries, and if encountered, decide whether to cross (if not, return amount of distance left to move and try moving again)
	oldMove	function	simplified movement routines when animals never leave a patch (ignores matrix)
	oppositeDir	function	move animal in a direction opposite to its current direction (used if an animal becomes “trapped” at a position)
PARAMETER	valFileID	string	unique ID of landscape file

Class Name	Member	Type	Description
	valFileName	string	name of IDRISI GIS file
	valNumAnims	int	population size for simulation run
	valStepDistance	int	maximum stepping distance for each move at each time step
	valSteps	int	number of iterations (time steps) per simulation run
	valWrite	boolean	export movement output to vector GIS file (true or false)
	fileID	function	return valFileID
	filename	function	return valFileName
	numAnims	function	return valNumAnims
	setFileID	function	define valFileID from user input
	setFileName	function	define valFileName from user input
	stepDist	function	return valStepDist
	steps	function	return valStepDist
	write	function	return valWrite

Figure 2.1: A very generalized representation of the model components. Boxes represent individual classes or objects contained in the model.

Figure 2.2: A generalized universal modelling language (UML) diagram of key model components showing the detailed structure and interaction of model objects. See Table 2.1 for a description of variables and functions.

Figure 2.3: Sample images of typical forest GIS maps that were used as landscapes in the simulation models. Forest maps were digitized from vegetation polygons in 1:50,000 topographic maps from southern Ontario, and each map is based on a 10 x 10 km landscape. In the model, each landscape is scaled to 512 x 512 pixels (each pixel edge is 20 m), providing a high degree of resolution necessary to distinguish very small and very irregularly shaped patches characteristic of natural landscapes.

Figure 2.4: Illustration of the difference between (a) a binary map of habitat (black) and non-habitat (white), and (b) a landscape mosaic composed of many landscape types (expressed as different shades of grey).

CHAPTER 3

EVALUATION OF METRICS OF PATCH ISOLATION FOR PREDICTING ANIMAL MOVEMENT IN BINARY LANDSCAPES

3.1 CHAPTER SUMMARY

Habitat isolation can affect the distribution and abundance of wildlife, but is an ambiguous attribute to measure. Presumably, isolation is a characteristic of a habitat patch that reflects how spatially inaccessible a patch is to dispersing organisms. In this chapter, I reviewed four types of isolation metrics (nearest-neighbour distance, Voronoi polygons, proximity index, and habitat buffers) and evaluated their ability to predict animal dispersal, using a spatially-explicit simulation model. The model simulated the movement of organisms in two types of landscapes: (1) artificially-generated point-pattern landscapes where patch size and shape are consistent and only the arrangement of patches varies, and (2) realistic binary landscapes derived from forest-vegetation maps where patch size, shape, and isolation vary. I tested the performance of the four isolation metrics by examining the strength of the correlation between observed immigration rate in the simulations and each patch isolation metric. I also evaluated whether each isolation metric would perform consistently under varying conditions of patch size/shape, total amount of habitat in the landscape, and proximity of the patch to the landscape edge. Area-based isolation metrics, such as the amount of available habitat within a given radius of a patch, were most successful at predicting immigration. The results indicate that the commonly-used distance-based metrics (e.g., nearest-neighbour distance) did not perform adequately when patch size and shape were

variable. Overall, the use of area-based metrics is advocated despite the limitation that these metrics require parameterization to reflect the movement capacity of the organism studied.

3.2 INTRODUCTION

Patch isolation is a key component of most patch-based approaches that seek to explain spatially subdivided populations. Examples of such approaches include the theory of island biogeography (MacArthur & Wilson 1967) and metapopulation theory (Levins 1970, Hanski & Gilpin 1991). Patch isolation is also a key consideration in numerous studies that have examined the influence of habitat fragmentation on wildlife populations (Table 3.1). However, patch isolation is a difficult attribute to quantify. Patch isolation, from a landscape ecology perspective, refers to the inaccessibility of a habitat patch for migrants moving from other patches. If one assumes that the land between patches (matrix) is homogeneous, then inaccessibility should be some function of the spatial relationships of patches (i.e., the configuration of habitat). Patch characteristics such as patch shape and size may also be a factor because larger, non-compactly shaped patches may "intercept" more immigrants than small, compact patches, particularly if there is some random component to an organism's movement behaviour. A number of metrics have been used in the literature to describe patch isolation (Table 3.1), but I am not aware of any studies that have attempted to evaluate the efficacy and reliability of different isolation metrics. Thus, the goal of this study was to determine which isolation metric provides the most reliable measure of patch isolation as it relates to dispersing organisms. I also evaluated how useful isolation is for predicting animal movement under different types of landscape scenarios, and I made the distinction between isolation (spatial configuration) effects and patch character (size and shape) effects on patch (in)accessibility.

3.2.1 Types of landscapes

Landscapes can be modelled (i.e., mapped) in at least four ways, and the different approaches affect how one employs and interprets patch isolation metrics. Figure 3.1 illustrates four approaches to modelling landscapes, which can be viewed as a progression of increasing complexity and realism.

The first landscape type is the point-pattern landscape (Figure 3.1a). In this approach, patches of habitat are discrete and exist in a homogeneous matrix. The sizes and shapes of the patches are either consistent or deemed to be unimportant. The configuration of patches (i.e., spatial pattern) is of central interest. The second type of landscape is the realistic binary landscape (Figure 3.1b). It is an extension of the point-pattern, except that patches have realistic, possibly irregular shapes of varying sizes. Note, however, that there are still only two states of landscape composition, habitat and non-habitat, which identifies it as a "binary" landscape. The third type of landscape that can be considered is the mosaic landscape (Figure 3.1c). Unlike binary landscapes, mosaic landscapes have more than one category of land type. There is a discrete number of landscape element types expressed (e.g., different levels of habitat suitability or matrix hostility). These types of landscape models are viewed as more "realistic" because they reflect a greater degree of landscape heterogeneity that cannot be expressed in a simple binary map. The final type is the raster image approach (Figure 3.1d) which does not use a categorical scheme to define patches of varying landscape types. The best examples of this approach are scanned aerial photographs and unclassified satellite images. This approach uses individual points or cells in a raster grid that can be represented by a nearly continuous range of grey levels to compose a complete image or map of a landscape. Because there is no categorization of landscape type, patches are not represented as discrete entities, and landscape elements can show a gradation from one type to the next (e.g., forest to

shrubs to grassland). This approach is the most realistic representation of the four landscape types we consider, but it is also most difficult to apply the concept of patch isolation because patches are not defined as unambiguously measurable objects.

In this study, I evaluated the performance of four general types of isolation metrics in the first two types of landscapes discussed above: point patterns and realistic binary maps. Point patterns serve as a type of "control" for initial evaluations of isolation metrics because these types of maps only reflect differences in the spatial configuration of habitat maps. Binary maps are more realistic, but introduce additional factors into the concept of patch inaccessibility because the size and shape of a patch can influence how accessible it is to dispersing organisms, independent of its isolation. Thus, I compared the ability of the different isolation metrics to predict patch inaccessibility to dispersers in both types of landscapes, to assess how reliable each metric was as the realism and complexity of the landscapes is increased.

3.2.2 Types of metrics

There are many different metrics that have been used in the literature to quantify patch isolation (Hargis et al. 1998, see descriptions in Gustafson 1998). There has also been a recent proliferation of statistical and GIS-based software packages for calculating all sorts of spatial pattern metrics, such as FRAGSTATS (McGarigal & Marks 1995), LEAP-II (Perera et al. 1997), Patch Analyst (Elkie et al. 1999), and APACK (Mladenoff & DeZonia 2000). Here I evaluate the four most common types of isolation metrics (Table 3.2) that can be calculated manually or by using packages such as the ones listed above.

The first type of isolation metric is the distance-based metric, such as the nearest-neighbour distance. Nearest-neighbour distance is the most straightforward of all the metrics I evaluated: it is simply a measure of the distance between a patch and its closest neighbour

(Figure 3.2a). I used patch edge-to-edge distance, but this metric could also be calculated by measuring the distance between the centres of neighbouring patches. This metric is simple to use but may be unreliable because it does not consider the proximity of other neighbouring patches beyond the closest patch.

Spatial tessellations are another way to measure patch isolation. Voronoi polygons, derived from the Dirichlet tessellation, use Euclidean distance as a criterion for defining the "area of influence" surrounding each patch (Figure 3.2b; see also Diggle 1983). This metric was suggested as an alternative to nearest-neighbour metrics by Krebs (1989), but has not been widely used in ecology. Unlike nearest-neighbour distance, Voronoi polygons are calculated by obtaining the distance to all proximate patches in the neighbourhood, and polygons are defined around each patch to delimit the space adjacent to each patch that is closer to it than any other patch in the landscape. Thus, the proximity of neighbouring patches is reflected in the size of a Voronoi polygon: small polygons indicate many proximate neighbours whereas large polygons indicate a greater degree of isolation.

A third type of isolation metric is based on the amount (area) of habitat that is within a specified distance of a patch. The greater the area proximate to the patch, the less isolated the patch. Such measures are easily obtained using a GIS to "buffer" a region around the patch and then determine how much additional habitat falls within that buffer region (Figure 3.2c). From a biological perspective, this approach makes a lot of sense because it provides a direct measure of how much habitat, that could be a source of dispersers, is within the proximity of a patch. However, one must parameterize this metric by selecting a threshold distance that determines how proximate the buffer region will be. The optimal buffer distance should reflect the dispersal capacity of the organism (Brennan et al. in press), but often this capacity is unknown and the buffer distance must be set arbitrarily.

A related type of areal metric is the proximity-based index (Gustafson & Parker 1994, McGarigal & Marks 1995). There are different forms of this index, but all use a distance-weighting scheme to calculate the amount of area within a distance threshold from a patch that contains habitat (Figure 3.2d). The proximity index sums the ratios of patch area to distance for all habitat patches that fall at least partially within some specified distance of the focal patch. This metric is also biologically realistic because it reflects the number of sources of dispersers that are proximate to a patch, as a function of their sizes and distances. However, like buffer metrics, the proximity index must be parameterized by specifying a threshold distance.

3.2.3 Characteristics of a useful metric

To be a useful metric of isolation, a measure must accurately and reliably reflect how spatially inaccessible a patch of habitat will be to dispersers. I suggest that to satisfy this definition, a useful metric must satisfy the following conditions. First, the isolation metric should be highly correlated with immigration rates, i.e., it must be a good predictor of immigration. Second, if isolation is to be used to predict immigration, then the relationship between these two factors should be proportional (i.e., linear). If the relationship between an isolation metric and immigration is non-linear, this is less useful because one may have to parameterize and back-transform the isolation metric to obtain predicted immigration. Without movement data, however, it could be quite difficult to perform the transformation. Finally, the metric should be robust enough that it performs consistently across different landscape patterns and is not influenced by factors such as the complexity of patch shape or the total amount of habitat in a landscape.

3.3 METHODS

3.3.1 Model Implementation

To determine how the various patch isolation metrics reflect immigration rate, the movement of “generic” animals was modelled in 100 simple simulated landscapes and 95 realistic (GIS) landscapes. The model was constructed to simulate the movement of organisms across different landscapes and recorded the number of successful immigrations for each patch in the landscapes. Because I was only concerned with dispersal movement, simple demographic parameters were used so that births equalled deaths, and the number of emigrants out of the landscape equalled new immigrants into the landscape, which greatly simplified the modelling and interpretation of results. For each run, the population size began with 250 animals placed randomly within habitat patches and the population size remained constant. Any animal that moved beyond the boundaries of the landscape was replaced by a new animal that appeared at a randomly selected location along the landscape boundary. Sex of the organism was not considered and every animal was potentially reproductive.

Each run of the model simulated the random movement of animals across the landscape. The goal was to record all new immigration events at each habitat patch. A patch immigration event occurred when an animal moved out of its patch of origin and encountered unoccupied habitat in another patch. Following immigration, each animal reproduced exactly one new individual and then died. New individuals were then free to move within or outside of this patch, and matrix mortality was not included. Each simulation run was performed for 1000 time steps, and 500 replications of each simulation were performed on every landscape. The total number of immigrants to colonize each habitat patch was recorded for every landscape, and the mean (across replicate runs) total number for each patch within each

landscape was used as the dependent variable to describe patch accessibility in subsequent statistical analyses.

At each time step, an animal could move up to 5 pixels in distance in any (360°) randomly chosen direction. The animal would move that full 5 pixels distance if the landscape composition along the route was homogeneous. However, if a boundary was encountered, then the animal would stop at that boundary and have to make a “decision” about whether to continue on its current path. The remainder of its maximum per-step movement distance could be used to continue moving in its current direction or in a new direction, depending on the outcome of the “decision”. A semi-permeable patch boundary was incorporated to simulate the preference that animals may have for remaining within habitat rather than entering matrix. In this model, a semi-permeable patch boundary was defined as a boundary that could only be crossed by animals (arbitrarily) 50% of the time when leaving a patch. There was no restriction enforced when an animal entered a patch, however.

Two types of landscapes were used in the simulations (see examples in Figure 3.3). The first landscapes were simple, pseudo-randomly generated maps, each containing 90 equal-sized circular patches. A clumping algorithm was used to vary the arrangement of patches in each landscape. The clumping algorithm had two parameters: first, a random number (3-12) of clusters of patches was selected, and a “seed” location was picked for each using randomly selected coordinates. Second, the degree of clumping was set by choosing a random number to be the maximum distance a patch could occur from its associated seed location. Each landscape was generated by distributing the 90 habitat patches among the seed locations, and the locations of the patches were determined by choosing random coordinates about each “seed” location that satisfied the maximum distance criterion. This method ensured that the only difference among the 100 simple landscapes was the configuration of patches, which

served as a control to isolate the effect of patch accessibility from the effect other patch characteristics (patch size and shape) that could affect immigration rates. The second type of landscape that I used was the “realistic” binary landscape in which the sizes and shapes of patches were not consistent. These 95 landscapes were obtained from 10 km x 10 km forest vegetation maps from agricultural regions in southern Ontario, Canada (described in Trzcinski et al. 1999). All landscapes were 512 x 512 pixels in size, providing considerable resolution for small and complex patch features (Figure 3.3).

3.3.2 Analysis of Model Output

A list of the patch isolation metrics that were evaluated is in Table 3.2. To determine which metrics were the best descriptors of isolation, squared Pearson product-moment correlations, r^2 were calculated between each metric in Table 3.2 and immigration rates obtained from the simulations. Each patch was described by the mean number of total immigrants to colonize it across the 500 simulation runs. To minimize the lack of statistical independence among patches within a single landscape, a nested design was used to calculate r^2 for patch indices by nesting mean patch immigration rates within each unique landscape. This method does not completely correct for lack of independence, but it does make it fair to compare individual patch-level responses in a relative fashion, which was my sole purpose here. Although it is standard practice to linearize data (e.g., log-transform) prior to correlation and regression analysis, this was not done in my analysis because one of my evaluation criteria (above) was to find a linear predictor of immigration rate.

There were some factors that could have confounded my results when analyzing the realistic binary (forest) landscapes. Immigration success may be related to characteristics of a patch that are independent of patch isolation (e.g., patch area, shape, length of perimeter), and it also may be influenced by the total amount of habitat in each landscape. I investigated how

large an effect patch characteristics should have on immigration by performing stepwise linear regressions on the following patch characteristics: patch area, perimeter length, perimeter/area ratio, patch shape index (Patton 1975, as implemented by McGarigal & Marks 1995), and the double-log fractal dimension of the patch. The latter three indices are different metrics that measure the complexity of the shape of a patch. If it appeared that any of these patch characteristics influenced immigration rate, these confounding effects were eliminated with residual analysis to statistically correct for their effects prior to subsequent analyses of the isolation metrics.

The total amount of habitat in a landscape might also influence my results because, all else being equal, it is to be expected that there will be higher immigration rates in landscapes that have more habitat (but only given my limited range of habitat amounts). This effect can occur simply because organisms spend less time searching in non-habitat areas. If immigration rates are much higher in some landscapes than others, there will be more extremely high immigration rate values in some patches, and therefore, there will be a greater possible range of observed values. Because it is easier to detect statistical relationships when there is a greater range of values to regress, the statistical relationship between isolation and immigration will be more apparent (see Opdam 1991, Hill et al. 1996). This situation is not an issue if all isolation metrics perform consistently, but is a concern if a particular metric is sensitive to a bias introduced by variability in habitat amount. To investigate this effect, the unexplained (residual) error was examined to see if it was related to the amount of habitat in a landscape.

One other factor that could have a confounding effect in both the artificial and realistic landscapes was the proximity of a habitat patch to the edge of the landscape. In my simulations, new individuals were allowed to enter the landscape at the boundary to exactly replace the animals that left the landscape. This introduces a potential discrepancy between

immigration and patch accessibility/isolation because the isolation metrics do not consider a patch's proximity to the landscape boundary, which is an artificial source of potential immigrants. This issue is also relevant to field studies that do not consider patches which fall outside the arbitrary landscape boundary when one measures isolation. This boundary proximity effect was assessed by examining the statistical relationships between a patch's distance to the boundary and the predictive ability of each isolation metric.

3.4 RESULTS

Figure 3.4 summarizes the correlations obtained from the independent relationships between mean immigration rate and each patch isolation metric for the point-pattern landscapes. The r^2 values are a direct measure of how well a patch isolation metric predicts the (in)accessibility of a patch to dispersers. Note that the direction of the relationship cannot be obtained from squared correlation coefficients. However, in all of my analyses in both types of landscapes, the relationship between each isolation metric and immigration rate was in the predicted direction: immigration rate increased as nearest-neighbour distance and Voronoi polygon area decreased, and immigration rate increased as buffer area and proximity scores increased.

In the forest landscapes, patch size and shape characteristics accounted for approximately one half of the variability in patch immigration rate (Table 3.3), and as expected, there was considerable correlation among characteristics (Table 3.4) indicating that the inclusion of some variables may have been redundant. The effects were statistically removed using multiple regression and residual analysis. Two analyses were then performed: one correlation analysis between each isolation metrics and the *raw* immigration rates, and one correlation analysis on the immigration rates corrected for the effects of patch size and shape.

Figure 3.5 summarizes the correlation scores obtained for each metric using both the uncorrected and corrected immigration rates. Generally, squared correlation coefficients were much lower using the realistic landscapes in comparison to the point-pattern landscapes, presumably because things other than patch configuration also influenced immigration rates (e.g., patch size and shape). Patch characteristics and patch isolation can also be entered into a multiple regression/correlation model as simultaneous predictors to determine, overall, how predictable immigration rates are in realistic landscapes (Figure 3.6). Taken together, patch size/shape characteristics and patch isolation do explain a large proportion of the variability in immigration rate (up to ca. 85%), and the R^2 values from these multivariate analyses are actually quite comparable in magnitude to the r^2 values obtained for the point-pattern landscapes where patch characteristics are consistent (Figure 3.4). Note that hereafter, I use the notation R^2 to indicate the squared multiple correlation coefficient, and r^2 to indicate a squared Pearson product-moment correlation coefficient or squared partial correlation coefficient, following the notation of Steel and Torrie (1980).

There was little evidence that the amount of habitat in a landscape affects the predictive ability of the isolation metrics evaluated (Table 3.5). However, only a fairly narrow range of habitat amount was evaluated (approximately 5 to 35% cover) and it is difficult to extrapolate to landscapes that contain more habitat. Yet, it may be that measuring isolation is not an issue above this amount because at higher levels of habitat amount, it is improbable that a highly isolated patch will occur (e.g., Gustafson & Parker 1992, Andrén 1994).

There did appear to be effects associated with measuring isolation for patches located near the edges of the landscapes. Figure 3.7 shows plots of the residual errors from the isolation-immigration rate regressions in the point-pattern landscapes. If a metric is unaffected by how far a patch lies from the landscape boundary, then one would expect to see an even

distribution of residuals across a gradient of distance. However, Figure 3.7 shows that for each metric, there is a preponderance of negative residuals for patches that are close (ca. < 30 pixels) to the edge of the landscape. This result indicates that immigration rates tend to be overestimated by patch isolation for patches very close to the landscape boundary. Voronoi polygons appear to be affected the most, likely because the delineation of a polygon is dependent on the position of the landscape boundary for peripheral patches. Beyond the 30 pixel threshold, all metrics seemed to perform fairly consistently. Figure 3.8 shows similar plots for the realistic landscapes. It appears that boundary effects have little influence in the realistic landscapes; the spread of residuals seems fairly consistent along the gradient of distance from edge.

3.5 DISCUSSION

The area-based metrics, buffer area and proximity index, clearly out-performed the other isolation metrics in both landscape scenarios (Figures 3.4 and 3.5). This result is not particularly surprising because nearest-neighbour distance and Voronoi polygons are calculated using only the distance to neighbouring patches, and they do not account for the *amount* of habitat that occurs within the neighbourhood. In my simulations, the presence of suitable habitat represents a potential source of migrants, so there should be a link between the amount of nearby habitat and the amount of immigration. The problem with distance-based metrics is that they cannot account for the amount of proximate habitat, which must influence the number of migrants in the neighbourhood, so they are poor predictors of immigration. For the point-pattern landscapes, the amount of proximate habitat is only a function of the number of patches within the neighbourhood, because all patches were of equal size. Distance metrics fail if they cannot reflect this function. The nearest-neighbour metric is an extreme example of

this because it does not look beyond one neighbouring patch. For the realistic binary landscapes, patch shape and size are irregular so the amount of proximate habitat is not necessarily reflected by number of patches or the distance to them, which explains why the area-based metrics perform so much better in these landscapes. Because the area-based metrics performed very well in both landscape scenarios, I conclude that these metrics are the most robust and reliable metrics across different types of landscapes.

A surprising result was that in the point-pattern landscapes, the simple nearest-neighbour distance was a better predictor of immigration than the Voronoi polygons. Nearest-neighbour distance should characterize patch isolation well if patches are fairly consistently spaced apart (Diggle 1983). However, if a clumpy distribution of patches occurs then the distribution of clumps themselves (particularly clumps composed of few patches) may determine the degree of isolation. Simple nearest-neighbour distance does not reflect the distribution of clumps of patches. It only reflects the distance from one patch to its closest neighbour, limiting its usefulness. Voronoi polygon area should be a better measure for assessing isolation because this metric is calculated by measuring the distance to all proximate neighbouring patches, and therefore, should better reflect how “clumpy” a distribution of patches is in a landscape. Yet, this was not supported in my results. Voronoi polygons were the worst predictor of immigration in point-pattern landscapes, with only about one-half the predictive power of the nearest-neighbour metric. In the realistic binary landscapes, they were about tied with the nearest-neighbour metric as the worst predictor of immigration. One problem is that Voronoi polygons are “unclosed” at the edge of the landscape for patches that lie adjacent to the boundary (see Figure 3.2b). My residual analysis that examined the influence of this boundary effect demonstrates that Voronoi polygons near the landscape edge tended to underestimate polygon area, and therefore, overestimate immigration rate in the point-pattern

landscapes (Figure 3.7). A similar effect was not observed for the realistic forest landscapes (Figure 3.8) but may have been masked by confounding patch characteristics that increase the variability of immigration rate and reduce the ability to detect a boundary effect.

An interesting result of the simulations was that patch isolation alone did not explain most of the variation in immigration rate. Rather, patch size and shape, which are unrelated to patch position, explained approximately one-half of the variation in immigration rate (Table 3.3). Thus, the accessibility of a patch can be strongly influenced by factors other than a patch's position in the landscape. It should be stressed that there are two components to accessibility that need to be considered: patch position and patch size/shape. Obviously, the relative importance of these two components will depend on the context of the landscape, and for highly isolated patches, the influence of patch size/shape may be slight. However, I demonstrate that immigration into the "average" patch was significantly determined by patch size and shape, and for very proximate patches, this component largely determines immigration success. It may not be necessary to consider all of the five patch shape/size characteristics that I used to characterize the patch shape/size component, especially since many of them are highly correlated (see Table 3.4). My results suggest that a reasonable surrogate would be to use either perimeter or the patch shape index because it was found that by themselves, each of these metrics explained most of the variation attributable to the overall patch size/shape component ($R^2 = 0.43$ and 0.44 , respectively). If two metrics are used, the patch shape index and patch area combined explain nearly the same amount of variation in immigration rate ($R^2 = 0.49$ for shape index and patch area vs. $R^2 = 0.52$ for all five patch characteristics combined).

In my simulations, I was able to statistically explain up to about 85% of the variation in immigration rate only if both patch size/shape and patch isolation components were taken

into account (Figure 3.2). This result represents a very high degree of predictability when one considers that the organisms simulated in this model were moving between patches in a random fashion. I expect that for more sentient organisms that move in a less random and unpredictable manner, one should be able to predict movement and immigration to an even higher degree. However, an interesting result (shown in Figure 3.5) was that by using buffer areas as the metric, one can still explain most (ca. 75%) of the variation in immigration rate without having to consider patch characteristics, provided that an optimal buffer distance is used (in this case, it was equal to the maximum distance that an organism could travel in five time steps of the simulation). This result demonstrates that buffer areas can be a powerful and robust metric if they can be parameterized correctly.

In conclusion, my results demonstrate that area-based metrics such as buffer areas and habitat proximity indices are superior predictors of immigration over commonly used distance-based indices such as the nearest-neighbour distance, or the distance-based spatial tessellations such as Voronoi polygons. The buffer and proximity metrics were both consistent and adequate predictors of immigration, and appeared to be relatively insensitive to variation in patch size/shape, distance to the landscape boundary, and the total amount of habitat within a landscape. In my evaluation, buffer area was the most predictive metric, but only if the buffer radius was correctly parameterized. Presumably, the optimal buffer radius is one that reflects the average dispersal distance of a migrating organism. However, average dispersal distances are rarely known and this may limit the actual usefulness of this metric unless one tries a variety of distances as I have done. Another option is to simply use the proximity metric, which appears to be relatively insensitive to correct parameterization. In this study, I simply chose a range of reasonable proximity distances for the metric and all the scores obtained were quite similar, suggesting that the proximity index will perform optimally if the distance

parameter is close to matching the dispersal ability of an organism. In either case, the area-based metrics are advocated for their predictive ability, reliability, and ease of calculation. The buffer-area operation is a fundamental operation of any geographic information system, and can be performed unambiguously. The proximity metric requires a little more work to calculate manually, but there is a wealth of readily available and free software that can be used to automate the process. These metrics are not as simple as measuring a nearest-neighbour distance, but I predict that as the popularity and wide use of GIS and software-based map analysis continues, area-based isolation metrics could replace the more commonly used distance-based metrics.

Table 3.1: Overview of recent patch isolation studies, applied patch isolation measures and results. Studies are assembled in descending chronological order. (Source: Bender et al., unpublished; prepared by L. Tischendorf).

Study	Patch isolation metric	Response variable(s)	Species	Results
Johannesen, Andreassen & Ims 2000	distance to nearest patch	degree of reproductive synchrony	root vole (<i>Microtus oeconomus</i>)	patch isolation favours within-patch reproductive synchrony
Delin & Andrén 1999	distance to the nearest habitat patch (>30 ha)	density	Eurasian red squirrel (<i>Sciurus vulgaris</i>)	no effect of patch isolation on density
Hokit, Stith & Branch 1999	$S_i = \sum e^{(-d_{ij})} A_j$ S_i : isolation of focal patch i (summed over all occupied patches) d_{ij} : distance between patch i and patch j A_j : area of patch j	occupancy	Florida shrub lizard (<i>Sceloporus woodi</i>), Racerunner (<i>Cnemidophorus sexlineatus</i>)	negative effect of patch isolation on <i>Sceloporus woodi</i> , but no effect on <i>Cnemidophorus sexlineatus</i>
Marsh, Fegraus & Harrison 1999	distance from experimental ponds to natural breeding ponds	occupancy and nest density	tungara frog (<i>Physalaemus pustulosus</i>)	negative effect of pond isolation on frequency of use and nest density

Study	Patch isolation metric	Response variable(s)	Species	Results
Hansson 1998	$S_i = \sum_{j=1}^n A_j e^{-\alpha d_{ij}}$ <p> S_i: isolation of focal patch i (sum over all occupied patches) d_{ij}: distance between patch i and patch j A_j: area of patch j α: constant, (2.3) </p>	colonization rate of various plant species	see Hansson (1998)	higher colonization rates into less isolated patches, effect of patch isolation depends on dispersal media of the species
Vos & Jardon 1998	<p>distance to nearest (occupied) pond,</p> <p>area of a) occupied ponds, b) moorland, and c) weighted roadlength within buffers of various width (250m - 2000m) surrounding focal patch</p>	presence/absence and density	moor frog (<i>Rana arvalis</i>)	area of moorland within 250m buffer best predictor, increasing buffer width did not result in higher correlation's
Bolger et al. 1997	distance to the nearest source canyon (>100ha)	species diversity	shrub inhabiting rodents, (e.g. californica mouse, cactus mouse, pocket mouse, desert woodrat)	no effect of patch isolation on species diversity

Study	Patch isolation metric	Response variable(s)	Species	Results
Cappuccino & Martin 1997	distance to the nearest shore, distance to the nearest point of land (island or shore), sum of distances to nearest land	density	birch tube-maker (<i>Acrobasis betulella</i>)	positive effect of patch isolation on larval density
Fitzgibbon 1997	distance to nearest wood patch, area of wood within 1km buffer surrounding focal patch, length of hedge within 400 m buffer	density	wood mice (<i>Apodemus sylvaticus</i>), bank vole (<i>Clithronomys glareolus</i>)	higher population increase in more isolated wood patches, more hedges support higher densities of both species
Grashofbokdam 1997	forest and length of wooded banks within buffers of 100m, 500m, 1000m widths surrounding focal patch	occurrence of plant species	see Grashofbokdam (1997)	higher probability of occurrence in less isolated patches
Luiselli & Capicci 1997	number of fencerows radiating from forest patch, distance to closest habitat patch, area of nearest patch, habitat area within 1km buffer surrounding focal patch	presence and abundance of species	various snakes	number of fencerows and distance to nearest patch affected presence of most species, generalist species less affected by patch isolation
de Vries, den Boer & van Dijk 1996	amount of heath within buffers of 500m, 1000m and 2000m surrounding focal patch	presence/absence	various ground beetle species	no effects of patch isolation variables on presence/absence

Study	Patch isolation metric	Response variable(s)	Species	Results
Hill et al. 1996	distance to nearest-neighbour patch	probability of colonization	silver-spotted skipper butterfly (<i>Hesperia comma</i>)	higher colonization probability into less isolated patches
Hijermann & Ims 1996	$S_i = \sum_{j \neq i} c_{i,j} A_j$ <p> S_i: isolation of focal patch i (sum over all occupied patches) $c_{i,j}$: distance based index (see ref.) A_j: area of patch j </p>	occupancy	wart-biter (<i>Dedalus verrucosus</i>)	probability of occupancy increased with decreasing isolation
Kinnunen et al. 1996	three isolation groups of patches (dependent on distance to nearest farmland patch)	presence/absence and abundance	farmland carabids	fewer individuals and species were caught in more isolated patches
Matter 1996	sum of the distances from a focal patch to all other patches	movement rates and distances, occupancy	red milkweed beetle (<i>Tetraopes tetraophthalmus</i>)	unoccupied patches were more isolated
Paillat & Butet 1996	total length of hedges in a 0.5km radius around sampling plot	abundance	bank vole (<i>Clethrionomys glareolus</i>)	patch isolation measure was best predictor of vole abundance
Dunning et al. 1995	distance to potential source patches	density	Bachman's Sparrow (<i>Aimophila aestivalis</i>)	isolated habitat patches were less likely to be colonized than nonisolated patches

Study	Patch isolation metric	Response variable(s)	Species	Results
Vos & Stumpel 1995	distance to nearest pond, various measures based on number of ponds, area of high herbs and area of shrubs within buffers of 100m and 2000m width	presence/absence	tree frog (<i>Hyla arborea</i>)	buffer measures gave better predictions of isolation than distance measures
Fitzgibbon 1993	area of wood within 1km buffer surrounding focal patch, distance to nearest wood, length of hedgerow within 400m buffer surrounding focal patch	drey density	grey squirrel (<i>Sciurus carolinensis</i>)	only distance to the nearest wood (> 0.5ha) influenced drey density
van Apeldoorn et al. 1992	area of nearest-neighbour woodland, distance to nearest wood area (> 25ha)	presence/absence, abundance	bank vole (<i>Clethrionomys glareolus</i>)	area of nearest woodland affects numbers of voles
Laan & Verboom 1990	number of pools within 0.5km radius from centre of a pool, several distances to nearest field, wood, shelter, pasture	presence/absence	various amphibian species	distance to nearest wood (>0.1ha) + distance to nearest old pool + distance to nearest field (>0.5ha) explained up to 28% of the number of species

Study	Patch isolation metric	Response variable(s)	Species	Results
Verboom & van Apeldoorn 1990	distance to nearest woodlot (> 5ha), distance to nearest woodlot (> 30ha), amount of wood in buffer rings of (i) 200-400m, (ii) 400-600m, and (iii) 200-600m widths surrounding focal patch	presence/absence	red squirrel (<i>Sciurus vulgaris</i>)	distance to nearest woodlot (>30ha) significantly affected squirrel presence
van Dorp & Opdam 1987	distance to nearest wood (>20ha), various buffer measures	abundance	forest bird communities	isolation variables explained small but significant parts of the residual variances in species number
Kozakiewicz 1985	distance of 400m to nearest compact forest area	reproduction, trappability, spatial organization	bank vole (<i>Clathronomys glareolus</i>)	habitat isolation decreased reproduction, increased trappability and influenced spatial organization
Opdam, Rijsdijk & Hustings 1985	distance to large forest area, distance to nearest mature deciduous wood (>20ha), area of wood within buffer of 3km width surrounding focal patch	spatial distribution	forest bird communities	no correlation between number of breeding bird species and isolation variables

Table 3.2: Description of the isolation metrics evaluated.

Name	Abbreviation	Description	Type of Metric
Nearest-neighbour distance	NDIST	Edge to edge distance to the nearest habitat patch	Distance-based
Voronoi polygon area	VORONOI	All area surrounding a given patch that is closer to it than any other patch	Spatial tessellation
Buffer area	BUFFER	Sum of all habitat cells within a buffer distance	Area-based
Proximity index	PROX	Sum of the ratio between area and inter-patch distance for all patches within a predefined buffer distance around a patch	Distance-weighted, area-based

Table 3.3: Statistical summary of stepwise multiple regression illustrating the relative influence of the different patch characteristics on immigration rate ($R^2 = 0.5251$, $n = 6761$, $p < .001$).

Patch Characteristic	Standardized	
	Regression Coefficient	Student's <i>T</i>
Area	0.312	7.223
Perimeter	-0.169	-2.573
P/A Ratio	-0.185	-21.133
Shape Index	0.763	13.349
Fractal Dimension	-0.237	-6.684

Table 3.4: Intercorrelations among patch characteristics and correlations between patch characteristics and isolation metrics. Values are Pearson product-moment correlation coefficients. Abbreviations are from Table 2.

	Area	Perimeter	P/A Ratio	Shape Index	Fractal Dimension
Perimeter	0.9548				
P/A Ratio	-0.2082	-0.2547			
Shape Index	0.6579	0.8020	-0.2695		
Fractal Dimension	0.4071	0.5363	-0.2180	0.9042	
NDIST	-0.0831	-0.0983	-0.0511	-0.1449	-0.1490
VORONOI	0.7025	0.7250	-0.2867	0.6048	0.4277
BUFFER05	1.0000	0.9552	-0.2086	0.6593	0.4085
BUFFER15	0.9969	0.9568	-0.2144	0.6711	0.4216
BUFFER25	0.9847	0.9513	-0.2236	0.6805	0.4347
BUFFER50	0.8953	0.8797	-0.2402	0.6656	0.4451
BUFR100	0.6120	0.6205	-0.2225	0.5162	0.3701
PROXIM05	0.1179	0.1314	-0.0093	0.1316	0.0938
PROXIM15	0.1189	0.1326	-0.0097	0.1328	0.0948
PROXIM25	0.1190	0.1327	-0.0098	0.1330	0.0949
PROXIM50	0.1190	0.1327	-0.0099	0.1331	0.0950
PROXM100	0.1190	0.1327	-0.0099	0.1331	0.0950

Table 3.5: Summary of relationships between amount of habitat area in a landscape for each isolation metric. A weak relationship indicates that an isolation metric is not sensitive to changes in habitat amount if used as a predictor or immigration rate. Most *P*-values are statistically significant, but it is more important to note that the absolute magnitudes of the effect (illustrated by squared Pearson product-moment coefficients and standardized regression coefficients) are practically negligible in all cases.

Isolation Metric	r^2	Standardized Regression Coefficient
NDIST	0.0013	-0.0359
VORONOI	0.0028	-0.0528
PROXIM05	0.0072	-0.2279
PROXIM15	0.0068	-0.0823
PROXIM25	0.0067	-0.0817
PROXIM50	0.0066	-0.0811
PROXIM100	0.0065	-0.0807
BUFFER05	0.0019	-0.0433
BUFFER15	0.0001	-0.0097
BUFFER25	0.0003	0.0168
BUFFER50	0.0010	0.0311
BUFFER100	0.0003	0.0163

Figure 3.1: Four different ways that landscapes can be mapped.

a. Point pattern

b. Realistic binary

c. Mosaic

d. Raster image

Figure 3.2: Illustrations of the four metrics tested in this study: a) nearest-neighbour distance (D); b) a spatial tessellation which produces many Voronoi polygons around each; c) buffer area, which is the amount of habitat that occurs within a fixed distance of the perimeter of a patch (grey polygons); and d) the proximity index which sums the ratios of patch area/distance (A/D) for all patches of habitat located within a fixed distance of a central patch of interest.

Figure 3.3: Sample landscapes illustrating simple point-pattern landscapes (a & b) and realistic forest landscapes (c & d), and spatially aggregated patches (b & d) and dispersed patches (a & c).

Figure 3.4: Summary of correlations between each isolation metric and observed mean immigration rate for the point-pattern landscapes. The height of each bar is a direct measure of how well a metric was able to predict mean immigration rate into a given patch. There are multiple bars for the buffer and proximity indices because these indices must be parameterized by defining a threshold distance from the patch perimeter. These distances were set in terms of the maximum distance an organism could move during each time step of the simulation. Thus, a 5-step buffer area defines all the available habitat within a distance from the focal patch that is equal to the maximum distance an organism could move in five time steps.

Figure 3.5: Summary of correlations between each isolation metric and observed mean immigration rate for the realistic binary (forest) landscapes. The gray bars indicate the squared correlation coefficients (r^2) obtained when patch shape and size characteristics are not accounted for. The black bars indicate the squared correlation coefficients obtained after statistically removing the effects of the patch characteristics (shown in Table 3).

Figure 3.6: The proportion of variation in mean immigration rate (expressed as R^2) that can be explained by patch characteristics and each isolation metric combined. In each case, patch characteristics account for the first 52% of variation in immigration rate, and the remaining explained variation in each vertical bar is attributable to the isolation metric.

Figure 3.7: Plots of the residuals from the immigration rate-isolation regressions against distance to edge for the point-pattern landscapes (see text).

Figure 3.8: Plots of the residuals from the immigration rate-isolation regressions against distance to edge for the realistic binary landscapes (see text).

CHAPTER 4

A SIMULATION STUDY TO EVALUATE THE INFLUENCE OF MATRIX HETEROGENEITY ON MOVEMENT

4.1 CHAPTER SUMMARY

The purpose of this second simulation study was to examine the influence of matrix heterogeneity on animal movement. Patch-based models, such as those based on metapopulation theory, do not incorporate information about features in the matrix. However, real landscapes (particularly terrestrial landscapes) normally have a complex structure that cannot be captured in a simple habitat/non-habitat view of the world. Whenever organisms respond to elements in the matrix while they are moving, the heterogeneity of the matrix should introduce unexplainable error into simple patch-based models. To examine this prediction, I performed movement simulations in landscapes with varying degrees of matrix heterogeneity, and compared them to landscapes with homogeneous matrices. I found that after introducing matrix heterogeneity, patch characters (patch size, shape, and isolation) became poor predictors of relative patch immigration rate. I varied three properties of the pattern of the matrix to determine the important aspects of heterogeneity: the scale of spatial pattern, the number of different types of matrix, and the amount of contrast between types (i.e., the degree of dissimilarity in hospitability values among types). The scale of pattern was the most influential property, and the number of different types of matrix also affected animal movement. Varying the contrast of matrix types had little effect. The simulations were also run using two types of dispersal behaviours: random movement and “directed” (i.e., correlated-random) movement. The response between random and directed movers was fairly

similar, although directed movement led to higher and more predictable immigration rates. This result suggests that my results are robust with respect to movement behaviour, and should be applicable to many different species with different dispersal behaviours.

4.2 INTRODUCTION

A patch-based view of the world is a dominant paradigm for scientists studying organisms distributed in a spatially subdivided manner. The theory of island biogeography (MacArthur & Wilson 1967) and metapopulation theory (Levins 1970, Hanski & Gilpin 1991) both stress the importance of island/patch size and isolation for structuring the abundance and distribution of organisms (see Chapter 2). This patch-based approach has become prevalent in the literature, particularly by those studying the effects of habitat fragmentation (Wiens 1995a). Typically, such studies survey animals in a fragmented landscape, define the spatial pattern in terms of patch size and isolation for every fragment, and then try to relate patch attributes to observed species abundance or species richness. However, these empirical relations are rarely consistent (see reviews by Mazerolle & Villard 1999) and are often opposite to the relations predicted from the theoretical models (Debinski & Holt 2000, and see also Bender et al. 1998).

Numerous explanations have been proposed to account for the apparent discrepancy between theory and the empirical literature, but two explanations are most important. First, the scale of pattern is important because it must match the scale of dispersal ability for the organism in question, or there will be no relation between spatial pattern and the abundance/distribution of the species. Doak et al. (1990) recognized this as a general problem in a review of fragmentation studies, and others have stressed the importance of scale in ecological studies (e.g., Levin 1992, Wiens et al. 1993, Malmer & Enckell 1994, Kareiva &

Wennergren 1995, Gustafson 1998). A second explanation for the inability of patch-based models to explain empirical distributions is related to variability of habitat quality and edge effects. The quality of a patch (i.e., its ability to support a species because of amount and quality of habitat or other resources) will largely determine the abundance of organisms within, and it will also affect site selection, movement, and the general distribution of organisms (e.g., Pulliam 1988, Danielson 1992, Danielson and Anderson 1999). If there is considerable variability in quality among patches, then this may be the over-riding factor determining abundance and distribution, and the effect of spatial pattern may be relatively weak or undetectable. Edge effects (e.g., Paton 1994, Villard 1998, Hartley & Hunter 1998) can compound this issue because they necessarily vary with patch size (see Bender et al. 1998), masking and/or confounding the effects of spatial pattern further.

A third and relatively unexplored reason to explain why patch-based models poorly predict species abundance and distribution in nature is the idea that there is too much complexity in real landscapes to be captured by a simple habitat/non-habitat model (Wiens 1997). Many patch-based models, particularly metapopulation models, view the matrix as homogeneous and either neutral or (to some degree) inhospitable. However, this is rarely the case in terrestrial landscapes where these models are being applied (Wiens 1995b). An animal's behaviour in the matrix may become unpredictable when there are elements within the matrix that affect movement, and the distribution of these elements is heterogeneous. That is, likely pathways for dispersal and barriers to movement are difficult to identify when the landscape matrix is composed of a complex mixture of land-cover types (Gustafson & Gardner 1996). For example, there may be many possible routes through the matrix that lead into or out of a particular patch, and there may be different landscape elements along each route (Figure 4.1). Depending on their constitution, the different routes of movement may have very different

probabilities of successful movement associated with them. There may (or may not) be barriers to movement, such as impassable streams or other bodies of water, or roads and built-up features that wildlife are unwilling to cross. Perhaps there are areas of exceptionally high mortality, such as barren ground, that make small mammals susceptible to predation by avian predators or amphibians susceptible to desiccation, or roads which may inflict exceptionally high mortality on small animals such as reptiles and amphibians (e.g., Fahrig et al. 1995). Conversely, corridors may connect patches of habitat facilitating movement and increasing the chance of successful migration. A simple patch-based model that considers only the size, shape, and arrangement of patches of habitat may not account for these matrix elements that affect movement. Also, a related effect is that of landscape complementation (*sensu* Dunning et al. 1992) which occurs when organisms require many different elements of the landscape over their lifetime. When this occurs, it is difficult to establish habitat vs. non-habitat in a simple binary map, effectively eliminating the possibility that a patch-based model can predict animal movement and distribution from a simple binary map of landscape structure, particularly where the spatial pattern of the different habitat types is complex and heterogeneous (Pope et al. 2000).

The heterogeneity of features in the matrix is the key, however. Even if the matrix contains areas associated with high mortality or has numerous barriers, patch-based models should adequately predict animal movement and distribution if elements of the matrix are distributed homogeneously (and assuming that some degree of movement between patches is possible). If matrix elements are homogeneously distributed (e.g., all areas of the matrix are similar in composition, or there is a regular fine-grained pattern of different types) then “all else is equal” and movement should be predictable by patch size, shape, and isolation. Therefore, “when all else is equal” and matrices are homogeneous, patch-based models should

perform much better at predicting relative amounts of movement than when the matrix is heterogeneous.

I examined the influence of matrix heterogeneity on animal movement using the same simulation approach that was presented in Chapters 2 and 3. In Chapter 3, I showed that patch area, patch shape index, and the buffer metric (calculated at a distance of 15 pixels) could predict about 80% of the variability in patch immigration rate in my simulated data. My approach in this chapter was to simulate movement in the same forest landscapes, but introduce varying degrees of heterogeneity into the matrix, to examine what relative effect it would have on movement. By contrasting movement in landscapes with homogeneous vs. heterogeneous landscapes, I was able to directly assess the influence of matrix heterogeneity on the predictability of movement. Also, heterogeneity can arise with respect to many different aspects of spatial pattern (Li & Reynolds 1994, Gustafson & Gardner 1996), so I also varied different components of matrix heterogeneity (see below) to determine which had the greatest influence on movement. In every case, the property of the matrix that varied (in some way) was the “perceived inhospitability” at a particular location. Every cell in the matrix was assigned a hospitability value that determined the likelihood that a moving animal would enter that cell (see Methods below). This procedure simulated the decision process that an animal might go through when it encountered areas of high risk to predation or other mortality, areas of restricted or energetically costly movement, or areas of relatively benign non-breeding habitat.

I also wanted to test the robustness of my results to different forms of movement behaviour. Movement behaviour may strongly influence how an animal responds to complexity of the landscape, and if true, then it would not be appropriate to generalize my results based solely on random movement. Therefore, I also modelled a second type of

movement that used a correlated random-walk routine to mimic the behaviour of an organism that moves in a much more directed fashion in the matrix (see Chapter 2). This type of behaviour produces movement pathways that are much less tortuous in the matrix because the animal tends to move in a fairly consistent direction, producing straighter routes between patches. I incorporated this type of movement to mimic the behaviour of habitat specialists which tend to move quickly and directly between habitat patches (Baars 1979, Rijnsdorp 1980, Wallin & Ekborn 1988, Wegner & Merriam 1990, Matter 1996, Charrier et al. 1997). My random dispersers behave more like a generalist species that have little aversion to the matrix. I contrasted these two types of movement by running identical, independent simulations using both types of movement. The goal here was not to test predictions about movement behaviour *per se*, but rather to determine how robust my modelling results were across these two types of movement behaviours. If both types of animals responded similarly to matrix heterogeneity, then this would indicate that it may be possible to generalize about matrix effects across different types of species.

4.3 METHODS

The modelling procedure used in this study was similar to that presented in Chapter 3 for the realistic forest landscapes. In this study, I added additional complexity to the model by varying the properties of the matrix. Note that the number of simulation replications per landscape had to be reduced from 500 down to 50 to accommodate the added dimensionality of the experimental design and the additional computation time needed to incorporate matrix heterogeneity into the model. The general method for each simulation was to take each forest landscape and superimpose it upon different matrix landscapes that had varying degrees of heterogeneity (refer to Chapter 2, illustrated in Figure 4.2). The results from these landscapes

were then compared to the results from landscapes with homogeneous matrices to determine if immigration rate was more predictable in the homogeneous matrix landscapes. Specifically, I compared the R^2 value for the overall regression models between immigration rate and patch size, shape, and isolation to contrast predictive ability.

I also explored how various components of heterogeneity affect the predictability of my patch-based statistical model. I systematically varied three aspects of matrix pattern that have been identified as important components of heterogeneity (Li & Reynolds 1994) to determine their relative effects: (1) diversity of matrix composition; (2) contrast among different types of matrix (with respect to inhospitability), and (3) the scale of the spatial pattern in the matrix (i.e., matrix “patch” size). In all cases, each different level of each aspect of matrix heterogeneity was applied to each of the 95 GIS landscapes (i.e., it was replicated 95 times) in a strictly “balanced” design.

The diversity of matrix composition (i.e., diversity of different types of land cover in the matrix) should have an effect on animal movement, because as the matrix becomes more diverse, there will be a greater number of potential decisions an organism will need to make as it finds a route between patches. Therefore, the number of possible routes should increase with increasing diversity of composition, making the prediction of that route more difficult. To test this prediction, I varied the number of land-cover types present in the matrix (Figure 4.3a). The property that changed in each of the different types of matrix was the “perceived inhospitability” of the matrix patch, which determines the relative tendency for a particular matrix type to be avoided by moving animals. The value of hospitability determined the probability that an animal would enter that patch, conditional upon the inhospitability of its current patch (see Chapter 2). For example, if an animal were to begin in a highly hospitable matrix patch (or a habitat patch), it would be unlikely to move into an adjacent patch that has a

very low hospitability score, whereas it would always enter an adjacent patch with a higher hospitability score (that is, if its movement path directed it there). Because it is possible that the overall or average hospitability of the matrix influences movement, I used landscapes where the average hospitability score across all matrix patches was approximately equal to an intermediate value of hospitability (ca. 0.5). As a baseline for comparison, I also ran simulations of movement in landscapes with a homogeneous matrix of intermediate (0.5) hospitability.

A second pattern that I varied related to the contrast or variability of matrix hospitability values around this mean intermediate value of approximately 0.5. I used matrix landscapes with a consistent number of types of matrix (four) and consistent pattern, and then varied the individual matrix patch hospitability values (h) from very similar ($h \in \{0.43, 0.48, 0.53, 0.58\}$, S.D.=0.07) to very dissimilar ($h \in \{0.05, 0.35, 0.65, 0.95\}$, S.D.=0.40) (see Figure 4.3b). In theory, a range of h values with a S.D. = 0 is a homogeneous pattern, so increasing contrast represents one aspect of increasing heterogeneity that animals *may* respond to while moving. I predicted that in low contrast landscapes, there would be fewer overall attempts to avoid inhospitable matrix patches than in high contrast landscapes, because the hospitability scores for matrix patches were more similar and the probabilistic decision algorithm for entering-exiting patches would be less influential on movement (i.e., the average probability of crossing matrix patch boundaries would be higher). Therefore, there would be less of an influence of the matrix on animal movement, and movement would be more easily predicted in low contrast landscapes than in landscapes where the contrast of matrix types was high.

The third matrix heterogeneity component I varied was the scale of the pattern (Figure 4.3c). In each matrix landscape, this parameter is simply the scale of subdivision, or the grain

size of the pattern. I varied the scale of pattern so that matrix landscapes varied from an 8 x 8 block (block size of 64 pixels) arrangement to a 128 x 128 block arrangement (block size of 4 pixels) (see Figure 4.3c). By doing so, I modified the size of the resulting matrix patches from large to small, and was able to examine how moving animals would respond to different scales of pattern. One would predict that when matrix patches are very large, patch-to-patch movement should be fairly consistent because there could be relatively few, if any, decisions to make as an animal moves. For example, if two habitat patches are close together and the underlying matrix pattern is very coarse, then the matrix composition between those two habitat patches might be homogeneous (but could differ in composition for another pair of habitat patches). However, when assessing the predictability of *overall* movement among all habitat patches in the landscape, matrices with coarse patterns of heterogeneity might be the most difficult to predict because pairs of patches will vary with respect to the type of matrix that occurs between them. The *average* matrix type intervening between two neighbouring patches embedded in a finely-grained matrix will tend to be more equivalent for all pairs because between patches there will be a large number of different matrix types. Averaging across these different types (for each pair of patches) will yield most similar “average” types of matrix elements needed to be passed-over to reach any neighbouring patch.

The effect of scale of matrix spatial pattern (i.e., subdivision) might also depend on how many types of matrix exist in the landscape (i.e., fine-grained matrices should be most complex and most unpredictable when there are many types of matrix present), so I simultaneously varied scale and diversity of matrix composition (while holding contrast constant) in a factorial design (5 scales of subdivision x 5 variants of number of matrix types x 95 landscapes) to assess any potential interaction between these two variables.

To analyze the data, I used PROC GLM in SAS (SAS Institute Inc. 2000) to determine the predictability (overall model R^2) of immigration rate from patch area, shape (patch shape index), and isolation (buffer area at 15 pixel distance threshold). These patch characteristics were chosen as predictors based on results from Chapter 3 that indicated they were the most powerful explanatory variables of animal movement. To compare how the predictability of movement was affected by diversity of matrix composition, scale of pattern, and contrast, I compared the fit of the predictive models (overall model R^2) across the different levels of a given variable of interest. To assess the degree of interaction between scale of pattern and diversity of matrix composition, I performed a two-way ANOVA on the immigration rate. As in Chapter 3, all statistical models were implemented as a nested (by landscape) design in SAS to facilitate the comparison of patch types across different landscapes. Note that in every case, I expected statistical significance due to the large sample size associated with the simulation data. Interpretation of statistical significance is, therefore, somewhat meaningless and instead I relied upon a qualitative approach.

4.4 RESULTS

To establish a baseline for comparing landscapes with homogeneous vs. heterogeneous matrices, I ran the simulation model on landscapes with homogeneous matrices of varying hospitability. Figure 4.4 illustrates that the average number of immigrants to reach a patch increased as matrix hospitability increased, but the overall predictive power of the statistical patch-based model was not affected in each case (i.e., the amount of explained variation in immigration rate did not vary). Although predictability of movement does not appear to depend on matrix quality, I nevertheless was consistent in creating matrix landscapes

that had an overall average hospitability that was consistent, regardless of how the pattern of that hospitability varied.

The degree of contrast in matrix hospitability values had surprisingly little effect on mean immigration rates or on the predictive ability of the statistical model (Figure 4.5). There was only a slight decrease in immigration rate and model R^2 with increasing contrast, contrary to my prediction. The trend was nearly identical for both random and directed movement.

The scale of pattern in the landscape and the number of matrix types constituting the matrix had the large effects on movement (Figures 4.6 and 4.7). Increasing the number of matrix types reduced the average patch immigration rate overall, especially when the scale of pattern in the matrix was quite fine-grained (Figure 4.6). The scale of pattern also influenced immigration rate, with the greatest degree of movement occurring when the pattern was very coarse, particularly for landscapes where the number of different matrix types was high (Figure 4.6). Inspection of the ANOVA table for these runs indicates that scale of pattern and number of matrix types had great effects on patch immigration rate (Table 4.1). These patterns were similar for both random and directed movement, although the directed movers experienced slightly higher movement rates.

Matrix heterogeneity had a large impact on the ability of the statistical model to predict immigration rate from patch size, shape, and isolation (Figure 4.7). The scale of pattern appears to have contributed more to the overall fit of the model (and thus, had a greater influence on the model R^2 values) than did the number of matrix types (Tables 4.1 and 4.2). In fact, the influence of number of matrix types seems to be dependent upon the scale of matrix pattern: the number of matrix types was positively related to predictive power for coarse patterns, and negatively related to predictive power for the fine-grained matrices.

The most important result, however, is that for all landscapes with any degree of heterogeneity, the patch-based statistical models performed more poorly than for landscapes with homogeneous matrices (Figure 4.7). In fact, when the matrix is heterogeneous and the scale of pattern is coarse, these models can only account for about half of the variation that is explained in landscapes that have homogeneous matrices. Table 4.2 illustrates the difference in predictive ability (expressed as the R^2 from the statistical models) in landscapes with homogeneous matrices and in landscapes with various degrees of matrix heterogeneity. This pattern was consistent for both random and directed movement.

4.5 DISCUSSION

Results from this simulation study demonstrate that the ability of a patch-based model to predict relative rates of immigration is greatly diminished when heterogeneity is introduced into the matrix (Table 4.2, Figure 4.7). On average, a patch-based statistical model using patch size, shape, and isolation could account for up to 70% - 75% of the variation in patch immigration rate if the matrix was homogeneous. However, when matrix heterogeneity was introduced into the landscapes, the amount of explained variation dropped to as little as 33%. The predictive power of the patch-based model was most dependent upon the scale of patchiness in the landscape, with the least predictable landscapes occurring when the pattern was coarse. The number of matrix types present in the landscape had a lesser and inconsistent effect, and the degree of contrast had a relatively small effect.

The first conclusion to be drawn from these results is that the matrix can matter! When the pattern of the matrix is coarse, the ability to predict relative immigration rates into a patch diminished to less than half compared to homogeneous matrix landscapes. Even when the smallest effect of heterogeneity was introduced (i.e., only two types of matrix and the finest

pattern of subdivision), predictive ability consistently declined from $R^2 = 0.70$ to $R^2 = 0.62$. When heterogeneity effects were large, predictive ability declined by almost one-half (i.e., from $R^2 = 0.70$ down to 0.38). The implication of these results is that patch-based models, such as those based on metapopulation theory, may not be appropriate when applied to terrestrial landscapes with a considerable degree of complexity, unless they explicitly consider elements existing outside of habitat patches. Classical metapopulation models and many other patch-based models assume that areas intervening patches of habitat have a negligible, or at least consistent effect on animals moving throughout a landscape. This assumption is violated when animals respond to elements in the matrix, and I have demonstrated (at least in theory) that this response can greatly diminish the capability of a patch-based model to predict the relative rates of movement among patches.

The effect of matrix heterogeneity on movement has also been investigated by Gustafson and Gardner (1996) in another computer simulation study. They simulated the movement of animals in random pattern landscapes and GIS landscapes that were defined to be either homogeneous or heterogeneous (with two degrees of heterogeneity). They found that in general, individual patches surrounded by homogeneous matrix had greater rates of immigration and emigration than did patches surrounded by a heterogeneous matrix. They also observed that immigration rates tended to be more variable in patches surrounded by a heterogeneous matrix, and that partial correlation coefficients with patch size and area tended to be smaller for patches surrounded by heterogeneous matrices. Although they did not explicitly test the prediction that patch immigration rate is less predictable in heterogeneous landscapes, they do reach this conclusion citing more variable immigration rates and smaller correlations as evidence. Their study agrees with my results, strengthening the idea that patch-based models will poorly predict animal movement when landscapes are complex with

heterogeneous matrices. However, this prediction has never been formally tested in the field. Chapter 5 presents a field study designed to test this prediction using the movement of small mammals in agricultural landscapes as an experimental system.

An interesting result of this study was that the pattern of response for two contrasting movement behaviours, random movement and directed movement, was consistent across all of the different scenarios I examined (see Figures 4.4 – 4.7). The two types of movement were designed to mimic the behaviour of a generalist and a specialist species. The consistency of response suggests that my modelling results are robust to different types of animals with different kinds of movement behaviour. In fact, the more specialist behaviour (directed movement) showed a consistently stronger response to landscape structure than the generalist. This suggests that departure from random movement makes an animal *more* predictable in its dispersal behaviour, and that random walks are a good baseline for study (i.e., if you find a response to landscape structure for random dispersers, you will also find it for more directional dispersers).

However, it should be stressed for both types of movement behaviours I simulated, each type had a large stochastic element to it. Even for the directional dispersers, the initial direction of movement out of a habitat patch was random, and none of the animals were able to “choose” optimal paths between patches in the landscape. There has been a great deal of attention paid to cognition and movement recently (e.g., Lima & Zollner 1996, Zollner & Lima 1997, Tyre et al. 1999, Zollner & Lima 1999, Conradt et al. 2000), and there is a growing belief that an animal’s response to landscape pattern might differ if it uses systematic movement behaviour rather than random behaviour. Although there can be a large random component in the movement behaviour of many organisms, particularly insects (Price 1976, Withers & Harris 1996, Goodwin unpublished, Keasar et al. 1996), it is certain that animals must select

their movement routes to some degree in response to their environment (see Zollner & Lima 1999). If true, factors that are important to random dispersers such as patch size and shape, may not be as important to highly cognitive dispersers. Also, the relationship between immigration success and patch isolation may not be clear if animals use very complex movement behaviours, such as “stepping stone” movement. Tyre et al. (1999) addressed such concerns in a modelling study that simulated many types of movement behaviour for animals dispersing through a fragmented landscape, but they found that every type of movement (even random dispersers) lead to strong responses to landscape structure. Perhaps we don’t need to model complex movement behaviour to determine predictable responses of animals to landscape structure (i.e., perhaps we can determine what aspects of spatial pattern are important using random movement only), but it would be very dangerous to make this conclusion without examining the movement characteristics of behaviourally dissimilar organisms to determine if their responses are consistent. Obviously, the interaction between animal movement behaviour, dispersal success, and landscape structure is an area of research that deserves greater attention.

Table 4.1: ANOVA results summarizing the association between log mean immigration rate and patch and matrix characteristics.

Source	<i>df</i>	Mean Square	<i>F</i> Value
Random Movement			
Area	95	752.0	514.52
Shape	95	51.7	35.36
Buffer	95	958.8	656.01
Landscape ID	94	27.41	18.75
No. of matrix types	4	2252.7	1541.25
Scale	4	5338.1	3652.18
Types*Scale	16	295.8	202.35
Directed Movement			
Area	95	765.4	682.19
Shape	95	47.2	42.14
Buffer	95	965.4	860.4
Landscape ID	94	26.9	24
No. of matrix types	4	1846.6	1645.79
Scale	4	3847.6	3429.13
Types*Scale	16	247.1	220.24

Table 4.2: Summary of the predictive ability (expressed as the overall R^2 values) of the patch-based statistical models for various types of landscapes. The R^2 values for the heterogeneous matrix landscapes were calculated separately by number of matrix types and scale. Only R^2 values for the two extremes of scale (block size of 64 pixels, 4 pixels) and number of matrix types (2 types, 32 types) are shown to illustrate the range of values produced by varying one parameter (and holding the other constant at its lowest level).

		Heterogeneous Matrix	
		Low Heterogeneity	High Heterogeneity
Random Movement	0.70		
No. of matrix types		0.42	0.41
Scale of pattern		0.35	0.52
Directed Movement	0.75		
No. of matrix types		0.47	0.47
Scale of pattern		0.38	0.62

Figure 4.1: An illustrated landscape to show how elements in the matrix affect the probability of inter-patch movement. In this example, the presence of barriers (a road or river) and corridors influences the probability that a chipmunk will move from the central patch to one of the adjacent patches (A, B, C, or D). However, a patch-based model would predict that there is equal probability of reaching each adjacent patch because patch size, patch shape, patch isolation, and patch quality are equivalent for every patch.

Figure 4.2: Graphical representation illustrating how heterogeneity was introduced into the matrix of forest landscapes.

Figure 4.3: Three components of heterogeneity that were systematically varied in the matrix landscapes.

Figure 4.4: Mean number of immigrants (bars) per patch by varying degrees of matrix hospitaibility where the matrix pattern was homogeneous. The line indicates the amount of immigration rate that was predicted by the statistical patch-based model using patch size, shape, and isolation as predictor variables. Random movement is shown in a, and directed movement in b.

Figure 4.5: Mean number of immigrants (bars) per patch by varying degrees of contrast of hospitability for elements in the matrix. The line indicates the amount of immigration rate that was predicted by the statistical patch-based model using patch size, shape, and isolation as predictor variables. Random movement is shown in a, and directed movement in b.

Figure 4.6: Log of mean immigration rate by scale of pattern of the matrix (i.e., the degree of subdivision of the matrix, coarse to fine-grained) and by number of matrix types constituting the matrix. Random movement is shown in a, and directed movement in b.

Figure 4.7: Amount of variation explained by the patch-based statistical model for varying degrees of scale of pattern of the matrix (i.e., the degree of subdivision of the matrix, coarse to fine-grained) and by varying number of matrix types constituting the matrix. Dashed line indicates the amount of explained variation that would be predicted in the absence of matrix heterogeneity. Random movement is shown in a, and directed movement in b.

a.

b.

CHAPTER 5

THE INFLUENCE OF MATRIX HETEROGENEITY ON THE MOVEMENT AND DISTRIBUTION OF SMALL MAMMALS

5.1 CHAPTER SUMMARY

In previous chapters (Chapters 3 & 4), I have shown that in theory, the movement of animals can often be predicted from patch characteristics (size, shape, isolation), but that the degree of predictability is a function of the complexity of the landscape (namely, matrix heterogeneity). This chapter investigates these predictions using an empirical approach designed to test my modelling results in a real-world system. I observed the abundance and movement behaviour of white-footed mice (*Peromyscus leucopus*) and Eastern chipmunks (*Tamias striatus*) in 20 agricultural landscapes near Ottawa, Ontario. I paired 10 agricultural landscapes that had relatively homogeneous matrix compositions with 10 complex landscapes to examine whether the abundance or movement of mice and chipmunks could be equally predicted in both types of landscapes using a patch-based statistical model. Small mammals were live-trapped, marked, experimentally relocated to nearby forest patches, and then re-captured to determine relative density and movement capability. A patch-based statistical model was constructed to explain abundance and movement as a function of patch size, shape and isolation. Although the model was generally unable to predict the relative density of mice and chipmunks, the movement of returning animals was predictable from patch characteristics. It was more difficult to predict movement in complex landscapes than in the more homogeneous landscapes. This result provides further evidence that matrix complexity can influence wildlife movement, and such information may be a missing factor in patch-based models like those based on island biogeography or metapopulation theory.

5.2 INTRODUCTION

In the previous chapters, I have presented two studies that used computer simulation modelling to examine the efficacy of a patch-based approach for predicting the movement and distribution of animals. In this chapter, I present “real-world” data that examine the distribution and movement of small mammals in agricultural landscapes. The goals of this empirical study were complementary to the goals of my modelling investigations, and the outcome of this study can be viewed as a test of the predictions of my theoretical work. Specifically, I was interested in addressing the three major predictions generated from my modelling studies: (1) that animal movement can be predicted from the patch-level characteristics that were identified as important in my simulation models (patch size, shape, isolation; see Chapter 3), (2) that inter-patch movement is less predictable from in landscapes with a heterogeneous matrix than in landscapes with a more homogeneous matrix (see Chapter 4), and (3) that the movement of a generalist species is more sensitive to landscape heterogeneity than movement of a specialist species (see Chapter 4).

The idea that the spatial pattern of habitat has an influence on the distribution and abundance of animals has become dogma in landscape ecology, and has been supported (at least in theory) by island biogeography theory and metapopulation theory (e.g., see Wiens 1995b). However, applications of island biogeography and metapopulation theory to explain real-world communities and populations have rarely been successful (see reviews by Harrison 1991, Harrison 1994, Debinski & Holt 2000). This failure to predict the distribution and abundance of organisms could arise for at least two reasons. First, the distribution and local abundances of a species may not reflect immigration and emigration rates among patches in the landscape. This could arise if local (i.e., patch) population dynamics are mostly asynchronous in the landscape because inter-patch movement is relatively infrequent, and

migration has a negligible demographic influence on each local population. This represents an “uncoupling” of the dynamics among local populations in the landscape and is actually a violation of the principal assumption of the classical metapopulation model. Conversely, many local populations may be completely synchronized (i.e., behave as one homogeneous population) if the subdivision of habitat is not great enough to prevent frequent and consistent inter-patch movement. Harrison (1991, 1994) recognized these as problems in field studies that inappropriately applied a metapopulation model to a system that was more appropriately defined as a collection of independent populations or as one homogeneous population. This is probably a common source of error in applying metapopulation models because complete information on the dispersal rates among patches, and even information on patch-level population dynamics, are not normally available for consideration.

A second, somewhat unexplored reason that might explain the shortcomings of applying a metapopulation-style or island biogeographic-style approach (i.e., a patch-based approach) relates to the heterogeneity of the matrix. Patch-based approaches view the landscape as a binary structure: habitat vs. non-habitat. Consequently, the matrix is assumed to be homogeneously neutral or inhospitable to some degree (see Chapters 1 & 4). Thus, among landscapes with different landscape structures, relative movement should be a function of patch characteristics, such as size, shape, and isolation (Chapter 3). However, if organisms also respond to elements in the matrix (e.g., corridors, barriers, mortality sinks), then heterogeneity in the matrix should lead to heterogeneous movement behaviour, and consequently, relative amounts of movement are not entirely predictable from patch characteristics alone (see Chapter 4, Figure 4.1). Thus, the first goal of this study was to determine whether these patch characteristics were significant predictors of the movement of small mammals in the different agricultural landscapes I surveyed. I also examined whether patch characteristics could predict

animal density, as predicted by metapopulation theory. The real question, however, was whether heterogeneity of the matrix influenced *how* predictable movement or density was from patch characteristics. Thus, the second goal of my study was to contrast two types of landscapes, simple landscapes with relatively homogeneous matrices and complex landscapes with heterogeneous matrices, to determine whether animal movement and density could be equally predicted in each case. If movement and/or density were significantly more predictable (or *only* predictable) in simple landscapes, then this would be further evidence that patch-based models may not be appropriate in terrestrial systems where landscapes are generally quite heterogeneous.

The final goal of this study was to compare the response of two behaviourally distinct species to landscape pattern to determine whether their response to patch characteristics and matrix heterogeneity was similar. I compared a forest habitat specialist, the Eastern chipmunk (*Tamias striatus*) and a habitat generalist, the white-footed mouse (*Peromyscus leucopus*). Specificity to habitat can be viewed as the converse to tolerance or utilization of the matrix. Therefore, I hypothesized that these two species should respond quite differently to composition of the matrix. In Chapter 4, I demonstrated that the movement of generalists (defined to have higher affinity to the matrix) was less predictable from patch characteristics when the matrix was heterogeneous. Thus, I also examined whether the movement and density of these two species were equally predictable for homogeneous and heterogeneous landscapes.

5.3 METHODS

5.3.1 Study Area and Site Selection

The study was conducted in the predominantly agricultural landscapes south and west of Ottawa, Ontario. Like much of eastern North America, this region was mostly forested

prior to European settlement (Curtis 1956). Today, only a small portion of this forest exists in the landscape following settlement and extensive agricultural development. What remains is patchily distributed forest remnants, hereafter referred to as woodlots or forest patches. These forest patches are embedded in a matrix of predominantly agricultural habitats, with the primary types being corn, soybean, alfalfa/hayfield, and pasture. Other common land-cover types are abandoned fields/old field habitats, early successional forest, and human developed/built-up areas. The composition and interspersions of these agricultural habitats and land-cover types varies greatly across the region. Some areas are dominated by one type (e.g., corn fields) whereas other places have a great diversity of composition with many different types being interspersed. I capitalized on this variation in composition and interspersions, and selected pairs of 2.5 x 2.5 km landscapes that represented contrasting landscape compositions: (1) "simple" landscapes that contained forest patches embedded in a relatively homogeneous matrix (usually one or two of corn, hay fields or pasture lands), and (2) "complex" landscapes where forest patches were embedded in a matrix composed of many different land-cover types (Figure 5.1).

I sampled small mammals (see below) in 20 landscapes between July and October of 1999. Each landscape was sampled for a one week period. Sampling sites were selected in pairs so that each week of trapping occurred in one simple and one complex landscape. The paired design was adopted to control for the increase in small-mammal density that was predicted to occur as the season progressed (Fahrig 1983, Wegner 1995, Henein 1995). I used the focal-patch sampling scheme advocated by Brennan et al. (In Press), and identified one central patch within each landscape for trapping (see Figure 5.2). Focal patches within landscapes were selected on a basis of accessibility (all landscapes except one were on private

lands necessitating landowner permission for access) and similarity in size and composition (all were deciduous forest).

5.3.2 Small Mammal Trapping

In the focal patch of each landscape, I used a systematic grid of aluminium box traps (Sherman traps) to capture small mammals. At each site, two pairs of parallel transects of traps (i.e., four transects in total) were laid out. Each transect began at 15 m from the forest edge (to be consistent and avoid edge effects), and each had approximately equal numbers of traps. Within each transect, traps were spaced at 5 m intervals. During the first half of the season (i.e., before 15 August), 100 traps were used per landscape. However, animal densities increased markedly over time, and the number of traps was reduced to 75 in the latter half of the season because logistically it was not possible to process the increased number of trapped animals. Traps were baited with birdseed (primarily millet and sunflower seed) and provided with Dacron wool for bedding material. Traps were run continuously for a 6 day period, and checked and re-baited between one and three times per day, as necessary. On the seventh day of sampling, traps were checked, recovered, and redeployed to the next sampling site.

I was particularly interested in the distribution and movement of two species: a forest habitat specialist, the Eastern chipmunk, and a habitat generalist, the white-footed mouse. These two species were identified as focal species because previous research in the same area (Fahrig 1983, Wegner 1995, Henein 1995) has shown that these are the most common small mammal species in the area, and that they have dissimilar use of the forest habitat. Wegner (1995) determined that white-footed mice could be found in many different land-cover types adjacent to the forest habitat, even though forest is the historical and preferred breeding habitat for this species. Occasionally, mice were even capable of breeding in agricultural fields, but generally this occurred only when provided with suitable cover (e.g., wooden nest boxes).

However, in a radio-telemetry study conducted in the same area, Merriam and Lanoue (1990) showed that mice rarely utilized such areas, suggesting that they are behaviourally plastic, and prefer to use forest habitat when available. By contrast, Henein (1995) showed that chipmunks rarely, if ever, ventured out of forest habitat. Generally, this species would only move between forest patches when there was some type of forested corridor for movement, such as a woody fencerow. Occasionally, chipmunks will take residence in woody fencerows, but such individuals tend to be juveniles or only temporary residents and not reproductive adults (Henein 1995).

When I captured white-footed mice or Eastern chipmunks (hereafter referred to as just mice or chipmunks, respectively), I used sequentially numbered Monel ear tags to uniquely mark these individuals. All other species were immediately released. Mice or chipmunks that were pregnant or lactating females, small juveniles, or individuals that did not appear healthy were also released. The remaining mice and chipmunks were relocated to adjacent woodlots that appeared to have similar forest habitat to the focal patch. Within each landscape, up to five relocation woodlots were selected by their accessibility and proximity. Woodlots were generally less than 1000 m from the focal patch of capture, which seemed like the farthest reasonable distance a mouse or chipmunk might move in a day or two (Merriam & Lanoue 1990, Henein 1995, J. Wegner, pers. comm.). Generally speaking, mice and chipmunks in this study area will attempt to return to their home patch following a relocation (K. Henein & J. Wegner, pers. comm.), although no one has investigated why this might occur. Regardless of the reason, I exploited this behaviour to gain insight into the movement capabilities of these two species. Specifically, I used the recapture rates of relocated individuals as a measure of the movement capability of each species in the homogeneous vs. heterogeneous landscapes I sampled.

5.3.3 Analysis of Capture-Recapture Data

I was interested in comparing information between landscapes on the (1) density and (2) the movement capability of mice and chipmunks. To estimate relative density, I calculated the total number of new captures for each species at each landscape divided by the number of traps that were deployed. This relative density score does not actually estimate the true number of mice or chipmunks that occurred within each woodlot because (1) it may underestimate density when some animals in the grid are not captured, and (2) it could also overestimate density when animals living outside the grid are drawn into traps from afar (e.g., they are attracted to the bait). However, I assumed that only animals within close proximity to the traps would be captured (certainly none from adjacent patches) and that the traps would perform with similar bias [i.e., (1) and (2) above] in every landscape, meaning that relative densities are still comparable across landscapes. Movement capability was simply calculated as the percentage of individuals of a species that returned to the focal patch subsequent to relocation.

I used a combination of multiple linear regression, residual analysis, and paired-sample t-tests to analyze my data. Multiple linear regression was used to identify key patch-level variables that influenced the relative density and return rates at each landscape, such as focal patch size and shape, and isolation. Derrane et al. (unpublished) also showed that the presence/intensity of roads between patches affected the movement rates of at least mice, so road density (landscape-level measurement) was also included in the statistical model in case it was an influential variable. Another landscape-level factor that can influence the local abundance of organisms is the total amount of habitat in the landscape (e.g., Robbins et al. 1989, Verboom & van Appledorn 1990, Fitzgibbon 1997, Vos & Chardon 1998), so this variable was also entered into the statistical model in case it was a confounding variable. A

final nuisance variable that was evaluated was understory vegetation cover. Although I attempted to select sites that were identical in composition, there were slight differences among sites with respect to the amount of understory vegetation, and I wanted to verify whether this factor influenced small-mammal densities. Multiple regression analysis was used to rank the importance of all these patch- and landscape-level variables. The effects of confounding/nuisance variables were statistically removed from the data, if significant, prior to assessing the significance of predictor variables of interest. I then used the residuals of the final regression model to reveal how well density and movement could be predicted from patch and landscape variables. By definition, the sum of the magnitude of the residuals reflects how closely the model predicts an observed phenomenon given one or more predictor variables. By examining the magnitude of the residuals, I could test the hypothesis that movement and distribution should be less predictable from patch characteristics in complex landscapes than in simple landscapes. I grouped the residuals by landscape type and used a paired-sample T-test to determine whether the absolute value of the residuals was significantly greater for the complex landscapes than the simple landscapes.

The analysis of the movement data was done in three steps. First, I was interested if immigration rates could be predicted from the patch characteristics of focal patch size (AREA), shape index (SHAPE), and patch isolation measured as the mean distance between focal and all relocation patches (MEANDIST). I also wanted to identify and eliminate the effects of any nuisance effects such as vegetation cover (VEGCOV) and the effect of roads (AVGROADS: average number of roads, and AVGTRAFF: average traffic intensity). Many landscapes (particularly those sampled towards the end of the season) had many more captures and returns than others, and obviously I had more confidence in landscapes where the counts

were higher. Therefore, I also weighted the fit of the regression by the number of captures that occurred in each landscape.

Once the important predictors of movement were identified, the second step was to contrast the fit of the best predictive model in the heterogeneous vs. homogeneous landscapes to test my prediction that movement is most predictable in homogeneous landscapes. If true, one would expect that the observed rates of return in homogeneous landscapes would be more similar than those predicted by the statistical model using patch size and isolation. A direct measure of this similarity is the size (i.e., absolute value) of the residuals from the return rate-patch size & isolation regression model, with smaller residuals indicating a close fit between the observed data and the model, and a large residual indicating a poorly predicted fit. Therefore, I tested whether the size of the residuals was consistently smaller for homogeneous landscapes than for heterogeneous landscapes using a paired-sample *t*-test.

Finally, I was interested in whether movement was equally predictable for both species. To evaluate this, I repeated the series of analyses above for the mice and chipmunk data independently and then I simply compared the results for each species to see if they showed similar relations. It should be made clear that my approach was to first examine the overall relationships of small mammals to landscape pattern and matrix heterogeneity, and then a secondary examination was to compare these relationships between the two species. To accomplish this, I performed two series of analyses on the data: one series on the pooled data for mice and chipmunks together, and then another series conducted independently for mice and chipmunks. The most straightforward analysis to examine *overall* relationships was to ignore species, and pool the movement data for mice and chipmunks into one data set. The advantage of doing this is that it is easy to interpret the overall response of the small mammals in each statistical test, and pooling also increases sample size and associated statistical power.

The danger in pooling data is that it *may* violate statistical assumptions regarding the independence of observations, and invalidate significance testing. To assess independence, I looked for significant correlations among the residuals from the regression models between mice and chipmunks. An absence of correlation would suggest that the mice and chipmunk data are independent. Regardless of the outcome of the correlation test, I also performed the analyses separately by species to compare the outcomes for a habitat specialist vs. a generalist species. I examined both approaches (pooled analyses and separate analyses by species) for consistency in outcomes before drawing conclusions. I urge the reader to consider the drawbacks of each approach (pooled, unpooled) when interpreting the results.

5.4 RESULTS

5.4.1 Number of captures and animal density

Over the course of the season, I captured 274 mice and 193 chipmunks. Of these, 180 mice and 103 chipmunks were suitable for relocation. The overall return rate of relocated animals was approximately 20% (22% for mice and 18% for chipmunks). Most of the relocated animals were males because the majority of females I captured were lactating and/or visibly pregnant, and therefore, were not chosen for relocation. Capture frequency (i.e., the number of captures/number of traps) increased for both species as the season progressed (Figure 5.3), and time was a highly significant predictor of animal densities (Table 5.1).

Although the magnitude of increase over time was fairly similar for both species (i.e., no significant interaction between species and time, Table 5.1), mouse densities were significantly higher than chipmunk densities throughout the season (Figure 5.3, Table 5.1). To statistically control for the effect of time on animal density, I refit the regression between animal density and trapping date for both species combined, and then used the residual values from this

regression as the dependent variable in subsequent analysis. The residual values can be thought of as “time-corrected” relative estimates of density. There was no evidence that the residuals were correlated between species ($r = 0.058$, $n = 20$, $p = 0.815$), suggesting that observed densities were reasonably independent between mice and chipmunks.

I used the RSQUARE model selection method of PROC REG in SAS to identify which of the following independent variables were associated with the corrected estimates of animal density: focal patch area (AREA), focal patch shape index (SHAPE), area-weighted mean distance between the focal patch and all other patches in the landscape (PROXIM) [a proximity index similar to (Gustafson & Parker 1994), see Chapter 3], amount (total length) of roads in landscape (ROADS), amount of understory vegetative cover (subjectively ranked from 0 to 5; VEGCOV), and heterogeneity (high or low) of the landscape (HETERO). I used the minimum AIC_c (Akaike's Information Criterion [with correction for small sample size], see Akaike 1973, Burnham & Anderson 1998) selection procedure advocated by (Burnham & Anderson 1998) to select the “best-fitting” model to the data. The variable(s) included in the best model were then identified as the most important predictors of animal density. However, after computing statistical models of all possible combinations of variables, none of the models (including the best-fitting model) were significant (Table 5.2). I also re-conducted the selection procedure by subdividing the data by species. Independent model selections for mice and chipmunks again revealed that there were no significant predictors of animal density. One model with the mice data ($R_DENSITY = SHAPE$) had a conspicuously lower AIC_c value than any other model, but the relationship was very weak and insignificant ($R^2 = 0.117$, $n = 10$, $p = 0.14$). I also looked to see if the return rates themselves were able to predict animal density, which asks the question whether movement itself predicts density. I found no correlation between animal-density and return rate ($r^2 = 0.013$, $n = 34$, $p = 0.535$; statistically

corrected for possible differences of matrix heterogeneity). Because animal density was not related to any patch characters (or any other variables), it did not seem reasonable to test whether such a relationship was dependent upon matrix heterogeneity, and the analysis of density data stopped here.

5.4.2 Movement data

Prior to analysis of the movement data, an assessment of data quality was performed. The two landscapes in week four were troublesome because return rates were anomalously low, mainly because all individuals that I relocated were captured on the second-to-last day of trapping, which did not leave sufficient time to re-trap animals. Using the DFFITS method of PROC GLM in SAS, the return rates (for both species) in week 4 were identified as strongly influential outliers and, therefore, removed from all subsequent analyses.

The best-fitting model to predict return rate included the variables AREA and MEANDIST (Table 5.3), and the summary of the fit of this model appears in Table 5.4. The residuals from this regression were saved for the second step of the analysis to determine whether movement is more predictable in homogeneous landscapes (below). The correlation analysis of the residuals for mice and chipmunks was not significant ($r = 0.164$, $n = 17$, $p = 0.560$) suggesting that the data for the two species was reasonably independent. I also used an ANCOVA model as a *post-hoc* diagnostic test to see if the best-fitting regression model was dependent on SPECIES. If true, it would not be reasonable to pool data from mice and chipmunks, i.e., the data could not be used to generalize across species. Return rate was modelled as a captures-weighted function of AREA, MEANDIST, and SPECIES. There was no effect of SPECIES or its interaction terms (Table 5.5), indicating that the relationship between return rate and patch size & isolation was similar for both mice and chipmunks, and the data was pooled with confidence.

The second step in the analysis of the movement data was to evaluate whether mice and chipmunk movement was more predictable in homogeneous landscapes than heterogeneous landscapes. The mean absolute size of the residuals, which indicates the degree of fit of the statistical model, was slightly but significantly larger for heterogeneous landscapes ($t_{one-tail} = 1.84$, $n = 18$, $p = 0.042$; Figure 5.4). For illustrative purposes, I also provide multiple regression summaries for predicting animal return rates from AREA and MEANDIST for homogeneous and heterogeneous landscapes separately (Table 5.6).

The third step was to repeat the analyses for mice and chipmunks separately to determine whether the strength of response in each analysis was similar for the two species. Separate regressions of return rate on AREA and MEANDIST were performed. A summary of the two regression analyses is presented in Table 5.7, and it is apparent that chipmunk return rates were much more predictable than those for mice. To statistically test this pattern, I used the regression model mean squared error (MSE) term as an estimate of explained variation, and used an F -test on the ratio of the two MSEs. This test was only marginally significant ($F = 1.86$, $d.f. = 17, 19$, $p = 0.098$). I also conducted separate paired-sample t -tests for mice and chipmunks to see if landscape heterogeneity influenced the predictability of their return rates. Landscape heterogeneity had a significant effect for mice ($t = 2.03$, $n = 9$, $p = 0.038$) but not for chipmunks ($t = 0.45$, $n = 7$, $p = 0.331$).

5.5 DISCUSSION

A fundamental goal of this study was to observe animal movement and examine the relative effects associated with landscape pattern and patch characteristics. According to the conventional wisdom of landscape ecology, movement should be influenced by the composition and configuration of the landscape. This study seems to support this belief, and

my results show evidence of compositional effects (matrix heterogeneity) and configuration effects (patch isolation). However, overall the results from the relocation data were more easily interpreted than the trapping density data. There was much less measurement error associated with counting returning individuals (even though my data must have consistently underestimated return rates), and the predictor variables of interest (e.g., patch size, isolation) are more likely to have direct effects on return rates than on density. Thus, I had much greater confidence in these data and I focus my discussion on these results.

5.5.1 Patch characters as predictors of movement and density

Patch isolation stands out as a clear predictor of inter-patch movement for mice and chipmunks. In a related study, Derrane et al. (unpublished) demonstrated (at the individual-level) that the probability of inter-patch movement by mice and chipmunks was strongly a function of inter-patch distance. Hence, distance appears to be a real determinant of successful animal movement, and therefore, it can be expected that inter-patch movement in the landscape can be predicted from isolation. This finding also agrees with my modelling study (Chapter 4). Patch area was also a significant predictor of movement success in this study (Table 5.4), but in the opposite fashion to conventional wisdom and opposite to my modelling results (Chapter 4). Mice and chipmunks were more likely to return and be recaptured in smaller patches than larger patches, which is the opposite of what theory predicts. One possible explanation is that recapture probability was much higher for very small patches, which might be true because the proportion of a patch covered by a trapping grid would have been greatest in the small patches. In large patches, the grid would only have sampled a fraction of the patch, and returning animals may have not have encountered any traps. However, there might be a biologically meaningful effect, as well. For example, Barrett et al. (1995) found that vole (*Microtus pennsylvanicus*) densities were higher in smaller, more

fragmented habitat patches in a manipulative study. Similar results were found in a study of deer mice (*Peromyscus maniculatus*) by Bowers and Dooley (1999). Bowers and Matter (1997) reviewed the patch size-density relation for small mammals, and reported that negative relations are quite commonplace. Explanations for this “opposite” result vary, but plausible ideas relate to differential habitat quality or avoidance of an ecological enemy that is most dense in the larger patches.

Another piece of conventional wisdom in landscape ecology is that animal movement will be reflected in patterns of abundance and spatial distribution (Forman & Godron 1986, Peles et al. 1999). In particular, small and isolated patches should have lower population densities and few immigrants, resulting in frequent extinctions. Therefore, small and isolated patches should, on average, have lower population densities than larger and/or well-connected patches. I found no evidence of this relationship for mice and chipmunks: density was unrelated to patch characters, nor was it related to immigration rate. Density was only predictable by time, and otherwise quite variable from landscape to landscape. Thus, it appears that patterns of abundance were not predictable from spatial pattern or movement for small mammals in this study. However, given the coarse nature of my estimates of patch density, I am reluctant to draw any definitive conclusions about whether patch and landscape variables are useful predictors of density.

5.5.2 Comparison of landscapes with homogeneous vs. heterogeneous matrices

The most interesting result of this study is that matrix heterogeneity seems to have a strong influence on the movement of small mammals. By statistically modelling inter-patch movement separately in heterogeneous and relatively homogeneous landscapes, it is clear that movement is much more predictable when the matrix is homogeneous (Figure 5.4, Table 5.6). If we examine the squared multiple correlation coefficients, R^2 in Table 5.6, we see that patch

size and isolation explains about 61% of the variation in return rates for mice and chipmunks in homogeneous landscapes, but only 17% in heterogeneous ones. This is a large difference! In fact, the relationship between return rate and patch size and isolation was not significant (i.e., not predictable) in the heterogeneous landscapes. This agrees with my modelling study (Chapter 4) that showed that there was a negative relationship between the degree of matrix heterogeneity and the predictability of movement from a patch-based statistical model.

The implications of these results are far-reaching. Patch-based approaches, particularly those with foundations in island biogeography or metapopulation theory, are very common methods for studying spatially subdivided populations (e.g., see reviews by Bowers & Matter 1997, Bender et al. 1998, Debinski & Holt 2000). The patch-based paradigm pervades the ecological literature (e.g., Wu & Loucks 1995, Wu & Levin 1997, Mazerolle & Villard 1999), and the majority of our analytical methods in landscape ecology are limited to dealing with a binary (habitat/non-habitat) view of the world (Gustafson 1998). Yet, habitat patches in terrestrial systems are rarely surrounded by a homogeneous, ecologically neutral or homogeneously inhospitable environment (Wiens 1995a). Binary, patch-based models can not incorporate information about properties of the matrix, even if they are important. In this study, I have shown that simply the degree heterogeneity of matrix composition greatly affects the performance of a statistical patch-based model to predict animal movement. Therefore, before one attempts to infer something about the movement or distribution of an organism from the spatial pattern of its habitat, one should also consider whether (1) there are elements in the matrix that will also affect the species movement or distribution, and (2) these elements are arranged in a complex or inconsistent pattern rather than a consistent (i.e., homogeneous) pattern. If both of these items are true, then there is reason to be sceptical that a patch-based approach will be useful.

5.5.3 Comparison between a habitat specialist vs. a generalist

The final goal of this study was to examine the distribution and movement of a habitat generalist (white-footed mouse) and a forest habitat specialist (Eastern chipmunk) to see if the predictions tested above were generalizable across species that represent two behavioural extremes. There was no evidence to suggest that the predictability of the distribution (density) of mice and chipmunks differed with respect to the spatial pattern of habitat or degree of matrix heterogeneity (it was always unpredictable for both species). This does not suggest that the two species necessarily respond the same; rather, my data may not have been refined enough to detect any differences that may or may not exist.

Analysis of the movement data did reveal some interesting differences between mice and chipmunks, however. Chipmunks were marginally more predictable in their movements based on knowledge of patch size and isolation than were mice. This seems reasonable because chipmunks have a strong preference to use forest or other wooded areas for movement (Henderson et al. 1985, Henein 1995) and therefore, they should respond more strongly to forest structure. The results from my simulation model also predicted that the movement of specialists would be more predictable from patch characters (Chapter 4). However, another simulation study by Tischendorf et al. (unpublished) predicted the opposite effect that generalists should be the more predictable species. It is difficult to explain why such a discrepancy exists between the Tischendorf model, and my field and simulation studies. One possibility lies in the way matrix effects were modelled in the Tischendorf et al. study. Unlike my model, Tischendorf modelled both matrix-specific movement and mortality. They defined specialists to have greater mortality rates in the matrix than generalists, which likely influenced the degree of successful movement through the matrix and among patches. Therefore, it is possible that movement can also be a function of species-specific mortality

rates in the matrix, which I have not modelled in Chapter 4 nor evaluated in this field study. The determination of the relative importance of heterogeneous movement effects vs. direct mortality effects is an area of research that deserves more attention, especially because each can potentially have great influence on species-specific dispersal rates and neither is generalizable from landscape pattern.

Mice and chipmunks also differed in their response to matrix heterogeneity. Despite the less predictable association between mouse movement to patch size and isolation, whatever degree of predictability existed was strongly influenced by matrix heterogeneity. Chipmunks were the opposite: their movement was highly predictable from patch size and isolation, but this predictability was not significantly influenced by matrix heterogeneity. One might reason that chipmunk movement was more predictable *because* they were relatively unaffected by heterogeneity in the matrix, and that mice are inherently less predictable because, being generalists, their movements are strongly influenced by different elements in the matrix. My results certainly suggest that this is true, although I cannot test it directly; to do so, I would have to know the actual movement paths taken by each species. However, in general it seems that a patch-based approach can be applied reasonably well to predict the movement behaviour of the specialist species, the Eastern chipmunk.

Where the patch-based approach appears to be unsuccessful is for the generalist, the white-footed mouse. My study suggests that to model the movement of generalists, knowledge of landscape structure (i.e., spatial pattern of habitat) alone is not sufficient when the matrix is heterogeneous. The landscape mosaic approach (*sensu* Wiens 1995b) or neighbourhood approach (*sensu* Gustafson 1998) are alternatives that explicitly consider elements of the matrix. However, very few studies have considered which elements of the matrix need to be measured and how they directly relate to species movements and

distribution. Of course, the obvious exceptions to this are research on movement corridors (e.g., Wegner & Merriam 1979, Fahrig & Merriam 1985, Lorenz & Barrett 1990, Bennett 1990, Bennett et al. 1994), movement barriers (Mader 1984, Wolff et al. 1997, Lovei et al. 1998), and complementary/supplementary habitats (e.g., Pope et al. 2000). What is apparent from mice is that we probably need to identify and incorporate information about the influential elements of the matrix before we can adequately predict the movement of a generalist species.

The greatest challenge will be to figure out how to incorporate information about the matrix into predictive models of animal movement when the matrix is heterogeneous. It is unlikely that the patch paradigm will be useful, because the only way one could incorporate matrix effects would be on a patch-by-patch basis. That is, when the matrix is heterogeneous, there will be a unique combination of matrix elements within the neighbourhood of each patch, necessitating that matrix influences be assessed on a patch by patch basis. For large landscapes with many patches, the information produced from a patch-by-patch analysis might be too complex to make generalizations from. Therefore, attempts to infer landscape-level dynamics from patch-level processes (e.g., see Bowers & Matter 1997) might only be possible in simple landscapes where matrix heterogeneity is low. The unfortunate situation is that we have insufficient knowledge to predict what matrix elements should be important to different species. Consequently, we can not reliably determine the threshold at which a landscape's matrix should be considered functionally homogeneous or heterogeneous. A challenge to future research will be to examine how organisms perceive elements of the matrix [and not just how they perceive landscape structure; see Taylor et al. (1993)] and determine reliable methods for assessing when landscapes must be analyzed as mosaics rather than using a much simpler patch-based approach.

Table 5.1. ANCOVA results summarizing the association between trapping date and species on relative density.

Source	<i>DF</i>	Mean Square	<i>F</i> Value	<i>p</i> Value
MODEL	3	355.6	5.89	0.002
STARTDATE	1	637.6	10.56	0.003
SPECIES	1	297.0	4.92	0.030
STARTDATE*SPECIES	1	132.2	2.19	0.148
ERROR	31	60.4		

Table 5.2. Model selection results to determine the best model that predicts relative animal density from landscape and patch characteristics (see text for description and abbreviations). Models with lower AIC_c values are deemed to be the better models following the approach of (Burnham & Anderson 1998). None of the models was statistically significant.

No. in Model	R ² Value	AIC _c	Variables in Model
1	0.0100	170.73	HETERO
1	0.0077	170.82	PROXIM
1	0.0075	170.83	AREA
1	0.0035	170.99	VEGCOVER
1	0.0004	171.11	ROADS
1	0.0001	171.12	SHAPE
2	0.0232	172.41	HETERO AREA
2	0.0177	172.63	HETERO PROXIM
2	0.0152	172.74	AREA VEGCOVER
2	0.0140	172.79	AREA PROXIM
2	0.0127	172.84	SHAPE PROXIM
2	0.0108	172.91	PROXIM VEGCOVER
2	0.0107	172.92	HETERO VEGCOVER
2	0.0103	172.93	HETERO ROADS
2	0.0101	172.94	HETERO SHAPE
2	0.0094	172.97	AREA ROADS
2	0.0088	173.00	PROXIM ROADS
2	0.0079	173.03	AREA SHAPE
2	0.0047	173.16	SHAPE VEGCOVER
2	0.0044	173.17	ROADS VEGCOVER
2	0.0006	173.33	SHAPE ROADS
3	0.0293	174.50	HETERO AREA PROXIM
3	0.0259	174.64	HETERO AREA VEGCOVER
3	0.0245	174.70	HETERO AREA SHAPE
3	0.0232	174.75	HETERO AREA ROADS
3	0.0222	174.79	HETERO SHAPE PROXIM
3	0.0210	174.84	SHAPE PROXIM VEGCOVER
3	0.0208	174.85	AREA PROXIM VEGCOVER
3	0.0195	174.90	AREA ROADS VEGCOVER
3	0.0182	174.96	HETERO PROXIM VEGCOVER
3	0.0178	174.97	HETERO PROXIM ROADS
3	0.0168	175.01	AREA PROXIM ROADS
3	0.0154	175.07	AREA SHAPE PROXIM
3	0.0152	175.08	AREA SHAPE VEGCOVER
3	0.0143	175.11	SHAPE PROXIM ROADS
3	0.0125	175.19	PROXIM ROADS VEGCOVER
3	0.0111	175.25	HETERO SHAPE VEGCOVER
3	0.0108	175.26	HETERO ROADS VEGCOVER
3	0.0104	175.27	HETERO SHAPE ROADS
3	0.0099	175.29	AREA SHAPE ROADS
3	0.0058	175.46	SHAPE ROADS VEGCOVER
4	0.0315	176.89	HETERO AREA PROXIM VEGCOVER

No. in Model	R^2 Value	AIC _c	Variables in Model
4	0.0295	176.97	HETERO AREA SHAPE PROXIM
4	0.0294	176.97	HETERO AREA PROXIM ROADS
4	0.0265	177.09	HETERO AREA ROADS VEGCOVER
4	0.0263	177.10	HETERO AREA SHAPE VEGCOVER
4	0.0262	177.10	AREA PROXIM ROADS VEGCOVER
4	0.0254	177.14	HETERO SHAPE PROXIM VEGCOVER
4	0.0252	177.15	AREA SHAPE PROXIM VEGCOVER
4	0.0246	177.17	SHAPE PROXIM ROADS VEGCOVER
4	0.0245	177.17	HETERO AREA SHAPE ROADS
4	0.0222	177.27	HETERO SHAPE PROXIM ROADS
4	0.0196	177.38	AREA SHAPE ROADS VEGCOVER
4	0.0182	177.43	HETERO PROXIM ROADS VEGCOVER
4	0.0182	177.43	AREA SHAPE PROXIM ROADS
4	0.0111	177.72	HETERO SHAPE ROADS VEGCOVER
5	0.0329	179.45	HETERO AREA SHAPE PROXIM VEGCOVER
5	0.0326	179.46	HETERO AREA PROXIM ROADS VEGCOVER
5	0.0314	179.51	AREA SHAPE PROXIM ROADS VEGCOVER
5	0.0297	179.58	HETERO AREA SHAPE PROXIM ROADS
5	0.0268	179.70	HETERO AREA SHAPE ROADS VEGCOVER
5	0.0264	179.72	HETERO SHAPE PROXIM ROADS VEGCOVER
6	0.0346	182.16	HETERO AREA SHAPE PROXIM ROADS VEGCOVER

Table 5.3. Model selection results to determine the best model to predict the proportion of individuals to return after relocation (see text for description and abbreviations).

No. in Model	R ² Value	AIC _c	Variables in Model
1	0.2542	-17.77	MEANDIST
1	0.1301	-12.54	AREA
1	0.1256	-12.36	SHAPE
1	0.0049	-7.97	AVGROADS
1	0.004	-7.93	VEGCOVER
1	0.0016	-7.85	AVGTRAFF
2	0.3483	-20.10	AREA MEANDIST
2	0.2781	-16.61	MEANDIST AVGROADS
2	0.2704	-16.26	SHAPE MEANDIST
2	0.258	-15.68	MEANDIST AVGTRAFF
2	0.2571	-15.64	MEANDIST VEGCOVER
2	0.1762	-12.13	AREA SHAPE
2	0.1609	-11.50	SHAPE AVGTRAFF
2	0.1379	-10.58	AREA AVGTRAFF
2	0.1351	-10.47	AREA AVGROADS
2	0.1318	-10.34	AREA VEGCOVER
2	0.1309	-10.31	SHAPE VEGCOVER
2	0.1294	-10.25	SHAPE AVGROADS
2	0.0236	-6.35	AVGTRAFF AVGROADS
2	0.0088	-5.84	AVGROADS VEGCOVER
2	0.0059	-5.74	AVGTRAFF VEGCOVER
3	0.3495	-17.74	AREA MEANDIST VEGCOVER
3	0.3495	-17.74	AREA MEANDIST AVGROADS
3	0.3486	-17.70	AREA SHAPE MEANDIST
3	0.3485	-17.69	AREA MEANDIST AVGTRAFF
3	0.2839	-14.48	MEANDIST AVGTRAFF AVGROADS
3	0.2813	-14.35	SHAPE MEANDIST AVGROADS
3	0.2808	-14.33	MEANDIST AVGROADS VEGCOVER
3	0.2705	-13.85	SHAPE MEANDIST AVGTRAFF
3	0.2704	-13.84	SHAPE MEANDIST VEGCOVER
3	0.2605	-13.38	MEANDIST AVGTRAFF VEGCOVER
3	0.2077	-11.04	AREA SHAPE AVGTRAFF
3	0.1914	-10.35	AREA SHAPE AVGROADS
3	0.1872	-10.17	AREA SHAPE VEGCOVER
3	0.1705	-9.48	SHAPE AVGTRAFF AVGROADS
3	0.1693	-9.43	SHAPE AVGTRAFF VEGCOVER
3	0.1395	-8.23	AREA AVGTRAFF VEGCOVER
3	0.138	-8.17	AREA AVGTRAFF AVGROADS
3	0.1375	-8.15	AREA AVGROADS VEGCOVER
3	0.1362	-8.10	SHAPE AVGROADS VEGCOVER
3	0.0289	-4.12	AVGTRAFF AVGROADS VEGCOVER
4	0.3504	-15.21	AREA SHAPE MEANDIST AVGROADS
4	0.3504	-15.21	AREA MEANDIST AVGROADS VEGCOVER
4	0.3498	-15.18	AREA MEANDIST AVGTRAFF AVGROADS

No. in Model	R ² Value	AIC _c	Variables in Model
4	0.3497	-15.17	AREA MEANDIST AVGTraFF VEGCOVER
4	0.3495	-15.17	AREA SHAPE MEANDIST VEGCOVER
4	0.3492	-15.15	AREA SHAPE MEANDIST AVGTraFF
4	0.291	-12.24	SHAPE MEANDIST AVGTraFF AVGRoads
4	0.2874	-12.06	MEANDIST AVGTraFF AVGRoads VEGCOVER
4	0.2821	-11.81	SHAPE MEANDIST AVGRoads VEGCOVER
4	0.2705	-11.27	SHAPE MEANDIST AVGTraFF VEGCOVER
4	0.2226	-9.11	AREA SHAPE AVGTraFF VEGCOVER
4	0.2086	-8.50	AREA SHAPE AVGRoads VEGCOVER
4	0.2078	-8.47	AREA SHAPE AVGTraFF AVGRoads
4	0.1772	-7.17	SHAPE AVGTraFF AVGRoads VEGCOVER
4	0.1397	-5.66	AREA AVGTraFF AVGRoads VEGCOVER
5	0.3508	-12.47	AREA SHAPE MEANDIST AVGRoads VEGCOVER
5	0.3506	-12.46	AREA MEANDIST AVGTraFF AVGRoads VEGCOVER
5	0.3505	-12.45	AREA SHAPE MEANDIST AVGTraFF AVGRoads
5	0.3499	-12.42	AREA SHAPE MEANDIST AVGTraFF VEGCOVER
5	0.2915	-9.50	SHAPE MEANDIST AVGTraFF AVGRoads VEGCOVER
5	0.2228	-6.35	AREA SHAPE AVGTraFF AVGRoads VEGCOVER
6	0.3509	-9.50	AREA SHAPE MEANDIST AVGTraFF AVGRoads VEGCOVER

Table 5.4. Summary of the fit of the multiple regression between proportion of returning individuals and patch size & isolation. The overall R^2 was 0.35.

Source	Parameter Value	DF	Mean Square	F Value	p Value
MODEL		2	0.634	8.73	0.001
AREA	-0.0154	1	0.319	4.40	0.044
MEANDIST	-0.0008	1	0.964	13.27	0.001
ERROR		31	0.072	.	.

Table 5.5. ANCOVA results summarizing the association between trapping date and species on capture frequency.

Source	DF	Mean Square	F Value	p Value
MODEL	5	2.145	4.16	0.005
AREA	1	2.336	4.54	0.041
MEANDIST	1	7.084	13.75	<.0001
SPECIES	1	0.170	0.33	0.569
AREA*SPECIES	1	0.105	0.20	0.655
MEANDIST*SPECIES	1	0.528	1.02	0.319
ERROR	31	0.515	.	.

Table 5.6. Summary of the fit of the multiple regression between proportion of returning individuals and patch size & isolation for homogeneous and heterogeneous landscapes separately.

Landscape Type	R^2	F value	d.f.	P Value
Homogeneous	0.61	12.51	2, 18	<.001
Heterogeneous	0.17	1.61	2, 17	0.232

Table 5.7. Summary of the fit of the multiple regression between proportion of returning individuals and patch size & isolation for mice and chipmunks separately.

Source	Mice ($R^2 = 0.19$)			Chipmunks ($R^2 = 0.74$)		
	Mean Square	F Value	P Value	Mean Square	F Value	p Value
MODEL	1.548	1.97	0.170	3.654	19.71	<.0001
AREA	1.128	1.43	0.248	1.833	9.89	0.007
MEANDIST	1.968	2.50	0.1322	5.475	29.54	<.0001
ERROR	13.375	.	.	2.595	.	.

Figure 5.1: A map of the study area showing the locations of 18 of 20 sample landscapes in the agricultural region south of Ottawa. Two additional landscapes (not shown) were situated to the west of Ottawa in a similar agricultural region. Landscapes are annotated as S (simple, relatively homogeneous matrix composition) and C (complex, relatively heterogeneous matrix). Note that although some landscapes appear to overlap, it was only necessary to re-use relocation patches on two occasions.

Figure 5.2: An example landscape (blue circle) and surrounding area illustrating the focal patch where mice were trapped, and relocation patches (numbered) that were selected from accessible, adjacent woodlots. Green polygons indicate forest patches, and red lines indicate roads. The blue circle indicates a 1250 m radius from the trapping location (black dot in focal patch) and defines the arbitrary extent of the landscape for analytical purposes.

Figure 5.3: Changes in relative density of mice and chipmunks (number of trapped animals per 100 traps) across the study period. Closed black circles and the solid trend line indicate data for white-footed mice, and open boxes and the dashed trend line indicates data for Eastern chipmunks. An ANCOVA revealed that the two trend lines do not differ significantly (Table 5.1).

Figure 5.4. Mean residual sizes from the relationship between patch characters (size, isolation) and return rates (see text) for heterogeneous and homogeneous landscapes. Error bars indicate ± 1 standard error.

CHAPTER 6

GENERAL CONCLUSIONS

6.1 CAN WE PREDICT ANIMAL MOVEMENT FROM LANDSCAPE STRUCTURE?

The goal of this thesis was to examine the relationship between animal movement and landscape structure to determine whether it is possible to predict movement/distribution from measuring spatial pattern of the landscape, particularly when that pattern is complex and difficult to measure. This relationship is a bit of a “holy grail” in landscape ecology because theory proclaims that this relationship should exist, but empirical research has not yet uncovered a consistent and general relation. Thus, we are faced with the knowledge that sometimes spatial pattern matters and sometimes it does not, but knowing exactly *when* it matters still eludes us. Some rules of thumb have been proposed to decide when spatial pattern should matter (Fahrig 1998), and such information is extremely valuable to planners and conservationists that wish to incorporate sound ecological knowledge into the management of wildlife and natural resources. Patch-based models, such as metapopulation-style models, are becoming very popular in management (e.g., see McCullough 1996) despite the fact that the theory is inconsistent with the empirical data (Doak et al. 1990, Harrison 1991, Harrison and Taylor 1997, Mazerolle & Villard 1999, Debinski & Holt 2000). Therefore, it is critical that we evaluate whether the patch-based approach is actually a useful method for studying wildlife populations in nature. This thesis evaluates one concern that arises when one wishes to apply patch-based models to wildlife populations in real landscapes: does landscape complexity affect our ability to measure and predict animal movement and distribution from the spatial pattern of the landscape?

In this thesis, I have identified two components of landscape complexity. The first is the structural complexity of habitat, which relates to the size, shape, and isolation of habitat patches. These are the fundamental variables of patch-based models, but they are not unambiguously measurable properties of a patch; they are concepts. Isolation is the best example of this: isolation is an intuitive property of the landscape that actually refers to a patch's inaccessibility to dispersers. There are many ways to measure this, all of which might provide a slightly different estimate of inaccessibility. Patch size and shape are similarly ambiguous properties: there are many metrics of patch shape (e.g., perimeter/area ratio, fractal dimension) and patch size could relate to area or perimeter length. I followed an experimental approach using simulated data to investigate how predictable animal movement actually is under different landscape scenarios, and I evaluated which metrics most accurately reflect this movement. Three indices, patch area, patch shape index, and the amount of habitat within a proximate distance of the patch (buffer area), proved to be consistent predictors of patch immigration when the matrix of the landscape was homogeneous. Results from a field study on small mammals showed that these properties can be measured in natural landscapes, and they do predict (at least to some degree) the movement of animals, particularly when the matrix is relatively homogeneous. However, my field data also showed some inconsistencies with the theory (patch area was *negatively* related to immigration rate), suggesting that although movement is related to landscape pattern, it may not necessarily be consistent or in the manner predicted from theory. Future research is needed to address how things like species-interactions or cognition and learning affect the movement and distribution of wildlife.

The second component of landscape complexity that I investigated was that of matrix heterogeneity. Patch-based models assume that the matrix of a landscape is homogeneously neutral or inhospitable, but this is rarely the case in terrestrial landscapes. The area between

patches of habitat is more often a mosaic of different elements, and whenever animals respond to these elements in the matrix, it can be predicted that matrix heterogeneity will lead to heterogeneous and unpredictable movement behaviours. I investigated how large an effect this might have on animal movement through another simulation study that compared the performance of a statistical patch-based model under varying degrees of matrix heterogeneity. My results showed that by introducing even low amounts of heterogeneity in the matrix, animal movement was less predictable from factors such as patch size, shape, and isolation. The field study tested this prediction by directly comparing the movement success of small mammals in simple landscapes with relatively homogeneous matrices vs. complex landscapes with heterogeneous matrices. I observed a strong effect of matrix heterogeneity on the ability to predict movement from patch area and isolation, lending further credibility to the idea that patch-based models are not likely applicable in landscapes with complex spatial pattern.

6.2 SHORTCOMINGS AND SUGGESTED FUTURE RESEARCH

Although I feel the research presented in this thesis contributes to our knowledge of animal movement in spatially-subdivided habitats, I can also identify some shortcomings, which I use as a basis for suggested future research. I believe there is convincing evidence that complexity in the landscape, particularly matrix heterogeneity, can seriously diminish our capacity to reliably apply patch-based population models. Two questions arise from this supposition: (1) “If patch-based models are not applicable in complex landscapes, *how* complex is too complex?,” and (2) “How do we account for this complexity so that we can accurately predict the distribution and movement of wildlife?” Unfortunately, I have not addressed either question in this research. It is relatively easy to identify situations where a theory or a methodological approach might not be applicable, but it is much more difficult to provide

answers about how we can *improve* our approach. Future research needs to identify rules of thumb for deciding when a landscape is “simple enough” for metapopulation-style models to be useful. This will not be an easy task because many factors influence how successful the metapopulation approach will be in application. These include difficulties associated with identifying the correct scale of observation, the confounding effects of habitat quality vs. pattern, and the complexity of movement behaviour that arises from specialized movement strategies and species interactions. A starting point for future research might be to investigate the relative impacts of each of these influences to determine which are the most important factors determining the distribution and abundance of organisms in the landscape.

We might also ask whether it is profitable to continue with the patch-based approach. Given that many factors diminish the capability of patch-based models to predict the movement and distribution of wildlife, perhaps patch-based models will *never* work unless we can account for matrix heterogeneity. Unfortunately, spatial heterogeneity has many components (Li & Reynolds 1994) which are difficult to measure and relate to animal movement and distribution (Gustafson & Gardner 1996). It is my belief that the structural complexity of terrestrial landscapes can be so great that there will be no way that we can “correct” for heterogeneity in patch-based models; all we can measure is how *much* heterogeneity exists and then use this information to evaluate the appropriateness of a patch-based approach. So what is a better solution? Perhaps we need a paradigm shift in our approach to studying spatially-subdivided populations. Terrestrial landscapes are probably more appropriately viewed as landscape mosaics rather than binary, habitat/non-habitat representations, and we need to develop theory and methodological tools that allow us to relate landscape-level properties (not patch-level properties) to animal movement and distribution. Such developments are still in their infancy (Gustafson 1998), and we are only

beginning to understand how things like landscape connectivity can be measured and related to animal distribution and movement (Tischendorf & Fahrig 2000, Tischendorf & Fahrig In press). There have been compelling arguments made to encourage us to consider a more landscape-level approach in our research (Wiens 1995a, Wiens 1995b, Wiens 1997, Gustafson 1998, Mazerolle & Villard 1999), but we need to better understand the link between measurable properties of landscapes and ecological processes that are related to them (Gustafson 1998, Tischendorf & Fahrig 2000). Future research needs to address this concern before we wantonly apply theoretical approaches to the conservation and management of wildlife populations in nature.

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