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LANDSCAPE CONNECTIVITY: THE INTERACTION BETWEEN INSECT MOVEMENTS AND LANDSCAPE SPATIAL STRUCTURE

by

Brett J. Goodwin, B.Art.Sci.

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

Doctor of Philosophy

Department of Biology

Carleton University

Ottawa, Ontario

May 5th, 2000

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ACCEPTANCE FORM

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

“Landscape Connectivity:
The Interaction of Insect Movements and Landscape Spatial Structure”

submitted by

Brett J. Goodwin, B.Art.Sci.

in partial fulfillment of the requirements
for the degree of Doctor of Philosophy

Chair, Department of Biology

Thesis Supervisor

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Carleton University
July 17th, 2000

ABSTRACT

I assessed a patch predictor of insect densities by summarizing tests of the Resource Concentration Hypothesis (RCH) using meta-analysis. Support was weak overall and very heterogeneous between studies. Analysis of moderator variables indicated RCH holds when: (1) resource concentration is manipulated as plant diversity or patch size; (2) plants are high in secondary metabolites detected by insects; (3) insects are adults; (4) insects detect host-plants from afar; (5) insects tend to remain in host-plant patches; (6) host-plant patches are artificial or have conspicuous edges; and (7) host-plant patches are accessible. This suggests that patch predictors of population levels are insufficient and interpatch movement behaviour needs to be considered.

I investigated environment-movement interactions with a goldenrod beetle (*Trirhabda borealis* Blake, Chrysomelidae) in mosaic microlandscapes of goldenrod, cut vegetation, and cut vegetation with camouflage netting patches. Beetles in: (1) goldenrod patches exhibited short bursts of fast, meandering movements interspersed with long periods of immobility, (2) cut patches exhibited longer bouts of slow, directed movements with short periods of immobility, and (3) netting patches exhibited short bursts (same as goldenrod) of fast, meandering movements with short periods of immobility between (same as cut). Using mark and release experiments I determined that *T. borealis* did not respond to patch edges, detect goldenrod from afar, nor exhibit density-dependent emigration. Movements in goldenrod patches maintain contact with food while movements in cut patches expeditiously cross inhospitable areas. Netting patch structural complexity both hindered movements and presented a resource (anti-predator defense) worth maintaining contact with.

I investigated the impact of landscape structure on landscape connectivity using a combination of simulation and empirical experiments. Landscape connectivity was based on individual movements, and was measured in six different ways. Different aspects of landscape structure influenced these measures, suggesting that: (1) connectivity is a poorly defined concept, and (2) the same landscape may have different connectivity values when different measures of connectivity are used. Two general predictions that held over all measures of connectivity were: (1) increasing isolation decreases connectivity and (2) matrix elements were insignificant in comparison to habitat elements. These simulation results were supported in the empirical tests.

DEDICATION

This thesis is dedicated to the two most important people in my life. My wife Trina, who has had to sacrifice and suffer like a graduate student but will get none of the rewards and still stood beside me during this consuming endeavour. And my new daughter Morgan, whose birth and growth this last year has pushed me on to finish.

ACKNOWLEDGMENTS

"No man is an Island, entire of itself; every man is a piece of the Continent, a part of the main..." - John Donne

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It has been said that academic pursuits are lonely pursuits. I would disagree. The landscape ecology lab at Carleton was a wonderful place to do graduate work because of the people there, who more than made up for the lack of windows and the sounds of rock saws from down the hall. I need to thank the following people, Darren Bender, Julie Brennan, Laurie Carr, Tom Contreras, Lenore Fahrig, Melanie Filotas, Kringen Henein, Jeff Holland, Ian Jonsen, Jean Langlois, Michelle Lee, Andy McAllister, Gray Merriam, John Pedlar, Shealagh Pope, Awegechew Teshome, Lutz Tischendorf, Kurtis Trzcinski, Lisa Veneir, and John Wegner, for the following things, good conversations, good arguments, great Ethiopian food, not so great Swedish fish, the lending of scythes and gas-powered trimmers, ideas about computers, games of pool, ideas about stats, Friday afternoon beer, ideas about teaching, lunch by the canal, and many good memories. I sometimes think this thesis took so long to finish because I didn't want to leave.

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Chapter 1

GENERAL INTRODUCTION

1.1 THE ECOLOGICAL IMPORTANCE OF MOVEMENT

Most organisms move during at least one stage of their lifecycle. Many phyla have certain life stages that seem specially suited for movement (e.g., plant seeds, insect adults, crustacean larval forms). Movement, whether active or passive, is one of the most common adaptations for surviving in a heterogenous world.. Movements can allow individuals, and by extension species, to escape from areas that are inhospitable due to lack of resources or environmental extremes. This importance of movement for survival in many species has led to the evolution of movement behaviours that range from short-duration, small-scale foraging in response to resource distribution, to long-duration, global-scale migrations in response to the seasons.

At its core, movement is an individual, behavioural decision. Many studies of animal movement have done so using a behavioural ecology standpoint. These studies consider movement behaviour as a function of decisions made by the organism to maximize fitness – searching and foraging theory (Zimmerman 1979, Stephens & Krebs 1986, Ims 1995), mate selection, home range or territory establishment and defence, and giving up densities (Bowers & Breland 1996). Movement can play a key role in population processes. Two of the four terms in the general demographic equation (immigration, emigration) require movement. This has been recognized from the very beginning of population ecology though

often populations are treated as closed to make analysis more tractable. More recently movement, and its role in population processes has become an explicit topic of research. Early work focused on how a collection of spatially disparate populations connected by a minimal amount of movement could persist longer than a large population due to spreading of risk amongst the smaller populations (den Boer 1968, Reddingius & den Boer 1970, den Boer 1981). Theory has suggested that a metapopulation, a collection of populations interlinked by movement, is stabilized relative to its constituent populations by dispersal (Levins 1970, Hanski & Gilpin 1997), though too much movement can counter-act metapopulation stability (Allen *et al.* 1993) and strict metapopulation conditions seem to be rare in empirical systems (Harrison & Taylor 1997). Empirical work, however, does suggest that immigration is important for rescuing small populations from extinction (Brown & Kodric-Brown 1977) and recolonizing patches where small populations have gone locally extinct (Henderson *et al.* 1985). Along with demographic effects, movements of individuals can have genetic effects through gene flow (Slatkin 1985, Lande 1988, Whitlock 1992, Thomas 1994, Dybdahl 1994, Hastings & Harrison 1994, Harrison & Hastings 1996) and can cause founder events (O'Brien *et al.* 1983, Olivieri *et al.* 1990, Stangel *et al.* 1992). Finally, movement seems to play a key role in avoiding inbreeding depression and its genetic consequences (Johnson & Gaines 1990).

Movements also play a key role in a species' ability to respond to anthropogenic landscape modification and/or global change. Anthropogenic alteration is a dominant feature of most landscapes (Wilcove *et al.* 1986, Kareiva *et al.* 1993, Groom & Schumaker 1993). Habitat loss and alteration are major causes of species extinctions and biodiversity loss (Wilcox & Murphy 1985, Groombridge 1992). To persist in the face of

these challenges, species must be capable of moving in these modified landscapes to meet its requirements for survival (e.g., foraging, mating, shelter; Bunce & Howard 1990, Merriam 1990). Also, organisms may need to shift or expand their geographic range (Demers 1993).

1.2 THE CONCEPT OF LANDSCAPE CONNECTIVITY

All landscapes are heterogeneous at multiple scales (Wiens 1976, Kotliar & Wiens 1990). Landscape structure refers to both the elements present in the landscape (composition) and how those elements are arranged in space (configuration). The field of landscape ecology, at least in North America, aims to understand how landscape structure influences processes occurring in the landscape (Wiens 1976, Turner 1989). This interest in landscape structure, along with an explosion in remote sensing and GIS technology, has led to a plethora of ways to describe landscape spatial structure (for a review see Gustafson 1998). However, exploration and understanding of the relationship between pattern and process seems to have lagged behind.

Landscape structure has long been appreciated by ecologists but until recently was treated as a nuisance that stood in the way of good experimental design or a statistical issue to be minimized (McIntosh 1991). Only recently have ecologists begun to consider the role and impact of landscape structure, often as patchiness, in its own right. Early approaches included spreading of risk (den Boer 1968, Reddingius & den Boer 1970), metapopulation dynamics (Levins 1970), and island biogeography (MacArthur & Wilson 1967). This soon led to considerations of the role of patchiness in processes such as predator-prey interactions (Hilborn 1975, Hastings 1977, Hastings 1978, Kareiva 1987, Morrison & Barbosa 1987,

Jones *et al.* 1993), species competition (Holt 1984, Pacala 1986, Tilman 1994), and population dynamics (Lomnicki 1980, Nachman 1981, Letourneau 1986, Hassell *et al.* 1991, Thomas 1991, Halley & Dempster 1996). Many of these processes rely on movements of individuals.

Merriam (1984) recognized that landscape structure and movement behaviour are inter-related and referred to the landscape property caused by that interaction as “connectivity”. Early research into landscape connectivity focused on presence and arrangement of movement corridors and both modelling and empirical studies suggested that changing landscape connectivity by manipulating corridors (both presence/absence and corridor quality) led to changes in population size and persistence (Fahrig & Merriam 1985, Lefkovitch & Fahrig 1985, Burel 1989, Henein & Merriam 1990). As the necessity of corridors was questioned (Merriam 1991a, Hobbs 1992) and the ability of organisms to move through matrix (i.e., non-habitat, often inhospitable) elements was appreciated (Reddingius & den Boer 1970, Wegner & Merriam 1979, Liro & Szacki 1987, Potter 1990, Szacki & Liro 1991, Johnson *et al.* 1992) the concept of connectivity expanded to encompass the influence of the entire landscape and “the degree to which the landscape facilitates or impedes movement among resource patches” (Taylor *et al.* 1993).

Interest in connectivity research has been growing (Figure 1.1) with a number of implications. The first is the adoption of the concept of connectivity into the literature. This appears through the number of studies that simply use connectivity as an explanatory variable for some other population or community process (42 of the 58 studies described in Table 1.1). At the same time, little work has been done to understand what can influence connectivity; that is, few studies have looked at the impact of

explanatory variables on connectivity. Adoption of the concept of connectivity may be premature if we do not understand how connectivity functions and how best to measure it. Along with the growth in use of the term connectivity, the meaning of connectivity has become diffuse and potentially contentious. There are two main approaches to researching connectivity: 1) a focus on patterns in the landscape, which has been strongly influenced by percolation theory and neutral landscape theory, and 2) a focus on patterns of organism movements (Table 1.1). These two approaches, landscape- vs. organism-focus, do not ask the same question. The landscape-focused approach describes connectivity in terms of landscape structure, typically focusing on patch isolation, the presence/absence of corridors, or the contagion/percolation of habitat cells in the landscape as measures of connectivity, and typically ignores organism movement behaviour. The organism-focused approach describes connectivity in terms of movements of individuals, which are summarized in many different ways (e.g., dispersal success, search time, cell immigration).

Purely landscape-focused approaches to connectivity (e.g., describing connectivity through landscape patterns regardless of movement behaviour) are flawed for a number of reasons. Many landscape-focused studies divide the landscape into habitat and a matrix element which the organism can not move through (With *et al.* 1997, Metzger & Décamps 1997, Tiebout & Anderson 1997), which may be unrealistic for most species. Landscape-focused studies that do allow for movement in the matrix may not change movement behaviour in the different landscape elements (Schumaker 1996), which is not the case for most real organisms (e.g., Baars 1979, Rijnsdorp 1980, Wallin & Ekborn 1988, Hansson 1991, Johnson *et al.* 1992, Matter 1996, Andreassen *et al.*

1996a, Charrier *et al.* 1997, Collins & Barrett 1997). Landscape-focused studies relying on percolation theory focus on spanning clusters (Green 1994, With & Crist 1995, With *et al.* 1997, Metzger & Décamps 1997, Tiebout & Anderson 1997) but spanning clusters refer to chunks of habitat that cross from one side of the landscape to another (Gardner *et al.* 1989) and may have no bearing on an organism's ability to move between habitat patches in the landscape (compare to the definition of connectivity in Taylor *et al.* 1993). Landscape structure is relatively easy to quantify making landscape-focused approaches to connectivity easy to do but these measures of connectivity may not be ecologically meaningful. While the organism-focused approach to connectivity is more relevant for ecological processes, measures of connectivity based solely on observing movements may be both difficult and costly to attain. This can be especially true if care is taken to study movements at the appropriate scale for the organism. Juvenile dispersal and migratory movements can cover very large distances making the movements difficult to study in any detail, though studying the movements of smaller organisms in an experimental model system (Wiens *et al.* 1993a) can circumvent some of the logistical problems of studying long distance movements. The question then becomes: is there a predictable link between landscape structure and organism movement? Testing for this link is the primary goal of this thesis.

1.3 SIMULATION AND EMPIRICAL APPROACHES TO STUDYING CONNECTIVITY

Much of the work investigating connectivity itself (i.e., not using a measure of connectivity to explain another ecological process or pattern) conducted thus far has been simulation studies, particularly for organism-focused studies of connectivity; 5 of the 7

studies which used organism movements as measures of connectivity and investigated things that influence connectivity were modelling studies (Table 1.1). There are two main advantages to simulation study approaches: 1) it is possible to completely manipulate the landscape structures used in the models thus giving the researcher much more control over the types of structures investigated, and 2) it is much easier to track the movements of individuals in the computer than in the field. Connectivity studies have simulated individual movements a number of ways: patch transition probabilities (Hof & Flather 1996, Hess 1996a), cellular automata (Green 1994), grid based movements (Schumaker 1996, Schippers *et al.* 1996, With *et al.* 1997, Henein *et al.* 1998, With & King 1999), and vector based movements (Tischendorf & Fahrig 2000). There are some concerns with cellular automata and grid based movement models, in that the movement may not be modelled very realistically (Tischendorf 1997) and the scale of movements are constrained to the scale of the grain of the landscape, which may not be appropriate. Vector based movement models seem most appropriate (Tischendorf 1997).

The main disadvantage with the simulation model approach is that movement may be modelled unrealistically or at least in such a manner as to miss some important nuance of the movement behaviour. Also, simulation studies are rarely coupled with empirical studies designed to test the simulation predictions (but see Fahrig & Merriam 1985, With & Crist 1995, Brooker *et al.* 1999, With *et al.* 1999) and empirical studies are rarely designed to test specific predictions of specific modelling studies (but see Wiens *et al.* 1997). This shortfall is even more apparent in studies that use organism-focused measures of connectivity where there are to date no cases of relationships between modelling and empirical approaches. In fact, simulation and empirical studies often measure connectivity differently; organism-

focused connectivity has been measured as dispersal success (Gustafson & Gardner 1996, Schumaker 1996, Schippers *et al.* 1996, Ruckelshaus *et al.* 1997) and search time (Doak *et al.* 1992) in simulation studies and as re-observation frequencies (Pither & Taylor 1998) in empirical work.

Empirical studies of connectivity are difficult to do and, particularly for organism-focused measures of connectivity, examples are few and far between. The studies can be divided into two approaches: 1) studies that look at organisms in their natural landscapes (categorized as E-O in Table 1.1) and 2) studies that look at organisms in artificially constructed landscapes (categorized as E-E in Table 1.1), where landscapes are constructed by mowing/cutting vegetation (Andreassen *et al.* 1996a, Andreassen *et al.* 1996b, Andreassen *et al.* 1998, Collinge & Forman 1998, Gonzalez *et al.* 1998, Browne *et al.* 1999), planting vegetation (Wiens *et al.* 1997, With *et al.* 1999), or placing out potted plants (Steffan-Dewenter & Tschamtkke 1999). Natural landscape studies have the problem that landscape structure cannot be manipulated directly and so causation is never certain. On the other hand, artificial landscape studies are almost always restricted to smaller scales and, by necessity smaller organisms (but see Browne *et al.* 1999). In some cases it might be argued that the scale of the constructed landscape is not appropriate relative to the scale of the organism. This may not be a problem as long as the researcher is only concerned about movements at the appropriate scale (e.g., daily foraging for finer scales). The restriction to smaller organisms need not be limiting as long as it can be argued that the smaller organism can act as a model system for a larger, less easily studied species (Wiens *et al.* 1993a).

Simulation studies alone do not tell us anything about the nature of the real world. Empirical studies of landscape phenomena are difficult and time consuming. Also, studies

investigating the role of landscape structure should be performed on multiple landscapes that vary in their structure. Such landscape replication is rarely done but if it were would make empirical studies even more difficult and time consuming. Without some direction as to what might be important in the field, empirical studies could spend much time and energy investigating unimportant factors which have no effect on connectivity; simulation results can allow empirical investigations to be more focused, and hopefully more productive. This is where a link between simulation and empirical approaches is powerful: simulations are used to explore possible relationships in a rigorous manner and then well-designed, focused empirical studies can either verify the simulation results or improve the simulations either in terms of their structure or parameter values.

To study the influence of landscape structure on connectivity I use both empirical and simulation approaches. I first use empirical studies of movement behaviour in the different landscape elements I am interested in to determine how to describe the movement behaviour. These movement parameters are then used in an individual-based simulation model which moves individuals through landscapes of various structure and calculates connectivity metrics. The predictions of this simulation are then tested with mark-release-resight experiments.

1.4 WHY THE *T. BOREALIS*-GOLDENROD SYSTEM IS A GOOD ONE FOR STUDYING MOVEMENT

To provide movement parameters for the models and to test simulation results, I decided to investigate a native chrysomelid beetle, *Trirhabda borealis* Blake, in mosaic microlandscapes consisting of three patch types, a habitat patch and two matrix path types. The patches were created in old-field vegetation by either leaving goldenrod

standing (the habitat patches) or mowing vegetation. In the areas that were mown the two matrix patches were created by either leaving the patch as a cut patch or by suspending camouflage netting in the patch to mimic vegetation structure. *T. borealis* is a relatively large (lengths around 1 cm) beetle of the Chrysomelidae family native to eastern Ontario. It is phytophagous and specializes on goldenrods (*Solidago* spp.), but will occasionally feed on asters (*Aster* spp.), during both the larval and adult life stages (Messina & Root 1980, Messina 1982a). Goldenrods are common, native perennials of disturbed areas and are found throughout eastern Ontario (Melville & Morton 1982), often dominating the herbaceous community on abandoned fields (Werner *et al.* 1980). *T. virgata*, a congeneric, and *T. borealis* often dominate the goldenrod herbivorous fauna in upper New York state (Messina & Root 1980, Root & Cappuccino 1992) and *T. borealis* was the dominant goldenrod herbivore at my study site (*personal observation*).

T. borealis overwinters as eggs, larvae appear in May passing through three instars while feeding on goldenrod plants, and eventually pupate in the soil at the base of the host plant in June (Messina 1982b). Flightless, teneral adults emerge from the pupae after a few weeks. After a few more days the cuticle has hardened enough for flight. The beetles then spend roughly two weeks in a pre-ovipositional dispersal phase (Messina 1982c), during which long distance flights (hundreds of meters) are common (Herzig 1995). The dispersal phase finishes when the females become gravid rendering them incapable of flight. The beetles spend the remainder of the summer feeding, copulating, and laying eggs until they succumb to the first frosts in September. During this time movement is primarily by walking (Messina 1982c), though they occasionally make short, descending flights from the tops of plants (*personal observation*).

There are a number of reasons why *T. borealis* was a good study organism for investigating landscape connectivity. Due to its specialist nature it was possible to divide the microlandscape into discrete habitat and non-habitat elements. This greatly simplified the identification of important landscape components, which in turn makes it easier to think about what is meant by landscape connectivity in that particular landscape. After pre-ovipositional flights the scale of movements of *T. borealis* individuals is very small and therefore becomes manageable for fieldwork. Many organisms are capable of impressive movements, which can make studying movement difficult if not impossible. Furthermore, I needed a system where I could measure relatively fine details of movement behaviour to parameterize the simulation models. Finally, *T. borealis* was the most common goldenrod specialist at my study site. The high abundance of the beetles allowed me to collect many individuals for both tracking and mark-release experiments. Though understanding landscape connectivity is important for understanding how threatened or rare species respond to landscape change, it would be difficult to get much data from studying such rare species.

1.5 OUTLINE OF THE THESIS

I begin, in Chapter 2, by assessing a patch-based predictor of insect population levels, namely the Resource Concentration Hypothesis (RCH). Essentially, the hypothesis predicts that increasing resource concentration will increase population densities (or loads) (Root 1973). I assessed the RCH by summarizing tests in the literature using meta-analysis. Using moderator variables in the meta-analysis allowed me to make some inferences about the mechanisms driving insect responses to resource concentration. Taken together, the analysis of moderator variables suggested that organism movements were important determinants of

population level responses to resource concentration. In other words, in most cases, resource concentration of a patch would be a poor predictor of insect population level. We need to understand the movement ability of the insects as well.

The first stage of trying to understand organism movements in landscapes is to understand how different patch types and other landscape features influence movement behaviour. Chapter 3 reports the results of a series of tracking and mark-release experiments that quantified *T. borealis* movement behaviour in response to patch types, edges between the patches, food patches from a distance, and density of conspecifics. This is a relatively novel approach to understanding movement as movement biology has been traditionally approached from the point of view of the organism making decisions to maximize fitness (Zimmerman 1979, Stephens & Krebs 1986, Ims 1995). Analyzing this sort of data was not straight forward, and this will continue to be a concern for movement analyses. Additionally, relating movement behaviour to landscape elements will be a necessary component of predicting organism responses to landscape alteration.

Having found that movement behaviour differed in the three different patch types, I postulated that spatial patterning of the landscape might then influence the ability of an organism to move through the landscape (connectivity). In Chapter 4, I tested for links between landscape spatial structure and landscape connectivity using simulation experiments that manipulated landscape structure and then simulated beetles moving through the landscapes using empirically determined movement parameters from Chapter 3. Since there is no consensus yet as to how to measure connectivity, I investigated six potential metrics. This also allowed me to compare the different measures. Finally, I verified my simulation

results with empirical experiments in which I created microlandscapes in the field and then released marked beetles into the landscapes.

Table 1.1: Summary of approaches to studying connectivity. Studies of connectivity have been divided into two groups: A) those which investigated things that influence connectivity (e.g., connectivity as dependent variable) and B) those which investigated the influence of connectivity on other things (e.g., connectivity as independent variable). Within each of the major classes, studies were further subdivided into connectivity described with either a landscape focus or an organism focus. The organism moving is identified (na refers to their being no specific organism while virtual refers to a non-specific model organism). The type of landscape is described. The design column reports the approach taken in studying connectivity; the first letter refers to the overall approach (E = empirical, M = simulation or mathematical model, C = conceptual model) and the second letter provides details about the implementation (for the empirical approaches: E = experimental, O = observational; and for the modeling approaches: I = individual-based movement model, M = metapopulation model, P = population model, C = cellular automata). The other variables investigated in relation to connectivity are described in the relationship column.

Study	Organism	Landscape	Measure of Connectivity	Design	Relationship
A. Studies that treat connectivity as the dependent variable					
i) Connectivity described through landscape pattern					
(Tiebout & Anderson 1997)	na	habitat/matrix grid	contagion	C	patch geometry
(Green 1994)	na	habitat/matrix grid	percolation thresholds	C	amount of active cells
(Metzger & Décamps 1997)	na	habitat/matrix grid	percolation thresholds	C	habitat amount and pattern
(Collinge & Forman 1998)	na	mown grassland	"straight line crossing" (Forman 1995)	E-E	habitat loss (amount, pattern)
(Andreassen <i>et al.</i> 1996a)	root vole (<i>Microtus oeconomus</i>)	mown meadow fragments	quality of corridors	E-E	distance moved, time in corridor
(Keitt <i>et al.</i> 1997)	na	forest patches	percolation cluster size	E-O	dispersal threshold
(Spetch <i>et al.</i> 1997)	na	old growth patches	proximity index	E-O	change with land management options

Study	Organism	Landscape	Measure of Connectivity	Design	Relationship
(With <i>et al.</i> 1997)	virtual	random & fractal virtual mosaic landscapes	percolation thresholds	M-I	type of landscape
(Hof & Flather 1996)	na	habitat/matrix grid	probability of moving between patches	M-P	arrangement to optimize connectivity and autocorrelation
ii) Connectivity described through organism movement					
(Andreassen <i>et al.</i> 1996b)	root vole (<i>Microtus oeconomus</i>)	mown meadow fragments	movement through corridors	E-E	corridor width, quality (predators, competitors)
(Pither & Taylor 1998)	damselflies (<i>Calopteryx aquabilis</i> & <i>maculata</i>)	forest and pasture	reobservation after displacement	E-E	behavioural history
(Schunaker 1996)	virtual	old-growth forest patches	dispersal success	M-I	landscape structure
(Ruckelshaus <i>et al.</i> 1997)	virtual	patches	dispersal success	M-I	error propagation
(Tischendorf & Fahrig 2000)	virtual	3 element mosaic landscape	dispersal success, search time, cell immigration	M-I	influence of connectivity on fragmentation
(Schippers <i>et al.</i> 1996)	badger (<i>Meles meles</i>)	central Netherlands	fraction of dispersers arriving at a patch	M-I	landscape structure, movement behaviour
(Doak <i>et al.</i> 1992)	virtual	hierarchically clustered patches	search time	M-I	inter-patch distance and scale of clustering

B. Studies that treat connectivity as the independent variable

i) Connectivity described through landscape pattern

(Metzger & Décamps 1997)	na	habitat/matrix grid	percolation thresholds	C	biodiversity
(Collinge & Forman 1998)	insect community	mown grassland	"straight line crossing" (Forman 1995)	E-E	insect density, richness, community structure

Study	Organism	Landscape	Measure of Connectivity	Design	Relationship
(Steffan-Dewenter & Tscharntke 1999)	pollinator community	potted plants in agricultural matrix	distance to source	E-E	pollination, seed-set
(Wiens <i>et al.</i> 1997)	tenebrionid beetle (<i>Eleodes obsoleta</i>)	grass and sand mosaics	percolation threshold	E-E	movement behaviour
(Andreassen <i>et al.</i> 1998)	root vole (<i>Microtus oeconomus</i>)	mown meadow fragments	presence/absence of corridors	E-E	interpatch movements, home range size and overlap
(Rosenberg <i>et al.</i> 1998)	salamander (<i>Desmognathus fuscescens</i>)	patches and corridors	presence/absence of corridors	E-E	dispersal
(Gonzalez <i>et al.</i> 1998)	microarthropod community	moss patches on bare rock	presence/absence of corridors	E-E	density
(Browne <i>et al.</i> 1999)	hispid cotton rat (<i>Sigmodon hispidus</i>)	clear cut patches in forest matrix	presence/absence of corridors	E-E	movement behaviour
(Bjornstad <i>et al.</i> 1998)	root vole (<i>Microtus oeconomus</i>)	mown meadow fragments	presence/absence of corridors	E-E	dispersal, space use
(Lecomte & Clobert 1996)	lizard (<i>Lacerta vivipara</i>)	enclosures with connecting corridors	presence/absence of corridors	E-E	dispersal behaviour
(Grashof-Bokdam 1997)	forest plants	forest patches in agricultural matrix	amount of forest in three zones around patch	E-O	plant community structure, occurrence of particular species
(Hutchinson & Vankat 1998)	Amur honeysuckle (<i>Lonicera maackii</i>)	forest patches in agricultural matrix	contagion	E-O	spread of invasive plant
(Zabel & Tschamtké 1998)	insect community	stinging nettle (<i>Urtica dioica</i>) patches in agricultural matrix	inter-patch distance	E-O	species richness, abundances
(Laan & Verboom 1990)	amphibians	pools	distance, presence of woods	E-O	occurrence, species richness

Study	Organism	Landscape	Measure of Connectivity	Design	Relationship
(Hijermann & Ims 1996)	wart bitter (<i>Delticus verrucivorus</i>)	un-grazed grassland in agricultural matrix	distance/area index	E-O	occupancy, persistence
(Petit & Burel 1998a)	forest carabid (<i>Abax parallelepipedus</i>)	woodland patches and a hedgerow network	Euclidean, network, and resistance weighted distances	E-O	abundance at site
(Fitzgibbon 1997)	wood mice (<i>Apodemus sylvaticus</i>), bank voles (<i>Clethrionomys glareolus</i>)	small woods in agricultural matrix	inter-patch distance	E-O	population abundance
(Farmer & Parent 1997)	Pectoral Sandpipers (<i>Calidris melanotos</i>)	wetlands in agricultural matrix	inter-patch distance, amount of habitat	E-O	movement behaviour
(Paillat & Butet 1996)	bank vole (<i>Clethrionomys glareolus</i>)	woody patches in agricultural matrix	length of hedges within a 0.5 km radius	E-O	abundance
(Clergeau & Burel 1997)	Short-toed Tree Creeper (<i>Certhia brachydactyla</i>)	rural landscapes	presence/absence of corridors	E-O	presence/absence
(Le Coeur <i>et al.</i> 1997)	plant community	hedgerow network	presence/absence of corridors	E-O	plant species composition
(Schmigelow <i>et al.</i> 1997)	breeding bird community	boreal forest patches in clear cut matrix	presence/absence of corridors	E-O	bird abundance, richness, community structure
(Arnold <i>et al.</i> 1993)	kangaroo (<i>Macropus robustus</i>)	patches and corridors of native vegetation	presence/absence of corridors and stepping stones	E-O	movement rates and distances
(Metzger 1997)	tropical tree community	forest fragments	presence/absence of corridors and stepping-stones	E-O	species diversity
(Petit & Burel 1998b)	forest carabid (<i>Abax parallelepipedus</i>)	woodland patches and a hedgerow network	resistance weighted distance	E-O	abundance at site

Study	Organism	Landscape	Measure of Connectivity	Design	Relationship
(Ault & Johnson 1998)	reef fish	small coral reefs	size of and distance to nearest neighbour	E-O	community structure
(With & King 1999)	virtual	fractal, habitat/matrix grid	percolation threshold	M-I	dispersal success
(Hencin <i>et al.</i> 1998)	eastern chipmunk (<i>Tamias striatus</i>), white-footed mouse (<i>Peromyscus leucopus</i>)	woodlots in agricultural matrix	presence/absence and quality of corridors	M-I	population size and persistence
(Demers <i>et al.</i> 1995)	virtual	woodlots and fencerows in agricultural matrix	presence/absence of corridors & amount of habitat	M-I	colonization success
(Lavorel <i>et al.</i> 1995)	virtual	binary, hierarchical	percolation threshold	M-I	population spread, dispersal distances
(With <i>et al.</i> 1999)	cricket (<i>Acheta domestica</i>)	grass/sand fractal landscape	percolation thresholds	M-I, E-E	movement behaviour
(With & Crist 1995)	two grasshoppers (<i>Xanthippus corallipes</i> & <i>Psoloessa delicatula</i>)	shortgrass prairie	percolation threshold	M-I, E-O	population distributions
(Brooker <i>et al.</i> 1999)	Blue-breasted Fairy-wren (<i>Malurus pulcherrimus</i>), White-browed Babbler (<i>Pomatostomus superciliosus</i>)	native vegetation in agricultural matrix	presence/absence of corridors and gap widths	M-I; E-O	gap crossing behaviour on dispersal success
(Hess 1996b)	virtual	connected patches	arrangement of connections	M-M	extinction probability with a disease present
(Swart & Lawes 1996)	samango monkey (<i>Cercopithecus mitis</i>)	forest patches	presence/absence of corridors	M-M	population persistence
(Hess 1996a)	na	abstract patches	ability to move between patches	M-P	population persistence
(Adler & Nuernberger 1994)	virtual	patch matrix	isolation (distance)	M-P	population persistence

Study	Organism	Landscape	Measure of Connectivity	Design	Relationship
(Root 1998)	Florida scrub jay (<i>Aphelocoryza coerulescens</i>)	scrub patches	nearest neighbour distance	M-P	abundance, persistence
(Lefkovich & Fahrig 1985)	white-footed mouse (<i>Peromyscus leucopus</i>)	woodlots and fencerows in agricultural matrix	presence/absence and arrangement of corridors	M-P	population size and persistence
(Henein & Merriam 1990)	white-footed mouse (<i>Peromyscus leucopus</i>)	woodlots and fencerows in agricultural matrix	presence/absence and quality of corridors	M-P	population size
(Fahrig & Merriam 1985)	white-footed mouse (<i>Peromyscus leucopus</i>)	woodlots and fencerows in agricultural matrix	presence/absence of corridors	M-P; E-O	population size
ii) Connectivity described through organism movement					
(Hof & Raphael 1997)	Northern spotted owl (<i>Strix occidentalis caurina</i>)	old-growth forest patches	influence of surrounding patches on population levels	M-P	abundance, persistence

Figure 1.1: Number of published connectivity papers (up to and including 1998) determined by a search of the Biosys database using the criteria “connectivity and landscape” in the keywords, title, or abstract. Only journal articles are included.

Chapter 2

EVALUATING THE EVIDENCE FOR THE RESOURCE CONCENTRATION HYPOTHESIS: A META-ANALYSIS.

2.1 CHAPTER SUMMARY

Using meta-analysis, I quantitatively reviewed support for the Resource Concentration Hypothesis in 51 studies that tested the relationship between herbivore density and resource concentration (host-plant density, host-plant patch size, or plant diversity of a host-plant patch). I found some support for the resource concentration hypothesis overall, but I also found a great deal of heterogeneity among studies in their support for the resource concentration hypothesis. I examined the source of this heterogeneity by incorporating moderator variables in the meta-analysis. My results indicate that the resource concentration hypothesis is most likely to be correct when: (1) resource concentration is manipulated as plant diversity or patch size; (2) plant species are high in secondary metabolites that are used by the insect species to help find host-plants; (3) insects are in the adult stage; (4) insects are capable of detecting host-plants from a distance; (5) insects tend to remain in host-plant patches once they are found; (6) host-plant patches are artificial or, if in a natural setting, have conspicuous edges; and (7) host-plant patches are accessible to the insect.

2.2 INTRODUCTION

Root (1973) postulated the Resource Concentration Hypothesis (RCH) to explain how the concentration of host-plant resources in a patch influences the herbivore population of that patch. Root measured resource concentration either as host-plant density (increasing density increases resource concentration) or plant diversity of a host patch (decreasing diversity of other plants increases resource concentration). Cromartie (1975) suggested that increasing host-plant patch size also increases resource concentration. Root (1973) predicted both species level and community level responses to resource concentration. At the species level, he predicted that increased resource concentration should cause increased densities of species that specialize on the resource. At the community level, he predicted that increased resource concentration should cause a decrease in herbivore diversity, as specialists would out-compete other, more generalist, insects. The RCH was quickly accepted into ecological “folklore” (Kareiva 1983) and proposed as the basis for agricultural pest-management (Risch *et al.* 1983), although early literature reviews found mixed empirical support for it (Kareiva 1983, Stanton 1983). My first goal was to see how well the species-level predictions of the RCH have stood up to over 20 years of testing, using meta-analysis to summarize these tests.

Meta-analysis, recently introduced to ecology (Gurevitch *et al.* 1992, Fernandez-Duque & Valeggia 1994, Arnqvist & Wooster 1995, Arnqvist *et al.* 1996, Leung & Forbes 1996, Bender *et al.* 1998), is a method used to quantitatively evaluate collections of experimental results. Meta-analysis avoids the pitfalls of vote counting procedures (Hedges & Olkin 1985, Gurevitch *et al.* 1992, Gurevitch & Hedges 1993). One can also investigate possible “moderator” variables (variables that could influence the strength of the relationship

between resource concentration and herbivore density; see Table 2.1 for examples) (Rosenthal 1991). My second objective was to incorporate moderator variables in our meta-analysis to determine the conditions under which the RCH is upheld.

Investigating moderator variables will point toward some of the mechanisms that drive insect responses to resource concentration. This is important as an understanding of the mechanisms driving insect responses to resource concentration will lead to predictions about insect responses to resource concentration in novel situations. Both Kareiva (1983) and Stanton (1983) pointed out in earlier reviews the need to understand the mechanisms behind the RCH. Earlier work elucidating mechanisms was limited (Risch 1980, Bach 1980a, Bach 1980b, Bach 1981, Risch 1981, Kareiva 1982) but there has been a greater interest recently (e.g., Bergelson & Kareiva 1987, Bohlen & Barrett 1990, Dingle 1991, Garcia & Altieri 1992, Costello 1995). The analysis of moderator variables should shed some additional light on the mechanisms driving the RCH. Furthermore, the meta-analysis approach will allow for an assessment of the generality of different mechanisms. For example, the RCH was postulated for species feeding on collards (*Brassica oleracea*) (Root 1973) but the generality of the hypothesis across different herbivore-host combinations needs to be assessed (Tonhasca & Byrne 1994).

I addressed the following questions (possible mechanisms) using meta-analysis with moderator variables:

1. Is the RCH more likely to be upheld for some forms of resource concentration (host-plant density, plant diversity, or patch size) than others?
2. Are the responses to resource concentration in natural and experimental settings (mostly using crop plants) the same? Experiments might show stronger support for

the RCH than surveys in natural settings, since experiments are designed to reduce extraneous variation.

3. Do particular insect orders or plant families show stronger responses to resource concentration? The RCH was originally postulated based on insect interactions with collards, a member of the Brassicaceae family (Root 1973). It is necessary to establish how well the RCH holds up across a broad spectrum of insects and plants before the generality of the RCH can be accepted (Tonhasca & Byrne 1994). Also, relationships between degree of response to resource concentration and plant and insect taxonomy may point to mechanisms driving the RCH (Stanton 1983).
4. Do densities of different insect life stages respond differently to resource concentration?
5. Do insects that eat different parts of the plant (vegetative tissue, saps or seeds) respond differently to resource concentration?
6. Does the effect of resource concentration increase as the degree of herbivore specialization increases? The RCH was initially postulated for specialist insects (Root 1973) and should hold most strongly for them. Still, there have been attempts to test the RCH on more generalist insect species (Stanton 1983).
7. Does the range over which resource concentration is varied influence the observed effect of resource concentration?

2.3 METHODS

I systematically surveyed the literature from 1973 to 1995 (see Table 2.2 for a list of journals searched) as well as additional papers referenced in three review papers (Kareiva

1983, Stanton 1983, Tonhasca & Byrne 1994). A paper was considered if it addressed the effects of host-plant density, patch size or plant diversity on the density of an insect herbivore, on a per-plant basis. I also used tests that reported the density of the insect herbivore on a per-area basis if the density of the host-plant was not changing concurrently with the measure of resource concentration.

Each paper provided one or more “effect size” for the meta-analysis. In meta-analysis the effect size functions as the dependent variable, and measures the degree of statistical support a single test provides for a hypothesis (here the RCH). There are several possible measures of effect size (Rosenthal 1991) but I chose the Pearson product moment correlation (r) between resource concentration and insect herbivore density, since the data tended to be correlative in nature. If r was not reported directly in the paper it was determined by either: 1) calculating it from raw data that were reported in tables, 2) converting other common tests (e.g., t values, ANOVA with 1 degree of freedom in the numerator, r^2 values, or the difference between two means) into r (see Rosenthal 1991, Rosenthal 1994 for conversion techniques), or 3) converting reported p values and degrees of freedom to an equivalent r . When resource concentration was measured as plant diversity of the host-plant patch I reversed the sign of the correlation between plant diversity and insect density since resource concentration increases with decreasing plant diversity. For analysis all r -values were converted to Fisher’s Z_r values following Rosenthal (1991).

Since one of the goals of the analysis was to determine factors that might influence the strength of the relationship between resource concentration and herbivore density, it was also necessary to determine values of the moderator variables in Table 2.1, for each test of the RCH. Values were assigned based on information contained within the paper itself or

from other literature. If the value of a moderator variable could not be determined for a particular test of the RCH, the associated effect size was excluded from the analysis involving that moderator variable.

It was often possible to extract multiple tests of the RCH from a single paper if that paper reported results for different values of the moderator variables. For example, a paper might report densities for both adults and larvae of two different herbivores, producing 4 tests of the RCH. Also, some papers reported multiple effects for a test of RCH, due to either reporting multiple densities in time (e.g., multiple days after planting) or in space (e.g., multiple locations). Since these multiple effect sizes were not independent, I selected the single effect size that most supported the RCH. This will skew the analysis toward detecting positive responses to resource concentration.

The effect sizes were analyzed using a meta-analytic approach analogous to multiple linear regression (Hedges & Olkin 1985, Hedges 1994). The transformed effect sizes (Z_r 's) were analogous to the "dependent variable" while different combinations of the moderator variables and their interactions were analogous to "independent" variables. The meta-analysis was performed using a weighted least squares, fixed effects approach, where the effect sizes were weighted by the inverse of the sampling variance (Hedges & Olkin 1985, Hedges 1994). This effectively weighted the studies with larger sample sizes, or greater statistical power, more heavily. Between-group comparisons were made by comparing 95 % confidence intervals, while multiple comparisons were conducted using a Bonferroni adjustment (Hedges 1994).

2.4 RESULTS

I found 166 studies investigating the RCH. Only 31% of the published papers (51 studies) provided enough information to be included in the meta-analysis. The most common problem leading to the elimination of studies from consideration was not reporting sample sizes. In addition, a few studies used designs in which the effect size could not be converted to r (e.g., ANOVAs with numerator d.f. > 1, Rosenthal 1994). From the 51 studies I extracted 139 effect sizes (Appendix A).

The grand weighted-mean correlation between resource concentration and herbivore density for all 139 tests of the RCH was small, positive, and significantly different from zero ($r = 0.0939$, 95% CI: $0.0715 < r < 0.1163$). The correlations were, however, highly heterogeneous ($Q_{TOTAL} = 2014$ [where Q has an asymptotic χ^2 distribution], $d.f. = 138$, $p = 0.0000$), indicating that individual tests of the RCH did not share the same correlation between herbivore density and resource concentration. The high heterogeneity suggested analysis of moderator variables would likely be fruitful.

Of all the moderator variables measured (Table 2.1), the form of the hypothesis tested (i.e., resource concentration measured as host-plant density, plant diversity, or patch size) explained the most heterogeneity in the correlations between resource concentration and herbivore density ($Q_{FORM} = 305$, $d.f. = 2$, $p = 0.0000$). Both plant diversity and patch size had significantly positive weighted-mean correlations while host-plant density had a significantly negative weighted-mean correlation (Figure 2.1). Even after taking the form of resource concentration into account there was still a great deal of heterogeneity ($Q_{WITHIN} = 2063$, $d.f. = 136$, $p = 0.0000$).

By constructing two-way models with each of the remaining moderator variables and the form of resource concentration, I considered the ability of the remaining moderator variables to explain the heterogeneity remaining after taking into account the effect of the form of resource concentration. In all of the two-way models the form of resource concentration was significant and behaved as it had in the single-variable model. All the two-way models had significant unexplained heterogeneity and, across all models, very few of the classes due to the interaction between moderator variables and form of resource concentration were homogeneous.

In addition to the form of resource concentration, the significant main effects were: (i) tests in experimental settings had more positive correlations than tests in natural settings ($Q_{\text{SETTING}} = 47.22$, $d.f. = 1$, $p = 0.0000$; Figure 2.2); (ii) lepidopterans, coleopterans and hemipterans all had positive correlations while the remaining insect orders had either non-significant or negative correlations ($Q_{\text{INSECT}} = 107.29$, $d.f. = 6$, $p = 0.0000$; Figure 2.3a); (iii) the Asclepiadaceae, Brassicaceae, Cucurbitaceae, Onagraceae, and Solanaceae plant families showed significant correlations while the remaining plant families had either non-significant or negative correlations ($Q_{\text{PLANT}} = 450.41$, $d.f. = 11$, $p = 0.0000$, Figure 2.4a); (iv) studies using insects that eat the leaves or steams of the plant were more likely to show positive correlations than those using insects that eat either the sap or the seeds ($Q_{\text{PART}} = 52.16$, $d.f. = 2$, $p = 0.0000$, Figure 2.5a); (v) insects in either adult or egg life-stages were more likely to show positive correlations than larval/nymphal insects ($Q_{\text{STAGE}} = 38.95$, $d.f. = 2$, $p = 0.0000$, Figure 2.6a); and (vi) herbivores that specialized at the genus or species level did not support the RCH (weighted-mean correlations were either non-significant at

the species level or negative at the genus level), while those who fed more broadly did support the RCH ($Q_{PHAGY} = 115.73$, $d.f. = 3$, $p = 0.0000$; Figure 2.7a).

Significant interactions between the form of resource concentration and other moderator variables were: (i) lepidopterans differed from the other insect orders in that the other orders had significantly more negative correlations when resources were measured as host-plant density ($Q_{INSECT \times FORM} = 153.90$, $d.f. = 12$, $p = 0.0000$; Figure 2.3b); (ii) when the plant eaten belonged to the Asteraceae or Brassicaceae families the observed correlations for patch size were not different from those observed for host-plant density while the remaining plant families either displayed no difference between the correlations for patch size and plant diversity or a more positive correlation for patch size ($Q_{PLANT \times FORM} = 176.68$, $d.f. = 22$, $p = 0.0000$; Figure 2.4b); (iii) herbivores feeding on leaves or stems were different from the other herbivores in that they had a non-significant correlation when resources were measured as host-plant density and the correlation for plant diversity was significantly more positive than for patch size ($Q_{PART \times FORM} = 99.33$, $d.f. = 4$, $p = 0.0000$; Figure 2.5b); (iv) larvae/nymphs differed from the other life-stages in that the weighted-mean correlations for all three forms of resource concentration were indistinguishable and not significantly different from zero ($Q_{STAGE \times FORM} = 93.91$, $d.f. = 4$, $p = 0.0000$; Figure 2.6b); (v) all of the weighted-mean correlations for the different measures of resource concentration for the most specialized herbivores were not significantly different from zero ($Q_{PHAGY \times FORM} = 153.90$, $d.f. = 6$, $p = 0.0000$; Figure 2.7b); and (vi) there was no significant effect of intensity of manipulation when resource concentration was measured as either plant density or patch size (plant density: $b = 0.00015 \pm 0.00042$; patch size: $b = 0.000004 \pm 0.000005$), whereas when resource concentration was measured as plant diversity the effect of intensity was negative

and significantly different from zero ($b = -0.01001 \pm 0.00286$), which indicates that the more diverse the polyculture in comparison to the monoculture the less positive the correlation between resource concentration and herbivore density ($Q_{INTENSITY \times FORM} = 32.02$, $d.f. = 1$, $p < 0.0000$).

2.5 DISCUSSION

I found the overall average correlation between resource concentration and herbivore density to be positive yet very small, explaining less than 1% of the variability in herbivore density. Also, the tests of the RCH were extremely heterogeneous (i.e., there was a great deal of variability in the correlations between resource concentration and herbivore density from test to test). This high heterogeneity suggests that other factors influence the correlation between herbivore density and resource concentration. Even when subdividing the effect sizes by two levels of moderator variables (the form of resource concentration and then any one of a number of moderator variables) there were few classes with homogeneous correlations. The combination of a low weighted-mean correlation and high heterogeneity suggests that the RCH is not very general and may only be correct under particular circumstances.

To be able to apply the RCH we need to understand how circumstances influence the correlation between resource concentration and herbivore density. In other words, we need to understand the mechanisms driving the RCH. Both Kareiva (1983) and Stanton (1983) pointed out the need to understand the mechanisms driving herbivore responses to resource concentration. Earlier work elucidating mechanisms was limited (Risch 1980, Bach 1980a, Bach 1980b, Bach 1981, Risch 1981, Kareiva 1982) but there has been a greater

interest recently (e.g., Bergelson & Kareiva 1987, Bohlen & Barrett 1990, Dingle 1991, Garcia & Altieri 1992, Costello 1995). The analysis of moderator variables also sheds some light on the mechanisms driving the RCH.

Plant quantity versus quality

Regarding the different forms of resource concentration, the meta-analysis results tended to agree with earlier work. I found the strongest support for the RCH when resource concentration was measured as plant diversity. This agrees with studies on the effect of crop diversification, which moderately supported the RCH (Risch *et al.* 1983, Tonhasca & Byrne 1994). I found that insect herbivore densities increased as patch size increased, as predicted by the RCH, though the correlation was weak. Similarly, Kareiva (1983) found that of 22 studies examining the influence of patch size on herbivore density 11 supported the RCH, 7 were inconclusive, and 4 were opposite the predictions of the RCH. A meta-analysis of the effect of habitat patch size on animal population density found an effect size of similar magnitude and direction (Bender *et al.* 1998). I found the mean correlation between host-plant density and herbivore density opposite that predicted by RCH. Similarly, Stanton (1983) found mixed support for RCH and Kareiva (1983) found only 2 of 13 studies examining host-plant density supported RCH.

The differences among results for different measures of resource concentration may be due to their different effects on host plant number and host plant quality. Increased host-plant density can lead to decreased leaf area and fewer reproductive parts (Harper 1977), sparser growth and earlier browning (Farrell 1976a), decreased height, stem diameter and stem moisture content (Luginbill & McNeal 1958), and slower rates of growth resulting in smaller plants (Mayse 1978). Lower quality of host-plants can decrease the number of

herbivore individuals, on a per plant basis, that the patch can support (Kareiva 1983), which would explain the negative correlation for host-plant density.

The effect of plant diversity on host plant quality is not as straightforward, which may account for the variation in results for this measure of resource concentration. Increased plant diversity in a patch can decrease host-plant quality through allelopathic or competitive effects, which lead to decreased plant growth or size (Müller-Schärer 1991), decreased foliage quality (Bach 1981), or reduced feeding activity due to changes in microclimate (Price 1976). Alternatively, if the herbivore can eat some of the other plants present then herbivore densities might increase with increasing plant diversity due to resource supplementation (especially if the host-plant's density remains constant). Increasing plant diversity could also increase herbivore densities by increasing resource attractiveness: Risch (1980) found the incidence of diseased host-plants, which were preferred, increased in polycultures.

Further support for decreases in plant quality counter-acting increases in resource concentration can be seen when comparing responses between sap feeding and tissue feeding herbivores. Insects feeding on sap (xylem and phloem) should be more sensitive to host-plant quality since plant saps are low in nutrients, especially nitrogen (Montllor 1991). For both host-plant density and plant diversity, sap feeder densities were more negatively correlated with resource concentration than other feeding styles. Only for patch size, which is less likely to affect plant quality, was there no difference in the correlation between resource concentration and herbivore density for the two feeding styles.

The role of movement

Arguably the most important component of the herbivore response to resource concentration that might vary from situation to situation is the movement behaviour of the herbivore (Kareiva 1983). Without explicitly considering searching or movement, the RCH makes implicit assumptions about these behaviours. In Root's (1973) formulation of the RCH, insects must preferentially find and then remain in patches of higher resource concentration.

Different herbivores use different cues to locate host-plant patches. Some species show little searching behaviour and land or bump randomly into host-plant patches (Dethier 1959, Root 1973, Price 1976, Cappuccino & Kareiva 1985), some use visual cues to find host-plants (Moericke *et al.* 1975, Smith 1976, Hamilton *et al.* 1978, Rausher 1981), and others use olfactory cues (Saxena & Saxena 1975, McKibbin *et al.* 1977, Ralph 1977a). If an herbivore cannot detect a host-plant until it is very close to the plant then herbivore density is less likely to correlate with resource concentration. Immature insect stages often have limited abilities to detect host-plants (Dethier 1959, Rausher 1981, Messina 1982d, Cappuccino & Kareiva 1985), have a high risk of mortality when dispersing (Dethier 1959, Ralph 1977b, Jennings *et al.* 1983), and move both less often and shorter distances compared to more mature stages (With 1994). These factors would tend to keep immature insect densities from responding to resource concentration, as they would diffuse out from oviposition sites (which may have been placed by adults responding to resource concentration) but not reconcentrate in areas of high resource concentration. In my meta-analysis, larval stages did not have significant correlations between resource concentration and density no matter what the measure of resource concentration. Similarly, many species

of aphids and thrips are deposited out of the air at random due to their small size (Price 1976) and I found the weighted-mean correlation for the Homoptera and Thysanoptera to be non-significant.

If herbivores search for host-plants visually they may use cues, such as leaf structure, that weaken in more diverse backgrounds (Papaj & Rausher 1983). Such a searching behaviour would produce results that support the RCH. However, it is more likely that herbivores respond to colour in general and then search within a favourable area (Stanton 1983). This may or may not produce herbivore distributions that support the RCH. For example, some aphids respond to light from the part of the spectrum congruent with leaf colour (Costello 1995). Interestingly though, they tend to land only in areas with some bare ground (Horn 1981, Bottenberg & Irwin 1992, Costello 1995) and show decreased landing rates on areas with any green ground-cover (plant or burlap) (Smith 1976). This could represent a response to avoid excessively dense plantings that result in reduced host-plant quality due to plant competition.

Often herbivorous insects are attracted to their host-plants by specific, volatile secondary metabolites (Finch 1980, Louda & Mole 1991, Städler 1992, Bernays & Chapman 1994). Increasing resource concentration can increase the effectiveness of olfactory cues: larger patches produce larger odour plumes which are more likely to be detected by herbivores (Stanton 1983), and more diverse patches may produce masking or repelling odours (Tahavanainen & Root 1972). Plant families high in secondary metabolites, or evolutionarily important secondary metabolites, should match the RCH better than plant families that do not have as many, or as important, secondary metabolites. In the meta-analysis the plants that tended to have more positive weighted-mean correlations are well

known for their specific secondary metabolites: glucosinolates in the Brassicaceae (Louda & Mole 1991), cucurbitacins in the Cucurbitaceae (Gershenzon & Croteau 1991), cardenolides in the Asclepiadaceae (Bernays & Chapman 1994), and particular alkaloids (solanine, atropine, nicotine) in the Solanaceae (Bernays & Chapman 1994).

Further complicating the issue of herbivores finding host-plant patches is the fact that patches are not equally accessible. The landscape in which a patch is embedded will influence the ability of an herbivore to access that patch. Patches that are more isolated from potential sources of herbivores will have lower herbivore densities, even if they are high in resource concentration. Patch isolation can be due to both distance and landscape resistance to movement through barriers and/or high risk of mortality during dispersal (van Dorp & Opdam 1987, Potter 1990, Sjögren 1991, Knaapen *et al.* 1992, Hanski *et al.* 1995). The presence or absence of supplementary or complementary resources in the landscape can also influence herbivore densities in patches (Dunning *et al.* 1992). Furthermore, the spatial pattern of the landscape can influence the ability, both positively and negatively, of herbivores to move through the landscape (Merriam 1984, Taylor *et al.* 1993). Variation in these characteristics from study to study could be partly responsible for the high heterogeneity of the correlation between herbivore density and resource concentration I observed.

The influence of the surrounding landscape on herbivore densities at a patch may account for our unexpected results for the degree of herbivore specialization. The RCH was originally formulated for specialist insect herbivores (Root 1973) and so the most positive correlations should occur for herbivores specialized at the species level. In fact I saw the strongest support for the RCH for species specialized at the family level. This may be due to

the fact that species that can use many plants in the landscape (i.e., a plant family) should move more easily than species that are restricted to a few plant species, as there should always be food patches nearby. For example, Jonsen and Fahrig (1997) found no effect of patch isolation on alfalfa specialist insects when a specialist was defined as feeding only on legumes. Insects specialized on a single species or genus might not be able to reach a host-plant patch and therefore will not respond to the resource concentration of that patch. Note, this does not explain the negative correlation I observed for species specialized at the genus level. That seems to be driven by the fact that over half of the genus level cases had resource concentration measured as host-plant density (Figure 2.7b).

An increase in the tendency of an herbivore to remain in a host patch, with increasing resource concentration, will result in a positive relationship between herbivore density and resource concentration. Sedentary species or species using rare host plants benefit from remaining in a resource patch (e.g., Tabashnik 1980, Kareiva 1982, Lawrence 1982). Herbivores remain within a host-plant patch by (i) turning more often following host-plant contact (Jones 1977, Wiens *et al.* 1995) and (ii) turning away from patch edges back into the patch (Lawrence 1982), which may depend on the edge being conspicuous (Ralph 1977a, Kareiva 1982, Turchin 1986). This may partially explain why tests of RCH in natural settings, where patch edges tend to be less discrete, show less support for RCH than in artificial settings, where patch edges tend to be conspicuous. Plant diversity can also influence movement behaviour by causing herbivores to make long movements after encountering a non-host plant (Bach 1980b, Turchin 1987, Elmstrom *et al.* 1988) and planting patterns (e.g., plants placed in rows) may direct herbivore movement (Bohlen & Barrett 1990).

In vagile species movement behaviour may be in response to selective forces other than resource concentration. Root and Kareiva (1984) showed that female movement patterns caused a negative relationship between *Pieris rapae* (Lepidoptera) egg density and host-plant density. Female *P. rapae* discovered patches of different densities at the same rate, landed only slightly more often in dense patches and their flights were very directional (little turning) resulting in quickly leaving host-plant patches. Fahrig and Paloheimo (1987) found similar results for *P. rapae* but in response to patch size. The probability of *P. rapae* females finding a host plant patch was directly related to patch size; however, the probability of leaving was unrelated to patch size, resulting in lower *P. rapae* egg densities in larger patches. For *Colias* butterflies Stanton (1983) found similar results for different reasons: the egg-laying butterflies landed more often in patches of dense host-plants up to a certain density, after which the butterflies did not respond to density. In both cases the movement patterns acted to spread reproductive effort over space in response to spatially unpredictable larval survival. Thus movement behaviours that have an adaptive significance other than resource finding can lead to patterns of herbivore density other than that predicted by the RCH.

The role of demographics

Decreased mortality and increased fecundity can also cause increased herbivore densities in areas of higher resource concentration. Few studies have actually looked at survival rate vs. resource concentration. Andow (1990) used a demographic analysis to determine that *Epilachna varivestis* (Coleoptera) egg survival was higher in monocultures of *Phaseolus vulgaris* than weedy polycultures. Increased rates of survival could, over a number of generations, lead to higher herbivore densities. Some of the non-significant or

negative tests of the RCH may be due to the short duration of the studies (one growing season, only a few generations of the insects at most) not allowing for differential population build-up among patches. It was impossible to address this in the meta-analysis since the vast majority of studies looked at herbivore density for a year or less.

There has also been a suggestion, the natural enemies hypothesis, that more diverse areas should harbour more generalist natural enemies and therefore lead to increased mortality of herbivores and decreased densities compared to more homogeneous patches (Pimentel 1961, Root 1973). Many studies have measured natural enemy populations in diverse habitats and tested for negative correlations between enemy abundance and herbivore densities (e.g., Letourneau & Altieri 1983, Buschman *et al.* 1984, Gold & Altieri 1989, Kemp & Barrett 1989, Helenius 1990, Letourneau 1990a, Letourneau 1990b, Coll & Bottrell 1995) with most of these studies finding little support for the natural enemies hypothesis (Kareiva 1983, Andow 1990). However, studies that actually measure mortality tend to find higher mortality rates in polycultures (reviewed in Russel 1989), nor does the natural enemies hypothesis and the RCH need to be mutually exclusive (Sheehan 1986).

The role of experimental design

One difficulty with performing a literature review is the necessity of comparing studies with different methodological approaches. I used the meta-analysis to evaluate whether there was a significant impact of methodology on support for the RCH results. I considered two aspects of methodology: 1) whether the investigator used a controlled experiment or a natural system and 2) the range over which resource concentration was manipulated.

Experimental settings tend to control for things like patch shape and edge contrast, and plant quality by watering and fertilizing. It is not surprising then that I found stronger support for the RCH in experimental settings. Also, I found the strongest support for the RCH when resource concentration was measured as plant diversity but none of the studies investigating plant diversity were performed in natural settings.

The intensity with which resource concentration was manipulated was extremely variable between studies. For example, Horton and Capinera (1987) only varied host-plant density by a factor of two while Reznik *et al.* (1994) varied density by a factor of 1600 (see Appendix A). For both host-plant density and patch size this variation in methodology had no detectable effect on the observed correlation between herbivore density and resource concentration. This was not the case for plant diversity where host-plant monocultures compared to host-plants grown in bi- or triculture showed stronger support for the RCH than monocultures, compared to host-plants grown with weeds. The added variability of allowing unspecified weeds to make up the polyculture seems to weaken the relationship. This is probably due to the weeds presenting potential food sources while the bi- or tricultures were chosen specifically to present unpalatable plants. This also suggests that the enemies hypothesis is not all that important since we would expect the opposite relationship - the weed polycultures would support more natural enemies and therefore we should see stronger support for the RCH the bigger the change in plant diversity.

2.6 CONCLUSIONS

My results demonstrate, first, that not all measures of resource concentration are equal. Resource concentration measured as plant diversity seemed to follow the predictions

of the RCH fairly well, patch size not quite as well, and host-plant density the opposite of what the RCH predicts. If the RCH is to be used in applied settings, such as pest control in crop fields, the focus should be on manipulating plant diversity. Increasing plant diversity of non-crop plants can decrease herbivore densities on the crop plant.

Second, many lines of evidence from the meta-analysis suggest that the bulk of the heterogeneity in herbivore responses to resource concentration is due to variability in movement behaviour. This suggests that it is necessary to understand herbivore search and movement behaviour, and how the landscape setting influences that behaviour, in order to use resource concentration to predict herbivore density. Kareiva (1983) recognized this but there is still little general theory regarding insect movement and searching behaviour.

Finally, the meta-analysis allows us to make predictions about when herbivore densities will increase as resource concentration increases. Specifically, I would expect herbivores in the following situations to respond as RCH suggests:

1. Resource concentration is manipulated as plant diversity or patch size and that manipulation has little or no impact on plant quality.
2. Plant species are high in secondary metabolites that are used by the insect species to help find host-plants.
3. Insects are in the adult stage.
4. Insects are capable of detecting host-plants from a distance (i.e., they do not rely solely on randomly encountering a host-plant).
5. Insects tend to remain in host-plant patches once they are found.
6. Host-plant patches are artificial or, if in a natural setting, have conspicuous edges.

7. Host-plant patches are accessible to the insect (i.e., they are not extremely isolated in the landscape).

Table 2.1: Moderator variables used in the meta-analysis.

VARIABLE	DEFINITION	VALUES
FORM	how the resource was manipulated	DENSITY = host-plant density SIZE = host-plant patch size DIVERSITY = plant diversity of the host-plant patch
SETTING	test in a natural or experimental system	EXP = experimental NAT = natural
INSECT	insect order of the herbivore	COL = Coleoptera DIP = Diptera HEM = Hemiptera HOM = Homoptera HYM = Hymenoptera LEP = Lepidoptera THY = Thysanoptera
PLANT	taxonomic family of the plant eaten	AQU = Aquifoliaceae ASC = Asclepiadaceae AST = Asteraceae BRA = Brassicaceae CHE = Chenopodiaceae CUC = Cucurbitaceae FAB = Fabaceae ONA = Onagraceae PIN = Pinaceae POA = Poaceae RUB = Rubiaceae SOL = Solanaceae
STAGE	life stage of the insect sampled	A = adult L = larvae/nymph E = egg
PART	part of the plant eaten by the insect	SAP = phloem or xylem SEED VEG = leaves or stems
PHAGY	degree of specialization of the insect	B = generalist F = specialized at the family level G = specialized at the genus level S = specialized at the species level
INTENSITY	degree resource was manipulated	maximum - minimum concentrations

Table 2.2: List of the titles of the journals along with years and volumes of each journal searched for studies testing the Resource Concentration Hypothesis.

TITLE	Date	Vol.
Agriculture, Ecosystems and Environment	1974-1995	1-54
Annals of the Entomological Society of America	1973-1995	66-88
Bulletin of Entomological Research	1973-1995	62-85
Ecological Entomology	1976-1995	1-20
Ecology	1973-1995	54-76
Entomologia Experimentalis et Applicata	1973-1980	16-28
	1988-1995	46-76
Environmental Entomology	1973-1995	3-24
Journal of Animal Ecology	1973-1995	42-64
Journal of Applied Ecology	1973-1995	10-32
Journal of Applied Entomology	1973-1987	73-104
	1994	117-118
Oecologia	1973-1995	11-104
Oikos	1973-1995	24-73

Figure 2.1: Weighted-mean correlations (r) and associated 95% confidence intervals for the three forms of resource concentration (host-plant patch size, host-plant density, and plant diversity). The numbers of tests used to calculate the mean effect size (k) are indicated.

Figure 2.2: Weighted-mean correlations (r) and associated 95% confidence intervals for the two different settings (experimental or natural). The numbers of tests used to calculate the mean effect size (k) are indicated.

Figure 2.3: Weighted-mean correlations (r) and associated 95% confidence intervals for (a) insect orders of the herbivores and (b) insect orders of the herbivores separated by the measure of resource concentration used (● = host-plant density, ▲ = plant diversity, ■ = patch size). The numbers of tests used to calculate the mean effect size (k) are indicated and * indicate groupings that were not significantly heterogeneous. Short forms as in Table 2.1.

Figure 2.4: Weighted-mean effect sizes (r) and associated 95% confidence intervals for (a) plant families and (b) plant families separated by the measure of resource concentration used (● = host-plant density, ▲ = plant diversity, ■ = patch size). The numbers of tests used to calculate the mean effect size (k) are indicated and * indicate groupings that were not significantly heterogeneous. Short forms as in Table 2.1.

Figure 2.5: Weighted-mean effect sizes (r) and associated 95% confidence intervals for (a) the part of the plant eaten by the herbivore and (b) the part of the plant eaten by the herbivore separated by the measure of resource concentration used (● = host-plant density, ▲ = plant diversity, ■ = patch size). The numbers of tests used to calculate the mean effect size (k) are indicated and * indicate groupings that were not significantly heterogeneous. Short forms as in Table 2.1.

Figure 2.6: Weighted-mean effect sizes (r) and associated 95% confidence intervals for (a) the insect life-stage sampled and (b) the insect life-stage separated by the measure of resource concentration used (● = host-plant density, ▲ = plant diversity, ■ = patch size). The numbers of tests used to calculate the mean effect size (k) are indicated and * indicate groupings that were not significantly heterogeneous. Short forms as in Table 2.1.

Figure 2.7: Weighted mean effect sizes (r) and associated 95% confidence intervals for (a) degree of specialization of the herbivore and (b) degree of specialization separated by the measure of resource concentration used (● = host-plant density, ▲ = plant diversity, ■ = patch size). The numbers of tests used to calculate the mean effect size (k) are indicated and * indicate groupings that were not significantly heterogeneous. Short forms as in Table 2.1.

Chapter 3

PATCH AND LANDSCAPE CONSTRAINTS ON THE MOVEMENT BEHAVIOUR OF A SPECIALIZED GOLDENROD BEETLE, *TRIRHABDA BOREALIS* BLAKE (COLEOPTERA: CHRYSOMELIDAE).

3.1 CHAPTER SUMMARY

To determine how patches and landscapes can influence *Trirhabda borealis* movement behaviour I tracked individual beetles through microlandscapes composed of three patch types (goldenrod, cut vegetation, and cut vegetation containing camouflage netting to a height of 50 cm) that differed in terms of available food resources and structural complexity. The results showed that: (1) individuals in goldenrod patches tended to move in short bursts of fast, meandering movements, with long periods of immobility in between, (2) individuals in cut patches tended to move in longer bouts of slow, directed movements with short periods of immobility, and (3) individuals in netting patches tended to move in short bursts (same duration as goldenrod) of fast, meandering movements but had more bouts of mobility due to short periods of immobility (same duration as in cut patches). Using mark and release experiments I determined that *T. borealis* edge crossing behaviour was not influenced by edge type, beetles did not detect goldenrod from a distance, nor did they exhibit density-dependent emigration from goldenrod patches. Movement in goldenrod patches can be understood in terms of the beetle's attempting to keep in contact with the food resource through long periods of

immobility and very brief meandering movements. Movement in cut patches can be understood in terms of the beetle attempting to move through an inhospitable patch through long bursts of movement and directed paths but having to exercise caution, through slower movements, possibly due to higher predation risk. Finally, movement in the netting patches can be understood in terms of the structural complexity of the patch, which interfered with movement due to physical hindrances, making beetles turn more frequently and shortening the duration of bursts of movement, and acting as a component of the *T. borealis* defence system, allowing the beetles to move with less caution (faster).

3.2 INTRODUCTION

Many ecological processes depend, to some extent, on movements of individuals. Two of the most obvious are the population processes of immigration and emigration, which are responsible for population redistribution (Myers & Campbell 1976, Pulliam *et al.* 1992, Dempster *et al.* 1995), recolonization following local extinctions (Henderson *et al.* 1985, Ebenhard 1991, Thomas 1994, Dunning *et al.* 1995), rescue effects (Brown & Kodric-Brown 1977), metapopulation persistence (Levins 1970, Hanski & Gilpin 1997), and stability of predator-prey interactions (Huffaker 1958, Crowley 1981, Kareiva 1987, Jones *et al.* 1993, Murdoch 1994, Holyoak & Lawler 1996). Movements of individuals influence the genetic structure of populations through gene flow (Gilbert & Singer 1973, Slatkin 1985, Lande 1988, Whitlock 1992, Dybdahl 1994, Hastings & Harrison 1994, Harrison & Hastings 1996), founder events or bottle-necks (O'Brien *et al.* 1983, Olivieri *et al.* 1990, Stangel *et al.* 1992), and avoidance of inbreeding depression (Moore & Ali 1984, Johnson & Gaines 1990, Bollinger *et al.* 1993). Much of behavioural ecology is

concerned with movements of individuals – searching and foraging theory (Zimmerman 1979, Stephens & Krebs 1986, Ims 1995), mate selection, home range or territory establishment and defence, and giving up densities (Bowers & Breland 1996). Processes which impact community composition, such as island-biogeography (MacArthur & Wilson 1967) and species spread (Hengeveld 1994, Kot *et al.* 1996), depend on movements of individuals. At the ecosystem level, movements of individuals can represent important fluxes of nutrients from one area to another (Dévai 1990).

Most movement studies consider movement behaviour as a function of decisions made by the organism to maximize fitness. Foraging and searching theory deals with organisms making decisions about movement behaviour in light of resource availability and predation risk (Zimmerman 1979, Stanton 1983, Root & Kareiva 1984). The impetus for dispersal, primarily juvenile, is thought to be driven by avoidance of parent/sibling competition (Arcese 1989, Davis & Howe 1992, Russell & Rowely 1993), avoidance of inbreeding depression (Moore & Ali 1984, Johnson & Gaines 1990, Bollinger *et al.* 1993), and/or spreading of risk (den Boer 1968, Reddingius & den Boer 1970, den Boer 1981, Sutcliffe *et al.* 1997).

However, constraints on movement are also imposed by the organism's surroundings. Animals may not be able to move into or through certain types of patches or may have to alter their movement behaviour within a patch due to physical barriers, physiological limitations, and/or behavioural responses (Mader 1984, Opdam *et al.* 1984, Opdam *et al.* 1985, Merriam *et al.* 1989, Mader 1990, Knaapen *et al.* 1992, Kozakiewicz 1993, Vos & Stumpel 1995, Matter 1996, Hill *et al.* 1996). For example, a densely vegetated area might be more difficult to cross than a sparsely vegetated area due to

individuals having to trace a tortuous path to move through the vegetation, even if it is in the organism's best interest to move in a relatively straight line, if it could. This environmental constraint not only influences the movements of a particular individual, but limits the possibilities upon which natural selection can act. This suggests that evolutionary questions should consider constraints imposed on movement by the structure of the environment.

These constraints on movement can be subdivided into the within-patch influence and the beyond the patch (landscape) influence. Within-patch constraints on movement are due to the interaction between patch characteristics and the organism's movement biology. Landscape influences on movement can be caused by either boundary effects on movements between adjacent patches, or effects of other (possibly distant) patches on within-patch movement behaviour (Wiens *et al.* 1985, Wiens *et al.* 1993a). Landscape influences on movement will be influenced by landscape structure since this will dictate the arrangement of patches including which patches are contiguous and thus what sorts of edges are present in the landscape.

The patch can constrain movement through three main mechanisms: 1) physical limitations placed on movement due to the structure of the patch, 2) presence or absence of various resources, and 3) risk of injury or death. Increased patch structural complexity (e.g., increased stems per unit area or increased plant complexity) could force organisms to either take more tortuous paths or to displace less in the horizontal plane with each move than they would in less structurally complex patches due to time spent moving up and down the vegetation and therefore not moving from one point to another. The presence of resources (primarily food) can lead to organisms changing their movement

behaviour to remain in contact with the resource (Jones 1977, Ralph 1977a, Tabashnik 1980, Kareiva 1982, Lawrence 1982, Turchin 1986, Wiens *et al.* 1995). The absence of resources will restrict possible movement behaviours since the organism needs to move out of the patch before depleting its resource stores. Risk of injury or death, due either to physiological stresses or predation, will place limits on the movement behaviour possible since movement rates or distances will have to be high enough to minimize exposure to the risk. In the case of predation, organisms may have to balance moving quickly through an area of high risk against being cautious enough (e.g., move slowly, less frequently) to avoid being preyed upon (Zollner & Lima 1999).

Landscape constraints on movement can occur via encounters with edges which may cause specific movement behaviours that are dependent edge type. Organisms in habitat patches may turn back from or avoid non-habitat edges (Lawrence 1982, Mills 1995), or movements may be directed along edges (Bohlen & Barrett 1990). Landscape constraints on movements need not be driven only by neighbouring landscape elements but can also be affected by distant landscape elements. For example, many herbivorous insects will use a wide range of sensory cues to detect host plants from a distance (e.g., Moericke *et al.* 1975, Saxena & Saxena 1975, Smith 1976, McKibbin *et al.* 1977, Ralph 1977a, Hamilton *et al.* 1978, Rausher 1981, Visser 1988; but see Dethier 1959, Price 1976, Cappuccino & Kareiva 1985, Fahrig & Paloheimo 1987 for counter examples). For organisms that can detect resource patches from a distance, we might expect that the degree to which surrounding resource patches influence movement behaviour would decline with increasing distance from the resource patch.

Finally, aggregations of individuals caused by the structure of the environment

may in turn influence movement through density-dependent impacts on movement behaviour. Individuals may be attracted to patches that are already inhabited by conspecifics (Turchin 1987, Stamps 1988, Smith & Peacock 1990) or aggregate in desirable patches due to behaviours that decrease emigration rates below immigration rates (Reeve & Murdoch 1985, Ray & Gilpin 1991, Morris *et al.* 1992, Godfray & Pacala 1992). Increasing densities in patches can lead to increased movement due to harassment (Odendaal *et al.* 1989) or dispersal to avoid competition and/or inbreeding (Waser 1985, Arcese 1989, Russell & Rowely 1993, Herzig 1995).

In this Chapter I describe a series of field experiments aimed at elucidating how different patch and edge types influence movement behaviour of a phytophagous beetle (*Trirhabda borealis* Blake) that specializes on goldenrod plants (*Solidago* spp.). Movements were studied in microlandscapes (*sensu* Wiens & Milne 1989; see Chapter 4) comprised of 3 patch types, which differed in their relative amounts of food resource and structural complexity (Figure 3.1). Patches were created by cutting old-field vegetation to leave standing goldenrod patches or cut patches. Cut patches could be further modified into netting patches by stringing camouflage netting with the top suspended approximately 50 cm above the ground. This created a panel of suspended netting (emulating the structure of standing vegetation) with the rest of the netting piled in the cell (emulating the structure of plant litter and ground-cover vegetation). Goldenrod patches were relatively high in both food resources and structural complexity due to the stems and leaves of the plants. The netting patches had high structural complexity due to the suspended camouflage netting but low food resources due to the lack of goldenrod plants. Finally, the cut patches were low in both food resources (no goldenrod) and

structural complexity (only stubble).

Natural history

T. borealis is a relatively large (lengths around 1 cm) beetle of the Chrysomelidae family, and is native to eastern Ontario. It is phytophagous and specializes on goldenrods (*Solidago* spp.), but will occasionally feed on asters (*Aster* spp.), during both the larval and adult life stages (Messina & Root 1980, Messina 1982a). Goldenrods are common, native perennials of disturbed areas. Members of the *Solidago canadensis* complex are found throughout eastern Ontario (Melville & Morton 1982), often dominating the herbaceous community on abandoned fields (Werner *et al.* 1980), but have persisted in the landscape historically in such naturally disturbed habitats as stream banks and gravel bars, alder swamps, and beaver meadows (Marks 1983). There is a diverse insect fauna associated with the goldenrods both as herbivores (Root & Cappuccino 1992) and as nectar and pollen feeders (Gross & Werner 1983). *T. borealis* and a congeneric, *T. virgata* often dominate the goldenrod herbivorous fauna in upper New York state (Messina & Root 1980, Root & Cappuccino 1992) and *T. borealis* was the dominant goldenrod herbivore at my study site (*personal observation*). *T. borealis* has a number of associated predators and parasites that mostly attack the larval stage. The adults avoid predation by dropping from the plant into the litter, and are also distasteful to vertebrates (Messina 1982b).

T. borealis overwinters in the egg stage. Larvae appear in May and pass through three instars while feeding on goldenrod plants and eventually pupate in the soil at the base of the host plant in June (Messina 1982b). Flightless, teneral adults emerge from the pupae after a few weeks. After a few more days the cuticle has hardened enough for

flight. The beetles then spend roughly two weeks in a pre-ovipositional dispersal phase (Messina 1982c), during which long distance flights (hundreds of meters) are common (Herzig 1995). The dispersal phase finishes when the females become gravid rendering them incapable of sustained flight. The beetles spend the remainder of the summer feeding, copulating, and laying eggs until they succumb to the first frosts in September. During this time movement is primarily by walking (Messina 1982c), though they occasionally make short, descending flights from the tops of plants (*personal observation*).

Hypotheses

Movement behaviour is typically measured in the two-dimensional, horizontal plane and described in terms of the probability of moving in a given, fixed amount of time (a time step), the step-length of a movement (measured as displacement per mobile time step), and the turn angle (the angle between the new direction of movement and the previous direction) (Kareiva & Shigesada 1983, Turchin *et al.* 1991, Wiens *et al.* 1993b). However, I found the probability of moving to be inappropriate to describe *T. borealis* movements due to temporal autocorrelation, that is time-steps with movements seemed to occur in runs longer than would be expected if time-steps with movement were randomly occurring during the tracking time (see 3.4 Results). Instead I used the duration of bouts of mobility (i.e., the number of consecutive time steps an individual displaced horizontally) and immobility (i.e., the number of consecutive time steps an individual was not detected to have displaced horizontally) as a measure of the tendency to move or not. Total time spent moving, say, can be related to the duration of bouts of mobility and immobility by determining how many bouts of mobility can be fit into a fixed time period

taking into account the lengths of the bouts of immobility in between. As such, any particular *T. borealis* trail could be described in terms of the distribution of durations of bouts of mobility and immobility and, during mobile events, step-length and turn angle distributions (Figure 3.2).

Movement behaviour could be influenced by either the presence/absence of resources (in this case food) or the presence/absence of structural complexity. Patches that contain food should engender movements that keep the beetle in contact with the food. Examples of such movement behaviour would be: i) shorter bouts of mobility (or conversely longer bouts of immobility) to keep from moving out of the patch, ii) a high degree of turning to produce a more tortuous path, which will tend to keep the beetle in the patch, and iii) slower movement (shorter step-lengths) when moving. Patches that lack food should have the opposite effect and engender movements aimed at moving quickly through the inhospitable patch. Examples of such movement behaviour would be: i) longer bouts of mobility (or conversely shorter bouts of immobility) to aid in moving through the patch, ii) a low degree of turning to produce a straighter path, which will tend to move the beetle through the patch, and iii) faster movement (longer step-lengths) through the inhospitable patch when moving. High structure patches should interfere with beetle movements and modify their movement behaviour in the following manner: i) shorten bouts of mobility (or conversely lengthen bouts of immobility) due to time spent moving up and down the structures and not displacing, ii) increase the degree of turning, producing a more tortuous path, due to having to wind through the structure of the patch, and iii) decrease movement speed when moving, as they find their way through the structures. Low structure patches should have the opposite effect and not interfere

with movement behaviour.

Based on the above, I would predict that movements in the goldenrod patches (high structure, high food) would consist of long bouts of immobility followed by short bursts of mobility and, when mobile, individuals would move slowly (via short step-lengths) and trace out tortuous paths due to turning frequently. Movements in the cut patches (low structure, low food) would consist of long bouts of mobility with short rests in between and, when mobile, individuals would move quickly (via long step-lengths) and trace out relatively straight paths due to turning infrequently. Finally, movements in the netting patches (high structure, low food) should be intermediate between the other two and would consist of an intermediate duration of bouts of both mobility and immobility (due to conflicting needs to have high mobility due to lack of food and being constrained to low mobility due to structure of the camouflage netting) and, when mobile, individuals would move more quickly than in goldenrod patches but not as quickly as in cut patches and should trace out somewhat tortuous paths (due to turning more frequently than in the cut patches but not turning as much as in goldenrod since the individual needs to move through the netting patch to find food).

Based on *T. borealis* natural history it is also possible to make predictions about the movement behaviour that will occur at patch edges. The lowest edge-crossing probabilities should be for crossing out of a goldenrod patch, as this would represent moving away from resources. The edge between a goldenrod patch and a netting patch may not be as conspicuous as the edge between a goldenrod patch and a cut patch. Accordingly there should be a higher probability of the beetle crossing a goldenrod-netting edge than a goldenrod-cut edge due to beetles not recognizing they are leaving a

goldenrod patch. Likewise, I predict the highest probability of crossing into a goldenrod patch from a cut patch than from a netting patch. The chance of a beetle moving from a netting patch to a cut patch should be low since this represents a loss of structural complexity (for predator defence). The chance of moving from a cut patch into a netting patch should be high, though not as high as the probability of moving into a goldenrod patch since the beetle should always prefer to move into a patch of food resources.

It is unknown whether *T. borealis* is able to detect goldenrod plants from some distance. If *T. borealis* is able to detect goldenrod from afar then movement responses to patch features will be tempered by responses to neighbouring goldenrod patches. Movements might become more directed towards the goldenrod patches and the speed and duration of movement events might increase. For these reasons it was necessary to assess the ability of *T. borealis* to detect goldenrod plants from a distance.

Finally, it is possible that *T. borealis* movement behaviour might change as the beetle density in a patch increases. A congeneric, *T. virgata*, displays density-dependent emigration during pre-ovipositional, long-distance dispersal (Herzig 1995), so the possibility of *T. borealis* doing the same during post-ovipositional, “trivial” movement needs to be considered. If this were the case, density-dependent movement behaviours would temper movement responses due to patch characteristics. To interpret *T. borealis* movement responses to patch type it will be necessary to know if density modifies movement behaviour.

3.3 METHODS

Field methods

Field experiments were performed in an abandoned farm field (approximately 20 years since abandonment) 6 km south of Ottawa, Canada. The vegetation consisted primarily of goldenrod (*Solidago* spp.), grasses, purple vetch (*Vicia americana*), raspberries (*Rubus* spp.), and milkweed (*Asclepias syriaca*) with some scattered shrubs (primarily willows [*Salix* spp.]) and young planted spruce (*Picea* spp.). Sixteen 5 by 5 m microlandscapes were constructed at 4 sites (4 microlandscapes per site) in the field. Microlandscapes consisted of three patch types: (i) patches of goldenrod (4% cover), (ii) cutting the vegetation and suspending camouflage netting in the patch (10 or 30% cover), or (iii) cutting the vegetation (remainder of landscape) (Figure 3.1). Each cluster of microlandscapes at a site was surrounded by 8 sticky traps (32 in all). Sticky traps were 1 m² in area and were mounted vertically with the bottom of the trap 2 m above the ground (Messina 1982c). Both faces of the trap (facing into and away from the cluster of microlandscapes) were sticky. Traps were monitored from July to September 1995 and checked every 2 to 3 days on average. *T. borealis* individuals were removed when captured and the traps were replaced when saturated with other insects.

Using the sticky traps I determined when *T. borealis* in the area were finished their pre-ovipositional dispersal flight phase (Messina 1982c). The sticky traps were no longer intercepting individuals in flight by the third week of July 1995 indicating the cessation of preovipositional dispersal flights (Messina 1982c). Additionally, only 3% of all movement events observed thereafter ($n = 645$) involved flying and all those flights were short, descending flights indicating that pre-ovipositional dispersal behaviour was

over. I then began tracking individuals to determine their movement behaviour (July 27 to September 6, 1995).

Using a sweep-net *T. borealis* individuals were captured from the surrounding vegetation between 15 minutes to 2 hours before being released and tracked. While waiting to be released beetles were held in a shaded container with fresh goldenrod leaves. Individuals were marked with a single dab of liquid paper on one elytron, ensuring that the elytra were not glued shut. This was done to make it easier to spot the beetle against the background vegetation, and was necessary due to the beetle cryptic colouring. Individuals were randomly assigned to start in one of the patch types in a randomly assigned landscape. In the course of the tracking season 30 individuals were captured, processed, and tracked. After preparation, individuals were released and allowed to wander for five minutes, to allow any effects of handling on movement behaviour to diminish, and were then tracked either until they were lost or for 49.5 minutes. During tracking, the beetle's activity (walking, resting, flying, or feeding) and patch type were recorded.

All tracking was performed between 10:00 AM and 4:00 PM on calm days. Individuals were not tracked at night, but from searching for marked individuals at night (see Chapter 4) it was apparent that the beetles were sluggish and immobile at night (*personal observation*). Movement trails were marked out with numbered surveyor's flags, which were placed in the ground every 30 seconds. To avoid disturbing or herding the beetles the surveyor's flags were displaced 10 cm in a constant direction that minimized the chance of shadows cast by the tracker falling on and disturbing the beetle (Turchin *et al.* 1991). The co-ordinates of the resulting path were mapped using

triangulation with a measuring tape from a fixed base line of known length (Turchin *et al.* 1991).

In a separate set of experiments, I assessed the behavioural response of *T. borealis* to patch edges. I released a known number of marked individuals (Table 3.2) within a patch of one type but within 2 cm of an edge with another patch type and then allowed them to move freely. Once an individual had moved 10 cm away from the edge (either back into the original patch or into the neighbouring patch) it was recaptured and scored as having either crossed or not crossed the edge. Again, individuals were caught from surrounding, natural vegetation using a sweep-net and marked with a single dab of liquid paper. This experiment was performed for all combinations of patch types.

I also assessed the ability of *T. borealis* individuals to detect goldenrod plants from a distance using an L-shaped arena constructed of polypropylene sheet. The arena had a potted goldenrod plant in one arm and the other arm was empty. Goldenrod plants were dug up from the surrounding field and consisted of 15 to 20 ramets each between 1 to 1.5 m tall. The goldenrod plant was in a pot that could be set flush with the ground. Individuals were captured and marked as in the edge crossing experiment and were released in the intersection of the two arms of the L and once individuals had moved into one arm or the other of the arena they were removed and scored as having either moved toward the goldenrod or not.

Finally, I assessed whether emigration rates from a goldenrod patch are density dependent. I potted 16 goldenrod plants (15-20 ramets each between 1 to 1.5 m tall) dug up from the surrounding field. After potting, each plant was shaken to remove any resident *T. borealis* individuals. I then placed *T. borealis* individuals, caught with a

sweep-net from the surrounding vegetation, at densities of 2, 5, 10 or 20 beetles per plant; densities of 20 beetles per plant were higher than anything I had seen in the field (highest density I observed was approximately 10 individuals per 20 ramets, *personal observation*). Before placing them on the goldenrod, the beetles were dusted with fluorescent powder to allow for a thorough search of the plants later. After 24 hours the potted plants were bagged, taken to the lab and frozen. Later the plants and soil in the pots were carefully searched, with the help of an ultraviolet lamp, to determine the number of beetles remaining on the plants.

Data analysis of the movement trails

The goal of the analysis of the movement trails was to summarize beetle movement behaviour (duration of bouts of mobility or immobility, step-length, turning angle) in response to patch type. Since some individuals crossed into different patch types during the tracking time (Figure 3.3), it was necessary to break each individual trail up into segments (of one or more steps) that were entirely in one of the three patch types before analyzing the influence of patch type on movement (Turchin 1998). Each movement trail then would consist of one or more path segments each of which would consist of a series of coordinates describing the path of an individual beetle as it moved through a specific patch type. These path segments could then be converted into the movement parameters: (i) duration of bouts of mobility or immobility, which are defined as the number of time-steps an individual remained mobile or immobile, respectively, (ii) step-length, which is defined as the displacement during a 30 second time-step where the beetle is moving, and (iii) turning angle, which is defined as the angular deviation from the forward direction when a beetle moves during a time-step, with 0° being

forward and positive angles indicating right turns and negative angles indicating left turns (Figure 3.2). The general approach to the analysis of the movement parameters was as follows: 1) test whether it is correct to pool the different path segments in the same patch type together (i.e., that individual path segments within a patch type were not significantly different) (Cain 1989), 2) test whether the multiple data points comprising each path segment were statistically independent to allow for correct statistical analysis (Turchin 1998), and 3) describe the movement parameter.

I assessed whether path segments in the same patch type could be pooled together by comparing the means and variances of the movement parameters (duration of bouts of mobility or immobility, step-length, turning angle) for each path segment. Means were compared using a Scheffé's test and variances using a Bartlett's test (Zar 1996). In the case of turning angles it was possible to compare the distributions directly using a non-parametric technique, the r -sample extension of the two-sample Uniform Scores test, and estimating the significance of the test statistic using a randomization approach (Fisher 1993). In the randomization the pool of observed turning angles were randomly assigned to path segments (maintaining the observed number of turning angles per path segment) and the test statistic calculated. This procedure was repeated 1000 times, generating the distribution of the test statistic under the hypothesis of random assortment of turning angles (i.e., all path segments are the same). The test statistic from the actual data could then be compared to the randomly generated distribution to estimate p .

To check that the series of data points making up a path segment were statistically independent I tested for temporal autocorrelation using a runs test for movement probabilities (Zar 1996) and examined the autocorrelation function (ACF) of the other

movement parameters (Diggle 1990). ACFs had to be determined for each path segment separately. ACFs for turn angles were determined following Fisher (1993) since turning angles are circular data and cannot be analyzed using traditional approaches. ACFs could only be constructed for pathway segments that were tracked for 4.5 minutes or longer as otherwise there would not be a long enough time series of data to calculate lagged correlations. Temporal autocorrelations were calculated for the lesser of the number of time lags equal to a quarter of the observations in a path segment or 10. It was then necessary to summarize the tests of temporal autocorrelation for a particular movement parameter across all the path segments in a patch type to ensure that all the data points for a particular movement parameter were statistically independent. This was done by either calculating a weighted-mean normal deviate of the number of runs from the expected number of runs under randomness (runs tests) or a weighted-mean correlation coefficient at each time lag (ACF) using meta-analytic techniques (Rosenthal 1991, Rosenthal 1994).

If heterogeneity between path segments and temporal autocorrelation within segments were ruled out, I quantified the different movement parameters. The duration of bouts of mobility and immobility were investigated using a survival analysis since some of the durations were censored, that is I stopped timing them before the event was actually over, since it extended past the 49.5 minute observation period. In such a case a survival analysis allows all of the data to be used and accounts for the censored data (Fox 1993). Differences in step-lengths in the different patch types were investigated using an ANOVA on log transformed step-lengths while Kolmogorov-Smirnov tests were used to assess the fit of theoretical distributions. Mean turn angles in each of the patch types were assessed using 95% confidence intervals (Batschelet 1981) and the fit of either a uniform

or von Mises (unimodal) distribution were assessed using the appropriate tests described in Batschelet (1981).

Goodness-of-fit tests were used to test if *T. borealis* individuals crossed any of the patch edges more or less frequently than would be expected under the null hypothesis of no response to the edge (i.e., 50% chance of crossing and not crossing the edge). Similarly, goodness-of-fit tests were used to evaluate the null hypothesis that *T. borealis* individuals did not detect, and therefore move toward, goldenrod plants from a distance (i.e., 50% chance of moving towards and away from goldenrod,). The influence of density on *T. borealis* emigration rate was analyzed using a linear regression of percent of beetles remaining after 24 hours, against initial density. Since I was regressing percentages I arcsine transformed the data to meet the assumptions of analysis of variance (Zar 1996).

3.4 RESULTS

Basic results

Over the course of tracking I caught and followed 30 beetles. Only 3 of the 30 beetles were not tracked for the full 49.5 minutes, due to being lost during tracking. The three lost individuals were tracked for 33.5, 36, and 36.5 minutes. Though individuals were released in equal proportions in all three patch types, since beetles were not tracked for the first 5 minutes after release, to allow any effect of handling to dissipate, the patch type within which the beetles were first tracked were not completely equal (37% in goldenrod, 30% in netting, and 33% in cut). Over the course of all the tracking the beetles did not spend equal amounts of time in the three patch types (43% in goldenrod, 18% in

netting, and 39% in cut). During tracking individuals were primarily immobile (approximately 70% of the time across all patches). This immobility was much more apparent than observed feeding (80.8% immobile and only 8.8% observed feeding; Table 3.1). When individuals were moving flights were rare (across all patch types only 0.8% of time steps had observed flights; Table 3.1), indicating that long-distance dispersal had ceased. Additionally, not all time steps with observed mobile behaviour (walking or flying) resulted in horizontal displacement. Overall, 74% of time steps with observed mobile behaviour resulted in a detectable horizontal displacement, though this varied between patch types with the cut patches having the highest percent of mobile behaviour resulting in displacement (90%) and goldenrod patches the lowest (55%; Table 3.1).

Due to some individuals moving from one patch type to another (three cases are illustrated in Figure 3.3) the 30 trails could be subdivided into 47 path segments each of which occurred in only one of the patch types. The duration of the path segments were highly skewed toward longer durations and, based on a Kruskal-Wallis test for a difference of medians, were significantly different between patch types ($\chi^2 = 10.3$, $d.f. = 2$, $p = 0.0058$) primarily due to the cutting patches having shorter duration path segments (Figure 3.4b). There were marginal differences between the measured displacements (straight-line distance between start- and end-points of the path segment) in the different patch types ($\chi^2 = 4.86$, $d.f. = 2$, $p = 0.088$) which this time were primarily driven by the path segments in goldenrod patches having shorter displacements (Figure 3.4a). Combining the two measures into a displacement rate blurred the distinction between the patch types ($\chi^2 = 2.783$, $d.f. = 2$, $p = 0.2486$). Next, I looked more closely at the movement behaviour within each of the patch types.

Duration of bouts of mobility and immobility

Many of the path segments showed temporal autocorrelation in the occurrence of horizontal displacement during a time-step. For netting and cut patches, path segments in general tended to have time-steps with movement and time-steps with non-movement events ordered significantly non-randomly (Figure 3.5), which necessitated the use of durations of bouts of mobility and immobility to describe whether an individual was moving or not. Within each patch type, mean duration of bouts of mobility were not significantly different nor were bouts of immobility (Scheffé's posthoc comparisons). The among path segment variability in the duration of both bouts of mobility and immobility were significant within cut patches (Bartlett's tests: $B_c = 36.6$ [where B_c has a χ^2 distribution (Zar 1996)], $d.f. = 13$, $p = 0.0005$ and $B_c = 35.1$, $d.f. = 17$, $p = 0.0006$ for mobility and immobility respectively). For the other two patch types there was no significant differences in among path segment variability of the length of bouts of mobility (goldenrod: $B_c = 13.1$, $d.f. = 9$, $p = 0.16$; netting: $B_c = 14.4$, $d.f. = 11$, $p = 0.21$) or immobility (goldenrod: $B_c = 9.88$, $d.f. = 11$, $p = 0.54$; netting $B_c = 15.2$, $d.f. = 12$, $p = 0.23$). This suggests that path segments within a patch type could be pooled to estimate the duration of bouts of mobility and immobility in that patch type.

There was no evidence of temporal autocorrelation in the duration of either bouts of mobility or immobility in any of the patch types (all 95% confidence intervals contained 0; Figure 3.6). This suggests that mobile and immobile bout duration data could be treated as statistically independent. In all patch types *T. borealis* individuals persisted in bouts of immobility longer than bouts of mobility (compare the scale of the x-axis for the two panels in Figure 3.7). Based on a survival analysis, there were

significant differences in the duration of bouts of both mobility and immobility among the different patch types (mobile: $\chi^2 = 7.65$, $d.f. = 2$, $p = 0.025$; immobile: $\chi^2 = 25.5$, $d.f. = 2$, $p = 0.0000$; Figure 3.7). Bouts of mobility lasted longer in cut patches than in the other two patch types while bouts of immobility lasted longer in goldenrod patches than the other two patch types.

Step-length

For all patch types, mean step-lengths per path segment were not significantly different among path segments (Scheffé's posthoc comparisons on log-transformed data). For both the cut and goldenrod patches, variances of log-transformed step-lengths were not significantly different among path segments (cut: $B_c = 16.9$, $d.f. = 18$, $p = 0.53$; goldenrod: $B_c = 8.50$, $d.f. = 11$, $p = 0.81$). The variances of step-lengths in the netting patches were significantly different among path segments ($B_c = 29.5$, $d.f. = 14$, $p = 0.009$) but removal of 3 path segments with extremely low variances left the remaining path segments indistinguishable ($B_c = 9.55$, $d.f. = 11$, $p = 0.57$). Since the step-lengths for these three path segments had both low variance and mean values near the overall mean I felt justified in pooling them with the other individuals.

For all patch types and all time lags, except for a time lag of 2 minutes in the cut patch, the weighted-mean temporal autocorrelations for step-lengths were not significant (95% confidence intervals contained 0; Figure 3.8). This suggests that it is reasonable to treat the step-lengths as statistically independent. Step-lengths in the three different patch types were significantly different (ANOVA on log transformed step-lengths: $F = 8.55$, $d.f. = 2$, $p = 0.0001$, $n = 635$; Figure 3.9). Surprisingly step-lengths in the cut patch were

the shortest. I tested a number of distributions and found that the gamma distribution fit the observed distribution of step-lengths best (Figure 3.10).

Turning angles

Some of the path segments in the cut patches were different from the others in terms of the distribution of turning angles ($W_r = 62.0$, $p = 0.001$ based on a randomization test with 1000 draws), but removal of two path segments with a stronger concentration of forward angles than the others removed this effect ($W_r = 40.8$, $p = 0.115$). There were significant differences among path segments in terms of turn angle distributions in goldenrod ($W_r = 43.1$, $p = 0.004$) that disappeared with the removal of a path segment with turn angles concentrated in the forward direction ($W_r = 18.1$, $p = 0.841$). There were no significant differences in the turn angle distributions among path segments in the netting patch ($W_r = 38.0$, $p = 0.085$), which suggests that the data could be pooled across individuals.

For all patch types and all time lags the weighted-mean autocorrelations for turning angles were not significant (95% confidence intervals contained 0; Figure 3.11). This suggests that the turning angles are statistically independent and can be treated so when describing them. For all patch types the mean turn angle was not significantly different from 0° , based on 95% confidence intervals, indicating that the beetles did not favour either left or right turns. Turn angles in the goldenrod patches were uniformly distributed both with ($V = 1.06$, $p > 0.15$; Figure 3.12) and without ($V = 1.45$, $p > 0.15$; Figure 3.12) the path segment that was different from the rest. Turn angles in the netting patch were also uniformly distributed ($V = 1.53$, $p > 0.15$; Figure 3.12). Turn angles in the cut patch were not uniformly distributed ($V = 3.05$, $p < 0.01$ for all path segments and

$V = 2.09$, $p < 0.01$ with the two different path segments removed) but were described by a von Mises distribution with a mean turning angle of 0° ($K = 0.42$; $U^2 = 0.04$, $0.25 < p \leq 0.5$ for all the path segments and $K = 0.25$; $U^2 = 0.12$, $0.05 < p \leq 0.1$ with the two different path segments removed; Figure 3.12). A von Mises distribution is unimodal (Batschelet 1981, Fisher 1993), so this indicates that the turning angles in the cut patches were concentrated in the forward direction, which would produce more directed, less tortuous movement than a uniform distribution.

Edge crossing behaviour, goldenrod detection, and emigration vs. density

I could not detect *T. borealis* to edges. In all the release experiments there were no significant differences between the number of individuals moving into the neighbouring patch and the number remaining in the original patch (Table 3.2). Also, I could not detect a response of *T. borealis* to distant goldenrod plants. The only significant response to the goldenrod plant during the releases in the arena was at 0.5 m and that was away from the goldenrod (Table 3.3). Nor did the beetles increase their emigration rate as density increased. A linear regression of the percent beetles remaining on the plant after 24 hours (arcsine transformed) against initial density was not significant ($F = 0.12$, $p = 0.74$, $n = 16$; Figure 3.13).

3.5 DISCUSSION

Movement behaviour of T. borealis

To a *T. borealis* individual a goldenrod patch represents both the presence of food resources and the presence of structural complexity. A typical *T. borealis* individual in a goldenrod patch has long bouts of immobility followed by short bursts of movement.

When moving through goldenrod individuals move relatively slowly and trace tortuous paths due to a high degree of turning. The overall impression then is of a beetle that hardly moves and when it does movements are brief, relatively slow, and produce twisted paths (Figure 3.3). This behaviour can be understood as a response aimed at maintaining contact with the food resource. The long bouts of immobility could be due to time spent feeding or processing a meal and therefore not moving. However, feeding was only observed during 10% of the immobile time-steps ($n = 1106$), and seems unlikely to be solely responsible for the duration of the bouts of immobility in goldenrod. Another possibility is a response to satiation or an adaptive response to decrease the amount of movement in order to remain in the food-plant patch. Along similar lines, the tortuous paths in the goldenrod patches will tend to maintain contact with the food patch. Both predatory (Kareiva & Odell 1987) and herbivorous (Root & Kareiva 1984, Visser 1988) insects have been shown to turn frequently to stay in contact with resources.

Cut patches are low in both food and structural complexity. As such, they are adverse environments for *T. borealis* individuals (no food), which should be relatively easy to move through (low complexity). A typical *T. borealis* individual in a cut patch has relatively longer bouts of mobility with shorter rests between. When moving, individuals travel more slowly and trace straighter paths in the cut patches than in the goldenrod patches. The overall impression then is of a beetle that sustains relatively slow, directed movements (Figure 3.3). The sustained bouts of mobility would seem to be an attempt to move out of the inhospitable cut patch; without food on hand the beetles cannot afford to sit still. Tracing straight paths by turning less also seems to be a good strategy to cross an inhospitable patch quickly. Even so, the concentration of turning

angles in the forward direction was not extreme; there was no detectable temporal autocorrelation in turn angle (Figure 3.11). The logical conclusion from this line of reasoning would be that the beetles should also move quickly (long step-lengths) to aid in moving through the inhospitable patch. Other species have shown this response to non-host plants (Bach 1980a, Turchin 1987, Elmstrom *et al.* 1988), predators, or unfavourable locations (Rijnsdorp 1980, Matter 1996, Charrier *et al.* 1997, Pither & Taylor 1998). But this was not observed in *T. borealis*; in fact step-lengths were significantly shorter in the cut patches than the goldenrod patches. This apparent inconsistency may have been in response to risk, or perceived risk, of predation. Cut patches lack the vertical structure that *T. borealis* have evolved to use in anti-predator defence, by dropping off the plants and into the litter where they are camouflaged (Messina 1982b), potentially leaving *T. borealis* individuals open to predation. Without their natural defence system in place, individuals may move slowly and cautiously to both avoid detection and allow them to detect predators in advance (Zollner & Lima 1999). However, this explanation is highly speculative, as I have only observed a single predation event, when a beetle wandered onto a spider web. Most of the natural enemies of *T. borealis* prey upon the larvae, and adults are known to be distasteful to vertebrates (Messina 1982b).

Netting patches are low in food, like the cut patches, yet high in structural complexity, like the goldenrod patches. As such, they may allow us to distinguish *T. borealis* responses to food from responses to structural complexity. A typical *T. borealis* individual in a netting patch has brief bouts of mobility, as in the goldenrod patches, with short rests between, as in the cut patches. When moving, individuals move faster but trace a more tortuous path than they do in the cut patches. The overall

impression then is of a beetle that has many brief bursts of fast, meandering movements (Figure 3.3). Bouts of mobility had similar durations in both netting and goldenrod patches. This suggests that the absence of food does not necessarily cause individuals to sustain longer bouts of mobility. However, bouts of immobility were shorter in the netting patches than in the goldenrod patches. This suggests that the beetles may respond to a lack of food by spending less time not moving which may compensate for not being able to sustain long bouts of mobility. In fact, average displacement rates in cut and netting patches, both of which lack food, are indistinguishable. Furthermore, the structural complexity of both the netting and goldenrod patches could play an important role in limiting the duration of bouts of mobility by interfering with horizontal displacement. If beetles were spending much of their movement time moving up and down structures some of the time-steps would result in no detectable displacement. These no displacement time-steps would break up the run of mobile time-steps thereby shortening the duration of bouts of mobility. There is some support for this “interference role” of structural complexity in that there were many time-steps where the beetles were observed to be actively walking but were only moving up and down stems (10% of immobile time-steps in goldenrod) or strands of camouflage netting (19% of immobile time-steps in netting). The structural complexity of the netting patches could also be thought of as a resource since *T. borealis* requires the vertical structure for their anti-predator defences. This could explain why beetles moved more quickly (longer step-length) through the netting patches; they did not feel threatened by risk of predation yet needed to move to find food. Netting patches caused beetles to trace tortuous paths, by inducing a high degree of turning. Since I also saw this behaviour in goldenrod patches

this suggests that the proximate cause of increased turning is actually the structural complexity of a patch. When there are vertical stems and dense vegetation the beetle is forced to take a more tortuous path even if, as is the case in the netting patches, it is presumably to the beetle's advantage to travel in a relatively straight line to move through the inhospitable patch. *T. borealis* may respond to structural complexity in two different ways: 1) as a physical barrier causing movements up and down and around vegetation, and 2) as a component of the anti-predator defence system. It was impossible to separate these possibilities in the current study. It would be interesting to see how insects with different defences respond to structural complexity in patches.

It would seem reasonable to expect *T. borealis* individuals to respond to the edges of goldenrod patches so as to increase the time they spend on their host-plant. I did not detect any response by the beetles to any of the edges. Other insects have shown behavioural responses to remain on host-plants or in host-plant patches (Jones 1977, Lawrence 1982, Wiens *et al.* 1995). These responses sometimes depend on the patch edge being distinct (Ralph 1977a, Kareiva 1985, Turchin 1986), but even the distinct edge between a goldenrod and a cut patch did not elicit any response from *T. borealis* individuals. There is probably only strong selection to remain in a host-plant patch for species that are either relatively sedentary, thus unlikely to move into another host-plant patch after leaving a patch (e.g., Dethier 1959), or are historically associated with a rare, and therefore difficult to find, plant species (e.g., Tabashnik 1980, Kareiva 1982, Lawrence 1982). After pre-ovipositional dispersal flights *T. borealis* usually settle into areas high in goldenrod and goldenrod tends to be common when it is found; thus there is no need to either remain in or quickly move into a goldenrod patch, as the chances are

good of running into another. Also, despite having a reduced ability to move after pre-ovipositional dispersal flights, *T. borealis* individuals are still vagile enough to easily move between goldenrod patches.

One might expect that *T. borealis* should be able to detect their host-plant from a distance as many herbivorous insects can (e.g., Moericke *et al.* 1975, Saxena & Saxena 1975, Smith 1976, McKibbin *et al.* 1977, Ralph 1977a, Hamilton *et al.* 1978, Rausher 1981, Visser 1988). *T. borealis* apparently could not detect goldenrod plants from as close as 5 cm. Furthermore, there were a few occasions when I observed individual beetles fall off of a goldenrod plant and immediately walk away from it (*personal observation*). Other insects have displayed this lack of ability to detect their host-plant (e.g., Dethier 1959, Price 1976, Cappuccino & Kareiva 1985, Fahrig & Paloheimo 1987). It is possible that *T. borealis* did not detect goldenrod from any distances for similar reasons that they do not respond to patch edges - the host-plant is so abundant that there is no need to seek patches; a randomly moving beetle will bump into a goldenrod patch rather quickly.

Finally, there was no apparent effect of beetle density on emigration from a potted goldenrod. It has been demonstrated that a congeneric, *T. virgata*, has pre-ovipositional dispersal (long-distance flying) rates that are density-dependent (Herzig 1995) but *T. borealis* post-ovipositional, or “trivial”, movement rates are not density-dependent. This could be due to a difference between species or the differences between dispersal and trivial movements. Though there are many reasons an animal might increase dispersal in the face of increased conspecific density - to avoid competition for resources, to increase mating success, to avoid inbreeding - these did not seem to be important for

T. borealis individuals at the densities tested. There may be effects of density on emigration at higher beetle densities, but the beetles were already being placed onto the plants at densities higher than any I had observed in the field and would rarely, if ever, occur in a natural population.

General hypotheses of insect herbivore movement behaviour

Based on the behaviour of *T. borealis* adults and reports of movement behaviour in the literature it is possible to suggest the following hypotheses about the role of landscape structural constraints on movement behaviour of insect herbivores:

- 1a) In patches of abundant food resources insects should move in short, infrequent bursts and, when moving, do so slowly while tracing tortuous paths.
- 1b) In landscapes where resource patches are rare insects should behave as in (1a) with the addition of increased detection distances for host-plants, and/or decreased chances of leaving a patch of host-plants, possibly by actively turning back from patch edges.
- 2) In response to increased structural complexity in a resource patch insect herbivores should move in short, infrequent bursts due to time spent navigating the plant structures and, when moving, trace tortuous paths due to having to thread their way through the vegetation.
- 3a) Where the patch does not match the insect's evolved anti-predator defence strategy (e.g., lack of structural complexity when it is necessary for the defence scheme) and contains no food resources, insect herbivores should display caution in terms of slower

movements. Paths should be as straight as possible to quickly move through the inhospitable patch.

- 3b) Where the patch matches the insect's evolved defence strategy but contains no food resources, insect herbivores should move with less caution and will therefore move faster, relative to (3a).

These hypotheses need to be tested across a broad spectrum of species in heterogeneous landscapes. This may be difficult due to the difficulties of measuring and then analyzing movement paths. The reward will be a greater understanding of the underlying mechanisms behind movement behaviour, thus allowing better predictions of how insect species might behave under novel conditions. One of the ways that landscape spatial structure might affect the survival of a species is through impacts on movement behaviour. If we understand environmental constraints on movement behaviour then we are closer to understanding the influence of landscape spatial structure on species persistence.

Table 3.1: Summary of observed beetle activity for all 30 individuals, as number (percent) of 30 second time-steps in which an activity was observed, both subdivided by patch type and for all observations. Every time step was scored as having either been predominately resting, flying, or walking. The total for these three categories is also presented. Additionally, flying and walking are combined, the detection of horizontal displacement is counted and the number (percent) of time-steps during which eating was observed is indicated.

	Resting	Flying	Walking	Total	Flying or walking	Disp.	Eating
Goldenrod	1000 (80.8)	17 (1.4)	220 (17.8)	1237 (100)	237 (19.2)	131 (10.6)	109 (8.8)
Netting	314 (60.4)	3 (0.6)	203 (39.0)	520 (100)	206 (39.6)	133 (25.6)	na
Cut	703 (62.3)	3 (0.3)	422 (37.4)	1128 (100)	425 (37.7)	381 (33.8)	na
All patch types	2017 (69.9)	23 (0.8)	845 (29.3)	2885 (100)	868 (30.1)	645 (22.4)	109 (3.8)

Table 3.2: Number of *T. borealis* released and then either remaining in the release patch or crossing an edge into a different patch (G = goldenrod, N = netting, C = cut). χ^2 values, and their associated p values, are calculated for the null hypothesis that the beetles do not respond to the edge.

Patch type		Number Released	Remaining	Crossing	χ^2	p
From	Into					
G	N	24	14	10	1.08	0.30
	C	26	16	10	1.39	0.24
N	G	22	10	12	0.18	0.67
	C	30	12	18	1.20	0.27
C	G	29	11	18	1.69	0.19
	N	25	10	15	1.00	0.32

Table 3.3: Number of *T. borealis* individuals that were released at three different distances and either detected or did not detect a goldenrod plant. χ^2 values, and their associated p values, are calculated for the null hypothesis that the beetles do not detect the goldenrod from a distance.

Distance (m)	Number Released	Detected	Not Detected	χ^2	p
0.05	31	15	16	0.032	0.86
0.50	33	10	23	5.12	0.024
1.00	33	17	16	0.030	0.86

Figure 3.1: Illustration of the three patch types: a) goldenrod patches, b) cut patches with camouflage netting suspended to a height of 50 cm, and c) cut patches. Patch types are arranged according to the food resources and structural complexity each represent for *T. borealis* individuals.

Figure 3.2: Illustration of the components of a *T. borealis* movement trail. The dashed line represents the trail traced out by the beetle. Open circles represent the points that were marked on the trail, with the numbers indicating how long the individual spent at that spot (in number of 30 second time-steps). Thus this path segment would consist of a bout of mobility that lasted for 2 time-steps, a 9 time-step bout of immobility, and a 3 time-step bout of mobility. The dotted line indicates how the turning angle (θ) is determined.

Figure 3.3: Typical movement trails for three *T. borealis* individuals. All trails were traversed during 50 minutes of tracking. The background colour of the trail indicates the patch type traversed (■ = goldenrod, □ = camouflage netting, □ = cut). Note the three trails are from different landscapes and have been arranged for clarity of presentation.

Figure 3.4: Box-whisker plots of a) path segment displacements, b) duration of path segments and c) path segment displacement rates in the three different patch types; cut ($n = 18$), goldenrod ($n = 17$), and netting ($n = 12$). Whiskers represent the range, the boxes represent the interquartile range and the horizontal lines indicate the median value.

Figure 3.5: Weighted-mean values of the normal deviates (Z_c) from the mobile/immobile runs tests and their associated 95% confidence intervals for the three patch types. Means and confidence intervals were determined using meta-analytic techniques. The numbers of path segments used to calculate the weighted-mean Z_c are also indicated. The horizontal dashed line indicates the critical value of Z_c for $\alpha = 0.05$.

Figure 3.6: Autocorrelation functions for the duration of bouts of mobility in a) goldenrod, c) netting, or e) cut patches and bouts of immobility in b) goldenrod, d) netting, or f) cut patches. Weighted-mean autocorrelation coefficients and their associated 95% confidence intervals are plotted against time lag (number of 30 s intervals). Dashed lines represent the minimum correlation necessary to be considered significant ($\pm 2/\sqrt{n}$ where n varies by time lag).

Figure 3.7: Cumulative proportion of a) mobile or b) immobile bouts lasting for increasing amounts of time from a life table analysis of all mobile (or immobile) bouts in each of the patch types. Standard errors are indicated. Note the different time scales for the mobile and immobile plots.

Figure 3.8: Autocorrelation functions for *T. borealis* step-lengths in a) goldenrod, b) netting, and c) cut patches. Weighted-mean autocorrelation coefficients and their associated 95% confidence intervals are plotted against time lag. Dashed lines represent the minimum correlation necessary to be considered significant ($\pm 2/\sqrt{n}$ where n varies by time lag).

Figure 3.9: Mean step-lengths and their associated 95% confidence intervals by patch type. Means with the same letter were not significantly different according to a Scheffé's test.

Figure 3.10: Distributions of the observed step-lengths in a) goldenrod, b) netting, and c) cut patches. Curves indicate the fitted gamma distribution (Kolmogorov-Smirnoff goodness of fit tests for goldenrod: $d = 0.0865$, $p = \text{n.s.}$, netting: $d = 0.1015$, $p < 0.15$, cut: $d = 0.0778$, $p < 0.05$).

Figure 3.11: Autocorrelation functions for *T. borealis* turn angles in a) goldenrod, b) netting, and c) cut patches. Weighted-mean autocorrelation coefficients and their associated 95% confidence intervals are plotted against time lag. Dashed lines represent the minimum correlation necessary to be considered significant ($\pm 2/\sqrt{n}$ where n varies by time lag).

Figure 3.12: Turn angle distributions for *T. borealis* in a) goldenrod, b) goldenrod but with 1 different path segment removed, c) netting, d) cut, and e) cut but with 2 different path segments removed. The solid lines are fitted distributions (either uniform or von Mises). The forward direction is indicated by 0 degrees. These are wrapped distributions and I have shown two full revolutions (as suggested by Fisher 1993) so each histogram represents twice the sample size.

Figure 3.13: Linear regression of arcsin transformed percent of beetles left on a potted goldenrod plant after 24 hours against the initial density. The best-fit line is indicated ($F = 0.12$, $p = 0.7373$, $n = 16$) and the points are scaled to the number of observations represented.

Chapter 4

HOW DOES MICROLANDSCAPE STRUCTURE INFLUENCE CONNECTIVITY? SIMULATION AND EMPIRICAL APPROACHES WITH A SPECIALIZED GOLDENROD BEETLE (*TRIRHABDA BOREALIS* BLAKE).

4.1 CHAPTER SUMMARY

I investigated the impact of landscape structure on landscape connectivity using a combination of simulation and empirical experiments. For the field experiments I utilized a specialized goldenrod beetle (*Trirhabda borealis*) in mosaic microlandscapes containing three kinds of patches: goldenrod patches, patches of cut vegetation, and patches of cut vegetation containing camouflage netting strung vertically to a height of 50 cm. Landscape connectivity was based on movements of individual beetles, and was measured in six different ways. The simulations revealed that the six measures of connectivity were influenced by different aspects of landscape structure, suggesting that: (1) connectivity is a poorly defined concept, and (2) the same landscape may have different connectivity values when different measures of connectivity are used. There were two general predictions that held over all measures of connectivity: (1) increasing interpatch distance significantly decreases connectivity and (2) the influence of matrix elements on landscape connectivity is insignificant in comparison to the influence of habitat elements. These simulation results were supported in the empirical tests.

4.2 INTRODUCTION

Rates of anthropogenic alteration to natural landscapes (e.g., cutting of forests, insertion of agricultural fields, damming of rivers, draining of wetlands) have increased markedly in the last century (Wilcove *et al.* 1986, Groom & Schumaker 1993). Destruction and alteration of habitat is a major cause of species extinctions and biodiversity loss (Wilcox & Murphy 1985, Groombridge 1992). Landscape alteration changes landscape structure by changing landscape composition (the amounts of various kinds of elements in the landscape) and/or landscape configuration (the spatial arrangement of elements in the landscape). Landscape alteration can be divided into three components: i) loss of habitat, ii) fragmentation of habitat, and iii) insertion of new kinds of, often inhospitable, landscape elements (e.g., farm fields, roads). Though these components are often related, they can be altered independently, and they may have very different independent effects. For example, habitat loss and fragmentation are often considered together as a single process (e.g., Wilcox & Murphy 1985, Wilcove *et al.* 1986, Herben *et al.* 1991, Robinson *et al.* 1992, Perry & Gonzalez-Andujar 1993, Diffendorfer *et al.* 1995, Holt *et al.* 1995, Schumaker 1996), because in many cases loss of habitat also leads to a larger number of smaller patches (i.e., fragmentation). However it is possible to lose habitat around the edges of patches and not change the degree of fragmentation (i.e., the number of patches in the landscape remains constant). When considered separately, the influences of habitat loss on population abundance and persistence appears to be greater than the influence of fragmentation (McGarigal & McComb 1995, Fahrig 1997, Trzcinski *et al.* 1999). Therefore, it is worthwhile to consider each component of landscape alteration separately.

Landscape alteration can have many impacts on populations – increased amounts of edge can alter microclimates (Chasko & Gates 1982, Saunders *et al.* 1991), predation/parasitism rates (Rolstad 1991, Paton 1994, Haskell 1995, Andrén 1995, Taylor & Merriam 1996, Nieuwirth & Boyce 1997), and competition (Saunders & Ingram 1987); reductions in amount of habitat can depress population levels (van Dorp & Opdam 1987, Robinson *et al.* 1992, Arnold *et al.* 1993, Kattan *et al.* 1994, Andrén 1994, Bender *et al.* 1998), making them susceptible to environmental and/or demographic stochasticity (Shaffer 1987, Burkey 1995). Problems due to landscape alteration are exacerbated by the fact that the rate of change is often much faster than can be accommodated by evolutionary adaptation (Fahrig & Merriam 1994). The ability of individuals to survive and populations to persist in the face of these challenges depends partly on the ability of individuals to move through human-modified landscapes. Movements through the landscape allow a species to mitigate detrimental edge effects, rescue local populations before they become extinct (Brown & Kodric-Brown 1977), recolonize local extinctions after they occur (Henderson *et al.* 1985, McCauley 1989, Roininen *et al.* 1993, Thomas 1994, Sutcliffe *et al.* 1997), or forage successfully over multiple habitat patches (Pyke 1978, Kozakiewicz 1995).

Not only does landscape alteration place a premium on the ability of organisms to move but it also makes movement more difficult. Habitat loss increases the distance between patches, decreasing patch accessibility to dispersing/moving organisms, even to the point of totally isolating patches if they are far enough apart. Matrix (non-habitat) elements displace habitat, but they also influence movement behaviour (Baars 1979, Rijnsdorp 1980, Wallin & Ekblom 1988, Hansson 1991, Johnson *et al.* 1992, Matter 1996,

Andreassen *et al.* 1996a, Charrier *et al.* 1997, Collins & Barrett 1997) and can increase the risk of moving (Gaines & McClellan 1980, Krohne & Burgin 1987, Fahrig *et al.* 1995, Schippers *et al.* 1996, Charrier *et al.* 1997, Sakai & Noon 1997), making habitat patches even harder to reach.

An organism's ability to move through a landscape is a function of both the organism's intrinsic movement biology (set by physiology and behaviour) and the extrinsic influence of the landscape structure. Merriam (1984) recognized that these two processes are inter-related and introduced the term "connectivity" to refer to the landscape property resulting from the interaction between landscape structure and the organism's movement behaviour. Landscape connectivity was later defined as "the degree to which the landscape facilitates or impedes movement among resource patches" (Taylor *et al.* 1993). A simulation experiment, parameterized for *Peromyscus leucopus*, showed that increasing the connectedness of habitat patches increases population persistence (Lefkovich & Fahrig 1985). The model is supported by empirical work that found lower population growth rates in *P. leucopus* populations in isolated woodlots (Fahrig & Merriam 1985). Furthermore, low quality connections (i.e., higher risk of mortality when dispersing) can depress the landscape-wide population (Henein & Merriam 1990), though this can be modulated by the degree to which the species is dependent upon corridors for movement (Henein *et al.* 1998). Understanding a landscape's connectivity, and how it is altered by landscape change, is essential for predicting how a species will respond to landscape change.

Altering landscape composition and configuration could influence connectivity through many different means. Loss of habitat will increase the separation of patches,

making them harder to access. Fragmentation will make patches smaller, making them harder to find. Also the shape of habitat patches (patch-size distribution, edge to area ratio) could influence connectivity by affecting the probability of finding a patch (Capman *et al.* 1990, Cappuccino & Root 1992, Matter 1996) or leaving a patch (Kareiva 1985, Stamps *et al.* 1987, Buechner 1987a). Matrix elements could play a role in landscape connectivity if they alter an organism's ability to move through a landscape. If particular matrix elements have different "resistances", that is they are harder or easier to move through, then the amounts of those elements in the matrix will influence connectivity (Knaapen *et al.* 1992). Some matrix elements may act as absolute, or relatively absolute, barriers (Merriam *et al.* 1989, Baur 1990, Mader 1990, Kozakiewicz 1993), thus restricting possible paths through the matrix and altering landscape connectivity. All of these effects depend on the individual's movement response to particular landscape elements.

Though there has been increasing interest in landscape connectivity, we are still a long way from being able to synthesize general relationships between connectivity and landscape structure. Part of the problem has been a lack of consensus on just how to measure connectivity (Table 1.1; Tischendorf & Fahrig 2000). There have been many different approaches to connectivity research, some focusing on habitat characters such as contagion and percolating clusters (Green 1994, With *et al.* 1997, Metzger & Décamps 1997, Tiebout & Anderson 1997, Keitt *et al.* 1997) while others have focused on organism movements (Doak *et al.* 1992, Demers *et al.* 1995, Gustafson & Gardner 1996, Schumaker 1996, Schippers *et al.* 1996, Ruckelshaus *et al.* 1997, Pither & Taylor 1998). Also, simulation and empirical approaches tend to use different connectivity metrics. For

example, connectivity has been measured as dispersal success (Demers *et al.* 1995, Gustafson & Gardner 1996, Schumaker 1996, Schippers *et al.* 1996, Ruckelshaus *et al.* 1997) and search time (Doak *et al.* 1992) in simulation studies and as re-observation after displacement (Pither & Taylor 1998) in empirical work. There is a need to make the links between different measures of connectivity to allow for comparisons both between simulation and empirical studies and between different empirical systems.

The first goal in this Chapter was to investigate the relationships between landscape structure and measures of landscape connectivity. I did this using a combination of simulation and empirical experiments. Simulation experiments allowed me to investigate more landscape descriptors and vary landscape structure over a wider range than was possible in the field. The second goal was to compare different measures of connectivity. This was achieved by calculating six different measures of connectivity during each simulation run, and two of those measures during each empirical run. The different measures were then compared in terms of their responses to landscape structure. All simulations were based on empirically determined movement behaviour for the goldenrod specialist beetle *Trirhabda borealis* (see Chapter 3 for the natural history of the system and a description of the movement behaviour) in mosaic microlandscapes containing three kinds of patches: goldenrod patches, patches of cut vegetation, and patches of cut vegetation containing camouflage netting strung vertically to a height of 50 cm (Figure 3.1).

4.3 METHODS

I assessed the influence of landscape structure on landscape connectivity using three experiments. The first was a simulation experiment to assess the influence of habitat amount and configuration on connectivity (Figure 4.1). The second was a simulation experiment primarily to assess the influence of matrix composition and configuration on connectivity, but this experiment also included the aspects of habitat structure identified as important in the first (habitat only) experiment (Figure 4.2). It was necessary to split the simulations examining habitat and matrix structure into two experiments because otherwise there would have been too many parameters and the model runs would have taken too long (Fahrig 1991). The third experiment was a combination of simulation and empirical experiments that tested the main predictions from the first two experiments (Figure 4.3). Since I could not test as many aspects of landscape structure in the field as I could using simulations, I identified the most important aspects of microlandscape structure from the first two experiments, performed simulations focused on the identified landscape attributes, and then tested the hypotheses generated by that set of simulations with mark-release-resight experiments in the field.

Simulations of T. borealis inter-patch movement

All the simulations were conducted in two stages: 1) generation of the microlandscapes and 2) simulations of individuals moving through the microlandscapes. Virtual microlandscapes were generated using algorithms that manipulated microlandscape composition and configuration (see Table 4.2 for the parameters and algorithms for the habitat simulations and Table 4.7 for the matrix simulations). A stochastic, individual-based simulation model then moved virtual beetles through the

microlandscapes based on empirically determined movement behaviour (see Chapter 3 for details of movement behaviour).

All virtual microlandscapes were based on square grids of 10 by 10 cells, where each cell represented 0.25 m^2 and the entire microlandscape represented a $5 \times 5 \text{ m}$ area. The virtual microlandscapes for the habitat simulation experiment were created as follows. 1) The amount of goldenrod was set. 2) The number of goldenrod patches was set. 3) The size distribution of the habitat patches was determined. 4) The location for the first cell of the first habitat patch was chosen randomly. 5) The patch was placed on the microlandscape using a self-avoiding random walk to select the habitat cells for that habitat patch. The shape of the patch was determined during this process by a) the number of steps in the random walk (set by the patch size) and b) the chance of the random walk turning, which was varied to give more or less edge by having less or more turning. 6) To ensure that patches did not coalesce, a 1-cell buffer was placed around the patch. 7) After the habitat patch was placed, the random walk jumped a set distance, determined by a distance parameter and distance variance parameter, in a random direction, to select the first cell of the next patch. If a habitat patch could not be placed there then the microlandscape generator systematically searched for a suitable location at that distance. Steps 5) through 7) were repeated, jumping from newly completed patch to the next patch, until all the habitat patches were placed in the microlandscape. If at any time the microlandscape generator could not fit a habitat patch into the microlandscape it would back-track (removing habitat patches) until all of the patches fit. Microlandscapes for the matrix experiment were created in a similar manner except the arrangement of habitat patches was determined ahead of time (see Figure 4.2) and the matrix patches

were placed using the procedure above, with the difference that matrix patches started at randomly chosen points in the microlandscape (the random walk did not jump a set distance between each patch). This approach to generating microlandscapes produced slightly different values for landscape indices (e.g., coefficient of variation [CV] for patch sizes, edge to area ratios, mean interpatch distance, CV of interpatch distance) even given the same parameters for the algorithms, so once the landscapes were created the indices were measured and these measures of landscape structure were used in subsequent analyses. Finally, microlandscapes for the third experiment were created by setting the pattern of habitat ahead of time (see Figure 4.3) and randomly placing the cells for the least common matrix element.

Virtual beetles were then moved through each of the virtual microlandscapes. One hundred individuals were randomly placed in goldenrod patches in the microlandscape; for placement of individuals each microlandscape cell was further subdivided into 100 sub-cells, so in essence the microlandscape was a 100 by 100 sub-cell grid, where each sub-cell represents an area of 0.0025 m^2 . Movements were modeled using empirically determined movement parameter distributions (duration of movement or non-movement events, step-length, and turning angles; see Chapter 3 for methods and distributions) in a vector-based movement model. The movement model kept track of movement state (moving or not) and kept an individual in that state for a duration drawn from the empirically determined distribution. If the individual was moving, a turning angle and step-length were randomly chosen from element-specific distributions (see Chapter 3 for distributions). Movements were modeled using a 30 second time step. Models ran for a total of 5800 time steps, approximately equivalent to four 12 hour days in the empirical

system. During movements each individual was tracked and data for calculating connectivity indices were tabulated (Table 4.1), however for the third set of simulations connectivity was determined in the same manner as the field tests (see below). Microlandscape edges were tiled, so the surrounding landscape was like the focal microlandscape (Figure 4.4), except for the third set of simulations where the area surrounding the focal landscape was treated as cut matrix to emulate the cut buffer strips (see below) in the field study. Only movements in the focal microlandscape were counted toward connectivity measures.

Empirical test of model results

Microlandscapes for the field tests were 5 x 5 m squares consisting of 100 0.25 m² cells. Four microlandscapes were constructed at each of 4 sites in an old field south of Ottawa, Canada. Over the course of the field season (July 28 to September 9, 1997) each unique type of microlandscape (see Figure 4.3) was replicated 4 times ($n = 64$). To do this I ran 2 sequential replicates, 16 microlandscapes per replicate, at 16% goldenrod and then cut the goldenrod back to 4% and ran two more replicates. Microlandscapes were created in the field by cutting natural vegetation and leaving goldenrod patches uncut. The netting matrix patches were then created in the cut areas of the microlandscapes by stringing camouflage netting from corner to opposite corner of each netting cell. Netting was strung such that the top of the netting was suspended approximately 50 cm above the ground. As the netting was between 1 to 1.3 m in width this created a vertical panel of suspended netting (emulating the structure of standing vegetation) with the rest of the netting piled in the cell (emulating the structure of plant litter and ground-cover vegetation). At each site all the natural vegetation between microlandscapes, which were

separated by a minimum of 1 m) and a minimum 1 m buffer around the 4 microlandscapes was also cut. Between releases of beetles, any re-growth of vegetation in the cut or netting patches was trimmed back.

After *T. borealis* had finished pre-ovipositional long-distance dispersal (Messina 1982c) and had been observed engaged in short-distance, “trivial”, movements they were captured, marked by dusting with fluorescent powder, released into goldenrod patches, and their movements monitored. Into each microlandscape, 25 fluorescent-powder dusted beetles were released in a single goldenrod patch. I used a different colour of powder for each microlandscape at a site, so movements from a neighbouring microlandscape could be detected and not influence measures of movement within a particular microlandscape. The 4 sites were separated by a minimum of 50 m of old field vegetation, so the chance of beetles moving between sites was remote. Beetles were released in a small paper bag and allowed to find their own way out to allow any effect due to handling to have a minimal influence on their movements. Any beetles that had not left the paper bag by the first night of searching were removed at night when they are sluggish and unresponsive. For four nights following release the goldenrod patches in the microlandscapes were searched using a hand-held UV lamp. The numbers of beetles in each patch or cell were recorded.

I used the observed distributions to estimate cell or patch immigration rates as a measure of connectivity. I estimated immigration rates by determining the number of detectable immigration events, either at a patch or a cell level. This was done by comparing the number of observed beetles in a patch or cell to the number previously observed in that patch or cell. For both simulations and field tests there was an initial

release followed by four subsequent observations, spaced a day apart. To allow for a direct comparison of the simulation and empirical tests I calculated connectivity in exactly the same way in the field and in the simulations preparing for the field. I will refer to this measure of immigration as estimated immigration to distinguish it from the first two simulations where all immigrants were known absolutely.

4.4 RESULTS

The mean ($\pm$ standard deviation) and maximum displacement (distance from start-to end-point) across all individuals in a landscape were 3.63 ± 0.31 m and 4.65 m for the first simulation experiment (habitat only), 3.46 ± 0.37 m and 4.41 m for the second simulation experiment (primarily matrix structure), and 3.30 ± 0.51 m and 4.94 m for the third simulation experiment (predictions for field tests). Since individuals were not tracked during the empirical releases and only the microlandscapes were searched for marked individuals it was impossible to determine displacement values for the released beetles.

Habitat simulation experiment

Correlations among the landscape variables are shown in Table 4.3. Each of the six different measures of connectivity (Table 4.1) was regressed against the six landscape variables (Table 4.2); for patch based measures of connectivity, mean interpatch distance was used while for cell based measures mean intercell distances were used. Huge sample sizes gave such strong statistical power that calculated p -levels were uninformative, so the relative importance of each microlandscape variable was assessed using partial correlations. For all the measures of connectivity, except patch immigration, landscape

structure explained much of the variation in connectivity - R^2 for the overall model ranged from 0.85 to 0.94 except for patch immigration where $R^2 = 0.58$ (Table 4.6a), indicating strong relationships between connectivity and microlandscape structure.

Distance, either between goldenrod patches or goldenrod cells, was almost always important. Interpatch distance had the strongest influence on connectivity, based on partial correlation values, when connectivity was measured as patch transition probability (partial $r = -0.726$, Table 4.4a) or patch immigration (partial $r = -0.649$, Table 4.6a) and was the second most important variable when connectivity was measured as patch visits per individual (partial $r = -0.545$, Table 4.5a). Intercell distance was not as important for cell-level measures of connectivity; it was the second most important variable for connectivity measured as cell transition probability (partial $r = -0.341$, Table 4.4b) and cell immigration (partial $r = -0.690$, Table 4.6b) and fourth most important for cell visits per individual (partial $r = -0.293$, Table 4.5b). In all cases though, no matter what the relative importance, increasing distance decreased connectivity.

The variance in the distance between goldenrod patches was always less important than the mean distance itself (see Tables 4.4-4.6). Additionally, with the exception of patch transition probability (partial $r = -0.638$, Table 4.4a) and cell visits per individual (partial $r = -0.175$, Table 4.5b), the greater the variance in either between patch or cell distances, the larger the connectivity measures (CELPB: partial $r = 0.243$, Table 4.4b; PATVISIT: partial $r = 0.370$, Table 4.5a; PATIMM: partial $r = 0.332$, Table 4.6a; CELIMM: partial $r = 0.250$, Table 4.6b).

The amount of goldenrod in the landscape was relatively important for all of the cell-level measures of connectivity. Cell transition probability and cell immigration

declined as goldenrod increased while cell visits per individual increased as goldenrod increased (CELPB: highest partial r of -0.605 , Table 4.4b; CELVISIT: second highest partial r of 0.571 , Table 4.5b; CELIMM: third highest partial r of -0.622 , Table 4.6b). The amount of goldenrod in the microlandscape had a relatively small, yet positive, effect on all of the patch-level measures of connectivity (PATPB: partial $r = 0.211$, Table 4.4a; PATVISIT: partial $r = 0.090$, Table 4.5a; PATIMM: partial $r = 0.278$, Table 4.6a).

The number of goldenrod patches in the microlandscape was only really important when connectivity was measured as patch visits per individual (highest partial r of 0.816 , Table 4.5a). In this case connectivity actually increased when the goldenrod in the microlandscape was more fragmented. There was a similar, though weaker, effect when connectivity was measured as cell immigration (partial $r = 0.457$, Table 4.6b). Number of goldenrod patches was also moderately important, though in the opposite direction, when connectivity was measured as patch transition probability (partial $r = -0.301$, Table 4.4a). For the three remaining measures of connectivity the number of goldenrod patches was the least important measure of microlandscape structure.

The edge to area ratio of the goldenrod in the microlandscape had the strongest influence on connectivity when measured as cell visits (partial $r = -0.666$, Table 4.5b) and cell immigration (partial $r = -0.718$, Table 4.6b). In these two cases increasing the amount of edge caused connectivity to decline. For all the other measures of connectivity the goldenrod edge to area ratio was not as important but had a positive relationship indicating that more edge in the microlandscape increased connectivity (PATPB: partial $r = 0.181$, Table 4.4a; PATVISIT: partial $r = 0.068$, Table 4.5a; PATIMM: partial $r = 0.289$, Table 4.6a; CELPB: partial $r = 0.174$, Table 4.4b).

Finally, the goldenrod patch size distribution had at most a moderate influence on connectivity. Both the cell transition probability (partial $r = -0.243$, Table 4.4b) and patch visits (partial $r = -0.289$, Table 4.5a) decreased as the patches became less uniform in size (increasing patch size coefficient of variation). When connectivity was measured as cell visits less uniformly sized patches increased connectivity (partial $r = 0.296$, Table 4.5b). For the remaining measures of connectivity the relationship with goldenrod patch size distribution was weak.

Matrix simulation experiment

Based on their relative importance in the first simulation experiment (above) I chose to retain interpatch distance, amount of goldenrod, and number of goldenrod patches in the matrix simulation experiments. Goldenrod edge to area ratio was also a candidate to be included due to its important effects on cell visits and cell immigration but in order to manipulate matrix structure the amount of goldenrod in the microlandscape had to be relatively low, which precluded any reasonable manipulation of edge to area ratios. See Table 4.7 for a list of landscape indices investigated. Unlike the habitat simulation microlandscapes, there was little correlation among the landscape indices for the matrix simulations, with the exception of amount of goldenrod and goldenrod edge to area ratio ($r = -0.91$, Table 4.8) and the matrix dispersion and edge to area ratios ($r = -0.78$, Table 4.8).

Matrix configuration (matrix dispersion, matrix patch size distribution, and matrix edge to area ratio) had no impact on any of the six measures of connectivity (absolute value of all partial r 's < 0.013 , Tables 4.9-4.11). Matrix composition (proportion of matrix as net) was the only aspect of the matrix that had even a minimal impact on

connectivity. For all six measures of connectivity increasing the amount of netting in the matrix decreased connectivity, but this effect was weak in all cases (absolute value of all partial r 's < 0.125).

In most cases measures of habitat arrangement influenced connectivity in the same manner for the matrix simulation experiments as in the habitat simulation experiments. The major exception to this was that the amount of goldenrod in the microlandscape was often correlated in the opposite direction than it had been in the first experiment. This was due to the fact that increasing the amount of habitat also decreased the edge to area ratio ($r = -0.91$, Table 4.8). Therefore, changing the amount of goldenrod also caused edge to area ratio effects.

The habitat and matrix simulation experiment results clearly show that the six different measures of connectivity respond to different aspects of microlandscape (primarily habitat) structure. For example, connectivity measured as either patch transition probability or patch immigration was influenced mostly by interpatch distance, cell transition probability was influenced most by amount of goldenrod, patch visits was influenced most by the number of goldenrod patches, and both cell visits and cell immigration were most affected by goldenrod edge to area ratio. Furthermore, the relationships between the measures of connectivity were anything but clear: some measures showed almost no apparent relationship (e.g., connectivity measured as cell immigration vs. connectivity measured as patch immigration; Figure 4.6), some had relationships that varied as some aspect of the microlandscape varied (e.g., linear relationships between cell visits and cell immigration that change slope as the amount of habitat changes; Figure 4.7), and some had more complex relationships that changed as

the microlandscape changed (e.g., a curvilinear relationship between the patch transition probability and patch immigration that breaks down as the number of patches increases; Figure 4.8).

Simulation and empirical tests of predictions

To prepare for the field tests I chose the important measures of microlandscape structure from the first two sets of experiments, namely amount of goldenrod, number of goldenrod patches, distance between patches, and the amount of the matrix in the netting element. Distance had an important and consistent influence on both patch and cell immigration. Both amount of goldenrod and number of patches were important either directly or as surrogates for edge to area ratios when this was not controlled for in the matrix simulation experiments. Finally, the composition of the matrix (proportion in net) was the only aspect of matrix structure that was predicted to have any influence on either patch or cell immigration. I measured connectivity as estimated immigration at either the cell or patch level, as those were the only two measures of connectivity I could measure in the field.

Estimated patch immigration was consistently lower in the field releases than in the simulations (Kruskal-Wallis test: $\chi^2 = 49.5$, $d.f. = 1$, $p = 0.0000$). However, the impact of all four of the landscape parameters on patch immigration remained the same (). A similar pattern was observed for cell immigration. This suggests that though detection in the field was well below that capable in the computer simulations this did not alter the detected pattern of response to landscape structure.

The simulation results for connectivity measured as estimated patch immigration produced the following hypotheses (based on results from the ANOVA; Table 4.12a):

i) increasing the amount of goldenrod should increase estimated patch immigration, ii) increasing the number of patches should decrease estimated patch immigration, iii) increasing the distance between goldenrod patches should decrease estimated patch immigration, and iv) changes to the amount of netting in the matrix should have no detectable effect on estimated patch immigration rates. Additionally, there were significant interactions terms suggesting that increasing the amount of goldenrod should increase the effect of the number of goldenrod patches and decrease the effect of distance while increasing the number of patches will decrease the effect of distance on estimated patch immigration rates. All of these predictions agreed with the simulation results from the first two experiments. For the empirical tests I first removed the effects of the significant covariates, site location and within-site microlandscape location, since all the southerly sites and all the microlandscapes that were southerly within their site had higher patch immigration. The ensuing ANOVA revealed the only significant aspects of landscape structure to be distance between goldenrod patches and number of goldenrod patches. However, with the exception of number of patches, all of the microlandscape variables influenced patch immigration in the same direction as they did in the simulations (Table 4.12b). Only the interaction between goldenrod and number of patches acted in a different direction in the field tests than the simulation.

Similarly, the simulation results for connectivity measured as estimated cell immigration produced the following hypotheses (based on ANOVA results; Table 4.13a): i) increasing the distance between goldenrod patches should decrease estimated cell immigration, ii) increasing the number of habitat patches should decrease estimated cell immigration rates, and iii) changes to either the amount of goldenrod or the amount of

netting should have no detectable effect on estimated cell immigration. Additionally, there were significant interaction terms suggesting that increasing the amount of goldenrod should decrease the effect of both distance and number of goldenrod patches on estimated cell immigration. All of these predictions agreed with the simulation results from the first two experiments. As with connectivity measured as patch immigration, I began analyzing the empirical results by removing the effects of the significant covariates, site location and within-site location, since the southerly sites had higher cell immigration and the southwest microlandscape at each site had higher cell immigration. The ensuing ANOVA revealed that number of goldenrod patches, distance between patches, amount of netting in the matrix, the interaction between amount of goldenrod and number of patches, and the interaction between amount of goldenrod and distance were significant and all of the microlandscape variables influenced cell immigration in the same direction as they did in the simulations (Table 4.13b). The only discrepancy between the field tests and the simulations was a significant, negative effect of amount of netting on estimated cell immigration in the field, which was not significant in the simulations. However, in both cases netting had a negative effect on estimated cell immigration.

4.5 DISCUSSION

The influence of spatial patterning of habitat on connectivity

It is no surprise that distance was the most consistent and, as far as patch-level measures were concerned, strongest influence on connectivity. If patches are further apart they will be harder to move between. Distance has played a prominent role in theoretical

constructs such as island-biogeography (MacArthur & Wilson 1967) and metapopulation models (Hanski & Simberloff 1997). Also, effects of isolation on patch population levels have been detected in many empirical systems (van Dorp & Opdam 1987, Laan & Verboom 1990, Sjögren 1991, Dunning *et al.* 1995, Mills 1995, Vos & Stumpel 1995). To try to improve the relationship between interpatch distance and connectivity some researchers have added various weighting factors to account for the resistance to movement of the intervening areas (Knaapen *et al.* 1992, Petit & Burel 1998a), though the improvement can be quite small (Petit & Burel 1998a). In light of increasing anthropogenic habitat loss, which increases habitat isolation, an interesting question to ask is: can other aspects of landscape structure mitigate the effect of isolation? The answer, based on these simulations, appears to be not really, although for cell level measures of connectivity distance effects were secondary to the effect of habitat edge to area ratios.

It is common to interpret effects of patch isolation as fragmentation effects (Dodd 1990, Robinson *et al.* 1992, van Apeldoorn *et al.* 1992, Celada *et al.* 1994), though it has been argued that isolation is really an effect of habitat loss (Fahrig 1997). It is hard to imagine how habitat can be fragmented without increasing isolation by at least the minimum separation necessary to distinguish two patches in a landscape. On the other hand, habitat loss is necessary for patch isolation (there must be empty space to spread the patches out in). For the matrix simulations, amount of goldenrod, number of goldenrod patches, and interpatch distance were varied essentially independently (Table 4.8). In those simulations, at least for the patch level measures of connectivity, interpatch distance always had the strongest, negative effect on connectivity; the amount and

fragmentation of the goldenrod was not always important and sometimes acted in the opposite direction than was expected. This suggests that isolation alone has an important, negative effect on landscape connectivity and it does not matter whether that isolation is due to habitat loss or fragmentation. It follows that measures that decrease isolation, corridors (Merriam 1991b, Noss 1993, Rosenberg *et al.* 1998), stepping-stones (Potter 1990, Arnold *et al.* 1993), relocation programs (McCullough 1996) or habitat restoration (Holland *et al.* 1991, Fedorowick 1993), all have the potential to increase connectivity. Connectivity will only be increased though if the mitigation measure actually decreases isolation for the organism (e.g., individuals actually travel through corridors), which is rarely established (Hobbs 1992, Rosenberg *et al.* 1997).

The terms habitat loss (reducing the amount of habitat) and fragmentation (increasing the number of patches) have been used interchangeably in the literature, and many authors think of the two as being a single process (e.g., Wilcox & Murphy 1985, Wilcove *et al.* 1986, Herben *et al.* 1991, Robinson *et al.* 1992, Perry & Gonzalez-Andujar 1993, Diffendorfer *et al.* 1995, Holt *et al.* 1995, Schumaker 1996). It has been argued that the two should be separated (Fahrig 1997, Fahrig 1998). Both Trzcinski *et al.* (1999) and McGarigal and McComb (1995) separated the effects of habitat (forest) fragmentation and loss in actual landscapes and both studies found that habitat loss had a much stronger effect than fragmentation on bird species presence/absences or abundances. Using an individual-based, spatially explicit simulation model, which separated the effects of amount and fragmentation, Fahrig (1997) found amount of habitat had a greater effect than fragmentation on extinction probability. Similarly, the connectivity measures that I investigated responded differently to habitat loss and fragmentation, with most influenced

more strongly by amount of habitat than fragmentation, suggesting that the distinction between amount and fragmentation can be important. These simulation results tend to contradict the notion that arrangement of habitat could, to some degree, mitigate against detrimental effects of habitat loss (Kareiva & Wennergren 1995).

Intuition suggests that habitat fragmentation should reduce connectivity since fragmenting a set amount of habitat will reduce the average patch size. Smaller patches may be more difficult for moving organisms to find (Kareiva 1985, Capman *et al.* 1990, Matter 1996). Most measures of connectivity responded accordingly, but patch visits and cell immigration actually increased with fragmentation. This was particularly evident with patch visits, as number of patches was the most important measure of landscape structure. Patch visits increased with fragmentation since more patches offer more opportunities for individuals to visit new patches, thus fragmenting habitat would inflate the mean number of patches visited per individual.

Measuring connectivity at the patch-level has the paradoxical effect that a landscape with only a single large patch of habitat has no connectivity, because individuals cannot move to any new patches. This contradicts the usual notion that declining connectivity is associated with a degrading landscape. Measuring connectivity at the cell-level, particularly cell-immigration, has been suggested as a potential solution to this paradox (Tischendorf & Fahrig 2000). However, in my habitat simulations (first experiment), cell immigration and cell transition probability strongly declined as habitat amount increased. This is counter-intuitive, as landscape connectivity should decrease with habitat loss since it will become harder for moving individuals to find habitat when there is less of it in the landscape. This is due to a combination of movement behaviour in

habitat and dilution of individuals with increasing habitat amount. Individuals in goldenrod patches move infrequently in short bursts of tortuous, relatively slow movements (see Chapter 3). If there is more habitat in the landscape then beetles will be more likely to spend time in habitat and the average time spent in habitat during the habitat simulations does increase with increasing habitat ($r = 0.96$). Spending more time in habitat will slow individuals down due to their movement behaviour in goldenrod. The average time spent moving during the habitat simulations does decrease with increasing habitat ($r = -0.96$). In addition, cell immigration was calculated by averaging the number of immigration events across all cells. If the number of beetles is held constant and their movement behaviour is not influenced by the habitat then cell immigration would decline just because there is more habitat. This dilution effect is confirmed by the fact that the mean number of cell visits, which is not averaged over cells but individuals, increases as habitat amount increases. The counter-intuitive decline in cell immigration with increasing habitat amount argues against the use of cell immigration as it fails to detect landscape degradation. Interestingly, this result was also observed in another simulation model (Tischendorf & Fahrig, *unpublished manuscript*).

Cell-immigration increased as habitat amount increased in my matrix simulations (second experiment) and the empirical releases, opposite what occurred in the habitat simulations (first experiment) and Tischendorf & Fahrig's model (*unpublished manuscript*). A major difference between the two sets of experiments was that the habitat simulations, and Tischendorf & Fahrig's model (*unpublished manuscript*), allowed the shape of the habitat patches to vary while the matrix simulations and empirical releases fixed the habitat in rectangular patches, which caused the amount of habitat to be

strongly, negatively correlated with habitat edge to area ratio. This caused low amounts of habitat to occur as a few single-cell patches while high amounts of habitat occurred as a few multi-cell patches. In the low habitat case all habitat cells were non-contiguous while in the high habitat case there were at least a few other habitat cells contiguous with any habitat cell. Thus, in the case of fixed patch shapes reducing habitat to a low enough amount will spread all the habitat cells apart and reduce the number of immigrants into each habitat cell as any immigrant will have to traverse matrix.

Changes to habitat configuration can also occur via changes to patch size distributions (O'Neill *et al.* 1988, Riitters *et al.* 1995, Gustafson 1998). Patch-based measures of connectivity did not seem to respond to habitat patch size variability, but cell-based measures did. Number of cell visits and cell immigration rates declined as patches became more uniform. This was probably because when there were a few large patches individuals could relatively easily move between many cells in that large patch despite being slowed by their movement behaviour in goldenrod. These within-patch movements would inflate either the average number of cells visited per individual or the average number of immigrants per cell. This would suggest that maintaining heterogeneity in the landscape, especially regarding patch sizes, would increase connectivity. In contrast, cell transition probability increased as patches became more uniform in size and shape. This difference is most likely due to the cell transition probability weighting each possible cell-to-cell movement equally, such that any isolated, single-cell patch that is unlikely to exchange individuals with other cells will contribute extremely low probabilities of exchanging individuals with all the other cells. This large number of low values will depress the average cell transition probability over the entire

landscape. Increased chances of moving within the few large patches will not offset the many low probabilities due to isolated, single-cell patches as only the transition probabilities for pairs of cells in the patch will be increased.

The influence of spatial patterning of matrix elements on connectivity

There has been little work on the influence of matrix composition and, particularly, configuration on movements between habitat patches. There are suggestions that matrix characteristics can be important since different matrix elements have been shown to function as barriers to movement (Mader 1984, Merriam *et al.* 1989, Baur 1990, Mader 1990, Kozakiewicz 1993), influence movement behaviour (Baars 1979, Rijnsdorp 1980, Wallin & Ekblom 1988, Hansson 1991, Johnson *et al.* 1992, Mauremooto *et al.* 1995, Matter 1996, Andreassen *et al.* 1996a, Charrier *et al.* 1997, Collins & Barrett 1997), and cause different mortality rates (Gaines & McClenaghan 1980, Krohne & Burgin 1987, Fahrig *et al.* 1995, Schippers *et al.* 1996, Taylor & Merriam 1996, Charrier *et al.* 1997, Sakai & Noon 1997). Corridors could be viewed as matrix elements that aid in movement (Saunders & Hobbs 1991, Noss 1993, Rosenberg *et al.* 1997). It would seem reasonable then for the patterning of landscape matrix to affect landscape connectivity. At a minimum, as the matrix becomes more difficult to move through, due to increasing proportions of impervious matrix elements, connectivity should decline (Knaapen *et al.* 1992). In fact, theoretical formulations of the idea of connectivity seem to focus almost exclusively on the influence of the matrix (Merriam 1984, Taylor *et al.* 1993). However, my simulations and field studies found little effect of matrix composition and no effect of matrix configuration on landscape connectivity. The lack of any effect of matrix configuration suggests that we only need to know the proportion of

the matrix made up of a particular patch type and not the spatial arrangement of those matrix elements.

The simulations and field tests may have failed to find much effect of matrix structure on landscape connectivity because matrix structure might influence connectivity through means other than movement behaviour within matrix elements. Matrix structure may influence connectivity through its effects on edge crossing behaviour and/or mortality, components that were not present in the simulations or the *T. borealis* field test (Chapter 3). The way an organism responds to edges influences patch residence times (Kareiva 1985, Turchin 1986, Stamps *et al.* 1987, Buechner 1987a) and movement through corridors (Soulé & Gilpin 1991, Tischendorf & Wissel 1997), so it would seem reasonable to expect that matrix elements that influence edge crossing behaviour might have significant impacts on connectivity. Note, however, that another simulation model, which altered edge-crossing behaviour in the matrix, found only weak influences of matrix composition and configuration on connectivity measured as cell immigration (Tischendorf & Fahrig, *unpublished manuscript*). Similarly, different risks of mortality in different matrix elements should change connectivity, since movements will terminate with mortality events and movement behaviour can change in response to predation risk (Lima & Dill 1990, Sakai & Noon 1997, Zollner & Lima 1999). While not investigating connectivity *per se*, using a simulation experiment Fahrig (2000) found that varying mortality risk in the matrix had an important influence on extinction risk and in fact was more important than habitat fragmentation, suggesting that the importance of the matrix can be increased by considering mortality. Further investigation of the necessary conditions for the landscape matrix to influence connectivity would be fruitful.

How should connectivity be measured?

These simulation and empirical experiments demonstrated that different measures of connectivity respond to different aspects of landscape structure, and in some cases will respond differently to the same aspect of landscape structure. Currently there is no broadly accepted metric of connectivity and many different metrics have been used in the literature. Some authors have focused on describing landscape patterns as measures of connectivity (number and/or arrangement of corridors Lefkovitch & Fahrig 1985, Henein & Merriam 1990, Hess 1996b, Gonzalez *et al.* 1998, Browne *et al.* 1999; habitat spatial contagion Green 1994, With *et al.* 1997, Metzger & Décamps 1997, Tiebout & Anderson 1997), while others have focused on describing organism responses as measures of connectivity (dispersal success Demers *et al.* 1995, Schumaker 1996, Schippers *et al.* 1996, Ruckelshaus *et al.* 1997; search time Doak *et al.* 1992; reobservation after displacement Pither & Taylor 1998). Furthermore, different situations will necessitate the use of different metrics of connectivity, based on what is possible in that situation (e.g., I could only measure patch- or cell-immigration in the field study). To my knowledge there is no published work comparing these, or any other, metrics of landscape connectivity. Based on the fact that my six measures of connectivity responded to different aspects of landscape structure, were weakly correlated, and showed complex interactions, it is highly unlikely that all of the measures of connectivity in the literature are directly comparable.

All six of the connectivity measures that I investigated measure the ease with which individuals move through the landscape, which is part of the definition of landscape connectivity (Taylor *et al.* 1993). The fact that these potential measures of

connectivity respond differently to landscape structure suggests that connectivity is a poorly defined concept. Measures of connectivity should be feasible in an empirical setting and respond in an intuitive way to degradation of the landscape (i.e., decrease as habitat fragmentation increases and as habitat amount decreases). All six measures that I investigated could conceivably be measured in the field, though patch and cell immigration are much easier than the other four since the transition probabilities would require release of many individuals from each patch or cell, and number of visits would require tracking of individuals without breaks. Of the two most reasonable measures, patch or cell immigration, patch immigration is the current leading candidate due to a focus on patches in the connectivity literature (Fahrig & Merriam 1985, Lefkovich & Fahrig 1985, Henein & Merriam 1990, Doak *et al.* 1992, Arnold *et al.* 1993, Demers *et al.* 1995, Gustafson & Gardner 1996, Schumaker 1996, Schippers *et al.* 1996, Hof & Flather 1996, Swart & Lawes 1996, Hess 1996a, Ruckelshaus *et al.* 1997, Andreassen *et al.* 1998, Gonzalez *et al.* 1998, Petit & Burel 1998a, Browne *et al.* 1999). It is true that patch immigration dovetails well with the definition of landscape connectivity. However, patch immigration increases as the number of patches increases, which seems counter-intuitive. Additionally, the R^2 value for patch immigration was the lowest, suggesting that patch immigration does not respond as strongly to landscape structure as the other measures of connectivity. Cell-immigration has a different problem, namely that it declines with increasing habitat amount, which also seems counter-intuitive. This could have serious implications for populations since habitat loss (regardless of habitat pattern) is one of the major contributing factors to population declines and extinctions (Andrn 1994, Bascompte & Sol 1996, Fahrig 1997, Bender *et al.* 1998). A practical measure of

connectivity will most likely be based upon either cell or patch immigration but with some sort of correction to account for non-intuitive responses to habitat amount and/or fragmentation.

These differences between the six connectivity measures also suggest the possibility that different measures of connectivity may be more appropriate for different ecological processes. For example, metapopulation persistence is driven by patch immigration (Levins 1970, Hanski & Simberloff 1997) and so a researcher interested in landscape connectivity as it affects metapopulation persistence would be interested in measuring landscape connectivity as patch immigration. My simulations then suggest that patch immigration will respond primarily to interpatch distance. On the other hand, if successful dispersal for an individual requires finding a vacant territory (Buechner 1987b, Lamberson *et al.* 1994, Verhulst *et al.* 1997) and we can think of territories as cells in my simulations then a researcher interested in dispersal would want to measure connectivity as cell immigration. And my simulations suggest that connectivity, measured as cell immigration, will respond primarily to the shape of the habitat patches and secondarily to distance. The metapopulation processes would only be influenced by changes to interpatch distances while the dispersal process could be influenced by both changes to patch shape and changes to distance.

One of the advantages of the design of this study was that landscape connectivity was determined by modelling movement using movement parameters obtained for a real species. Most modelling studies of connectivity do not use empirically determined, organism specific movement behaviour (but see Schippers *et al.* 1996). This can lead to difficulties validating the modelling results through empirical tests. A drawback to this

approach is that only a single combination of movement behaviour, specific to *T. borealis*, was used when investigating the relationship between landscape structure and landscape connectivity. It is possible that the relationships observed in this study depend on the particular movement parameters of *T. borealis* and may not hold for all species. For example, the importance of interpatch or intercell distance might have declined if beetles were capable of detecting goldenrod patches from a long distance. Extreme edge crossing behaviour (e.g., never crossing from one matrix patch into another) may have made matrix structure more influential on landscape connectivity. This concern with the influence of the movement parameters chosen is also present in simulation studies that used an artificial movement behaviour (e.g., self-avoiding random walk) and did not vary the functional parameters. There are two main approaches that can be taken to assess the dependence of simulation results on the particular movement parameters chosen: i) model a number of general categories of species in terms of their movements (Tischendorf & Fahrig 2000) or ii) describe the movement parameters as simple distributions and perform a sensitivity analysis and/or more thorough exploration of the relationship between connectivity and landscape structure. The difficult part then would be empirically testing those more general modelling results across a large number of species.

To advance our understanding of landscape connectivity and how it is influenced by landscape structure we will need to be able to compare connectivity between different landscapes, between different species, and between simulation and empirical studies. Also, we will need to match the measure of connectivity to the ecological process of interest. Understanding the relationships between different measures of connectivity will be vital to advancing landscape connectivity research.

4.6 CONCLUSIONS

These results suggest two general points about the relationship between landscape structure and connectivity. First, the influence of habitat spatial structure seems much more important than the influence of matrix spatial structure on connectivity. This suggests that mitigation against the influence of habitat loss or fragmentation on landscape connectivity cannot be achieved by manipulating the matrix elements being inserted into the landscape. Second, all measures of connectivity declined when habitat patches were farther apart. This suggests that mitigation against landscape change will need to reduce, or at a minimum not increase, interpatch distances. Overall, the general relationships between landscape structure and connectivity warn that habitat loss should be avoided.

It could be argued that a third general point arose from this work: that there is little generality among measures of connectivity. Put another way, different measures of connectivity respond differently to landscape structure. Based on the most important relationships (strongest partial r 's): i) patch transition probability will decrease with increasing interpatch distances, decrease with increasing variance of interpatch distance, and decrease with increasing habitat fragmentation; ii) cell transition probability will decrease with increasing habitat and decrease with increasing intercell distances; iii) patch visits will increase with increasing habitat fragmentation and decrease as those fragments are further apart; iv) cell visits will decrease with increasing habitat edge and increase with increasing habitat; v) patch immigration will decrease with increasing interpatch distances and increase with increasing variance in those distances; and vi) cell immigration will decrease with increasing goldenrod edge to area ratio, increasing

intercell distance, and increasing amount of goldenrod. Based on what is easily measured in the field researchers should focus on patch and/or cell immigration as measures of connectivity, though both have problems that need to be addressed. There is no one set of rules, with the exception of keeping habitat patches close together, that will dictate how to structure a landscape to increase connectivity.

Table 4.1: Description and computation details for the six measures of connectivity investigated. In all equations n_p , n_c , and n_b are the number of patches, cells, or individuals in the landscape, respectively. p_{ij}^p is the probability of moving from patch i to patch j and is estimated by dividing the number of individuals that moved from patch i to patch j by the number of individuals available to move. p_{ij}^c is the probability of moving from cell i to cell j and is calculated similarly to p_{ij}^p . v_i^p and v_i^c are the number of patches or cells visited by individual i , respectively. Finally, m_i^p and m_i^c are the number of immigrants into patch i or cell i , respectively.

Variable	Description	Computation
PATPROB	Mean patch transition probability, averaged across all pairs of patches in the microlandscape	$\frac{\sum_{i=1}^{n_p} \sum_{j=1}^{n_p} p_{ij}^p}{n_p(n_p - 1)}, i \neq j$
CELPROB	Mean cell transition probability, averaged across all pairs of cells in the microlandscape	$\frac{\sum_{i=1}^{n_c} \sum_{j=1}^{n_c} p_{ij}^c}{n_c(n_c - 1)}, i \neq j$
PATVISIT	Mean number of visits to a new patch per individual	$\frac{\sum_{i=1}^{n_b} v_i^p}{n_b}$
CELVISIT	Mean number of visits to a new cell per individual	$\frac{\sum_{i=1}^{n_b} v_i^c}{n_b}$
PATIMM	Mean number of immigrants per patch	$\frac{\sum_{i=1}^{n_p} m_i^p}{n_p}$
CELIMM	Mean number of immigrants per cell	$\frac{\sum_{i=1}^{n_c} m_i^c}{n_c}$

Table 4.2: Description of the landscape indices for the habitat simulations. The generating algorithm is described as well as the minimum and maximum values attained. Units of measure are indicated.

Descriptor	Description Generating Algorithm; (Min., Max.)
AMOUNT OF GOLDENROD	Amount of goldenrod in the microlandscape (proportion of landscape) Set levels: 0.08, 0.12, 0.16, 0.20, 0.24, 0.28, 0.32; (0.08, 0.32)
NUMBER OF GOLDENROD PATCHES	Number of goldenrod patches Set levels: 2, AMOUNT/4, AMOUNT/2, 3*AMOUNT/4; (2, 24)
GOLDENROD PATCH SIZE DISTRIBUTION	Coefficient of variation (CV) of the goldenrod patch sizes Every patch gets one cell of habitat, start putting the remaining habitat in the first patch, probability of moving on to a new patch set at 4 levels: 0, 0.1, 0.25, 1; (0.00, 1.98)
GOLDENROD EDGE TO AREA RATIO	Ratio of total edge to total area for all goldenrod patches Patches are placed as self-avoiding random walks with 4 levels for the probability of turning: 0.75, 0.5, 0.25, 0.05; (0.88, 3.75)
INTERPATCH DISTANCE	Mean distance between goldenrod patch edges (cells) The base step distance from one patch to the next as they are placed in the landscape is set at 4 levels: 2, 4, 6, 8 cells; (0.00, 7.07)
VARIANCE IN INTERPATCH DISTANCE	CV of distances between goldenrod patch edges Two levels of variance: first level: no change in step distance; second level: randomly changed the step distance from -2 to +2 cells; (0.00, 1.41)
INTERCELL DISTANCE	Mean distance between goldenrod cell centres (cells) Set by placing patches; (1.84, 7.49)
VARIANCE IN INTERCELL DISTANCE	CV of goldenrod cell distances Set by placing patches; (0.37, 0.95)

Table 4.3: Pearson product-moment correlations between landscape indices calculated from the microlandscapes produced for the habitat simulations ($n = 3584$).

	NUMBER OF GOLDENROD PATCHES	GOLDENROD PATCH SIZE DISTRIBUTION	GOLDENROD EDGE TO AREA RATIO	INTERPATCH DISTANCE	VARIANCE IN INTERPATCH DISTANCE	INTERCELL DISTANCE	VARIANCE IN INTERCELL DISTANCE
AMOUNT OF GOLDENROD	0.48	0.22	-0.13	-0.05	0.24	0.27	-0.31
NUMBER OF GOLDENROD PATCHES	1	0.29	0.72	0.54	0.61	0.64	-0.42
GOLDENROD PATCH SIZE DISTRIBUTION		1	0.07	0.36	0.35	0.05	0.12
GOLDENROD EDGE TO AREA RATIO			1	0.61	0.59	0.67	-0.44
INTERPATCH DISTANCE				1	0.51	0.70	0.07
VARIANCE IN INTERPATCH DISTANCE					1	0.50	-0.37
INTERCELL DISTANCE						1	-0.37

Table 4.4: Multiple regression results for habitat arrangement simulation experiments with connectivity measured as mean transition probabilities for either (a) patches or (b) cells. All terms in both models were significant.

a) Dependent variable – Patch transition probability

Model - $F_{(6, 3577)} = 3921.2, p < 0.0000, R^2 = 0.8680$

	Coefficient	$t_{(3578)}$	Partial r
Intercept	0.3832	35.590	
INTERPATCH DISTANCE	-0.0635	-63.046	-0.7255
VARIANCE IN DISTANCE	-0.2584	-49.545	-0.6379
NUMBER OF GOLDENROD PATCHES	-0.0087	-18.896	-0.3013
AMOUNT OF GOLDENROD	0.0033	12.894	0.2107
GOLDENROD EDGE TO AREA RATIO	0.0417	10.992	0.1808
GOLDENROD PATCH SIZE DISTRIBUTION	0.0071	3.038	0.0507

b) Dependent variable – Cell transition probability

Model - $F_{(6, 3577)} = 3500.2, p < 0.0000, R^2 = 0.8545$

	Coefficient	$t_{(3578)}$	Partial r
Intercept	0.0963	25.600	
AMOUNT OF GOLDENROD	-0.0027	-45.398	-0.6046
INTERCELL DISTANCE	-0.0073	-21.674	-0.3407
GOLDENROD PATCH SIZE DISTRIBUTION	-0.0061	-14.989	-0.2431
VARIANCE IN INTERCELL DISTANCE	0.0611	14.964	0.2427
GOLDENROD EDGE TO AREA RATIO	0.0096	10.563	0.1739
NUMBER OF GOLDENROD PATCHES	-0.0004	-4.235	-0.0706

Table 4.5: Multiple regression results for habitat arrangement simulation experiments with connectivity measured as mean number of visits per individual to a new (a) patch or (b) cell. All terms in both models were significant with the exception of the number of goldenrod patches for mean cell visits per individual ($p = 0.8795$).

a) Dependent variable – Patch visits			
Model - $F_{(6, 3577)} = 9650.7, p < 0.0000, R^2 = 0.9418$			
	Coefficient	$t_{(3578)}$	Partial r
Intercept	0.1487	1.365	
NUMBER OF GOLDENROD PATCHES	0.3931	84.453	0.8161
INTERPATCH DISTANCE	-0.3956	-38.837	-0.5446
VARIANCE IN INTERPATCH DISTANCE	1.2565	23.811	0.3699
GOLDENROD PATCH SIZE DISTRIBUTION	-0.4240	-18.054	-0.2890
AMOUNT OF GOLDENROD	0.0139	5.419	0.0902
GOLDENROD EDGE TO AREA RATIO	0.1569	4.090	0.0682
b) Dependent variable – Cell visits			
Model - $F_{(6, 3577)} = 8791.9, p < 0.0000, R^2 = 0.9365$			
	Coefficient	$t_{(3578)}$	Partial r
Intercept	55.2412	54.729	
GOLDENROD EDGE TO AREA RATIO	-13.0518	-53.357	-0.6657
AMOUNT OF GOLDENROD	0.6553	41.643	0.5714
GOLDENROD PATCH SIZE DISTRIBUTION	2.0059	18.498	0.2955
INTERCELL DISTANCE	-1.6553	-18.352	-0.2934
VARIANCE IN INTERCELL DISTANCE	-11.6678	-10.640	-0.1751
NUMBER OF GOLDENROD PATCHES	0.0031	0.126	0.0021

Table 4.6: Multiple regression results for habitat arrangement simulation experiments with connectivity measured as mean number of immigrants into (a) patches or (b) cells. All terms in both models were significant with the exception of the goldenrod patch size distribution for mean immigrants per cell ($p = 0.8075$).

a) Dependent variable – Patch immigration			
Model - $F_{(6, 3577)} = 824.07, p < 0.0000, R^2 = 0.5802$			
	Coefficient	$t_{(3578)}$	Partial r
Intercept	16.8372	8.351	
INTERPATCH DISTANCE	-9.6053	-50.950	-0.6485
VARIANCE IN INTERPATCH DISTANCE	20.5754	21.066	0.3322
GOLDENROD EDGE TO AREA RATIO	12.8244	18.059	0.2891
AMOUNT OF GOLDENROD	0.8217	17.322	0.2782
GOLDENROD PATCH SIZE DISTRIBUTION	-5.2256	-12.021	-0.1971
NUMBER OF GOLDENROD PATCHES	-0.6430	-7.464	-0.1238
b) Dependent variable – Cell immigration			
Model - $F_{(6, 3577)} = 9219.3, p < 0.0000, R^2 = 0.9393$			
	Coefficient	$t_{(3578)}$	Partial r
Intercept	405.6917	87.753	
GOLDENROD EDGE TO AREA RATIO	-69.1686	-61.736	-0.7182
INTERCELL DISTANCE	-23.5375	-56.976	-0.6898
AMOUNT OF GOLDENROD	-3.4213	-47.470	-0.6217
NUMBER OF GOLDENROD PATCHES	3.5156	31.487	0.4659
VARIANCE IN INTERCELL DISTANCE	77.6952	15.468	0.2504
GOLDENROD PATCH SIZE DISTRIBUTION	0.1210	0.244	0.0041

Table 4.7: Description of the landscape indices for the matrix simulations. The generating algorithm is described as well as the minimum and maximum values attained. Units of measure are indicated.

Descriptor	Description Generating Algorithm; (Min., Max.)
AMOUNT OF GOLDENROD	Amount of goldenrod in the microlandscape (proportion of landscape) Set levels: 0.04, 0.16; (0.04, 0.16)
NUMBER OF GOLDENROD PATCHES	Number of goldenrod patches Set levels: 2, 4; (2, 4)
GOLDENROD INTERPATCH DISTANCE	Mean distance between goldenrod patch edges (cells) Set levels: near, far; (2, 10)
PROPORTION OF MATRIX AS NET	Proportion of the non-goldenrod landscape taken up by the netting Set levels: 0.1, 0.2, 0.3, 0.4, 0.6, 0.7, 0.8, 0.9; (0.1, 0.9)
MATRIX DISPERSION	Number of matrix patches Set levels based on the number of cells of the least common matrix element (LCM): 2, LCM/4, LCM/2, 3*LCM/4; (2, 28)
MATRIX PATCH SIZE DISTRIBUTION	Coefficient of variation (CV) of the least common matrix type patch sizes Every patch gets one cell of the least common matrix type, start putting the remaining matrix in the first patch, probability of moving on to a new patch set at 4 levels: 0, 0.1, 0.25, 1; (0.00, 0.22)
MATRIX EDGE TO AREA RATIO	Ratio of total edge to total area for all patches of least common matrix type Patches are placed as self-avoiding random walks with 4 levels for the probability of turning: 0.75, 0.5, 0.25, 0.05; (1.0, 3.6)

Table 4.8: Pearson product-moment correlations between landscape indices calculated from the microlandscapes produced for the matrix simulations ($n = 9216$).

	NUMBER OF GOLDENROD PATCHES	GOLDENROD INTERPATCH DISTANCE	GOLDENROD EDGE TO AREA RATIO	PROPORTION OF MATRIX AS NET	MATRIX DISPERSION	MATRIX PATCH SIZE DISTRIBUTION	MATRIX EDGE TO AREA RATIO
AMOUNT OF GOLDENROD	0.00	-0.15	-0.91	0.00	-0.04	-0.05	0.00
NUMBER OF GOLDENROD PATCHES	1	-0.10	0.39	0.00	0.00	0.00	0.01
GOLDENROD INTERPATCH DISTANCE		1	0.08	0.00	0.01	0.01	0.00
GOLDENROD EDGE TO AREA RATIO			1	0.00	0.07	0.04	0.00
PROPORTION OF MATRIX AS NET				1	0.00	0.00	0.00
MATRIX DISPERSION					1	-0.24	-0.78
MATRIX PATCH SIZE DISTRIBUTION						1	0.03

Table 4.9: Multiple regression results for matrix arrangement simulation experiments with connectivity measured as mean transition probability for either (a) patches or (b) cells.

a) Dependent variable – Patch transition probability

Model - $F_{(7, 9208)} = 7839.6, p < 0.0000, R^2 = 0.8563$

	Coefficient	$t_{(9208)}$	Partial r
Intercept	0.5836	155.401	
GOLDENROD INTERPATCH DISTANCE	-0.0436	-219.555	-0.9163
NUMBER OF GOLDENROD PATCHES	-0.0574	-102.871	-0.7312
AMOUNT OF GOLDENROD	-0.0021	-22.8100	-0.2313
PROPORTION OF MATRIX AS NET	-0.0256	-12.637	-0.1306
MATRIX DISPERSION	0.0000	0.336	0.0035
MATRIX PATCH SIZE DISTRIBUTION	0.0012	0.117	0.0012
MATRIX EDGE TO AREA RATIO	0.0000	0.030	0.0003

b) Dependent variable – Cell transition probability

Model - $F_{(7, 9208)} = 3456.1, p < 0.0000, R^2 = 0.7243$

	Coefficient	$t_{(9208)}$	Partial r
Intercept	0.3940	112.647	
AMOUNT OF GOLDENROD	-0.0118	-134.058	-0.8132
NUMBER OF GOLDENROD PATCHES	-0.0409	-78.644	-0.6339
GOLDENROD INTERPATCH DISTANCE	-0.0034	-18.506	-0.1894
PROPORTION OF MATRIX AS NET	-0.0058	-3.059	-0.0319
MATRIX EDGE TO AREA RATIO	-0.0008	-0.739	-0.0077
MATRIX DISPERSION	0.0001	0.566	0.0059
MATRIX PATCH SIZE DISTRIBUTION	0.0005	0.048	0.0005

Table 4.10: Multiple regression results for matrix arrangement simulation experiments with connectivity measured as mean number of visits to either (a) patches or (b) cells per individual.

a) Dependent variable – Patch visits

Model - $F_{(7, 9208)} = 4977.6, p < 0.0000, R^2 = 0.7910$

	Coefficient	$t_{(9208)}$	Partial r
Intercept	0.8424	54.959	
GOLDENROD INTERPATCH DISTANCE	-0.1332	-164.209	-0.8634
NUMBER OF GOLDENROD PATCHES	0.1587	69.701	0.5877
AMOUNT OF GOLDENROD	-0.0081	-21.159	-0.2153
PROPORTION OF MATRIX AS NET	-0.1142	-13.813	-0.1425
MATRIX DISPERSION	0.0005	1.073	0.0112
MATRIX PATCH SIZE DISTRIBUTION	-0.0202	-0.474	-0.0049
MATRIX EDGE TO AREA RATIO	-0.0021	-0.424	-0.0044

b) Dependent variable – Cell visits

Model - $F_{(7, 9208)} = 23732, p < 0.0000, R^2 = 0.9474$

	Coefficient	$t_{(9208)}$	Partial r
Intercept	13.3307	70.567	
AMOUNT OF GOLDENROD	1.6926	357.404	0.9658
NUMBER OF GOLDENROD PATCHES	-4.1002	-146.094	-0.8358
GOLDENROD INTERPATCH DISTANCE	-0.7545	-75.455	-0.6181
PROPORTION OF MATRIX AS NET	-1.4750	-14.475	-0.1492
MATRIX EDGE TO AREA RATIO	0.0341	0.551	0.0057
MATRIX PATCH SIZE DISTRIBUTION	-0.1260	-0.240	-0.0025
MATRIX DISPERSION	0.0009	0.166	0.0017

Table 4.11: Multiple regression results for matrix arrangement simulation experiments with connectivity measured as mean number of immigrants either (a) per patch or (b) per cell.

a) Dependent variable – Patch immigration

Model - $F_{(7, 9208)} = 9542.9, p < 0.0000, R^2 = 0.8789$

	Coefficient	$t_{(9208)}$	Partial r
Intercept	46.9549	134.003	
GOLDENROD INTERPATCH DISTANCE	-4.7695	-257.143	-0.9369
AMOUNT OF GOLDENROD	-0.2664	-30.330	-0.3014
PROPORTION OF MATRIX AS NET	-3.6294	-19.202	-0.1962
NUMBER OF GOLDENROD PATCHES	-0.6186	-11.882	-0.1229
MATRIX DISPERSION	0.0124	1.186	0.0124
MATRIX EDGE TO AREA RATIO	-0.0485	-0.423	-0.0044
MATRIX PATCH SIZE DISTRIBUTION	-0.3678	-0.378	-0.0039

b) Dependent variable – Cell immigration

Model - $F_{(7, 9208)} = 10758, p < 0.0000, R^2 = 0.8910$

	Coefficient	$t_{(9208)}$	Partial r
Intercept	244.2846	160.034	
NUMBER OF GOLDENROD PATCHES	-48.9985	-216.059	-0.9139
AMOUNT OF GOLDENROD	5.5027	143.792	0.8318
GOLDENROD INTERPATCH DISTANCE	-6.4672	-80.039	-0.6405
PROPORTION OF MATRIX AS NET	-10.8953	-13.232	-0.1366
MATRIX DISPERSION	0.0234	0.513	0.0053
MATRIX PATCH SIZE DISTRIBUTION	-1.9539	-0.461	-0.0048
MATRIX EDGE TO AREA RATIO	-0.2073	-0.415	-0.0043

Table 4.12: Results of ANOVA (single factors and all 2-way interactions) for the influence of microlandscape structure (see Figure 4.3) on estimated patch immigration in a) simulated microlandscapes to prepare for field tests ($n = 320$) and b) field tests ($n = 64$). Effects for significant factors from the simulation ($\alpha = 0.05$) are described.

a) Simulation results

Variable	<i>F</i>	<i>p</i> -level	Effect
Amount of goldenrod (PG)	408	0.0000	↑ goldenrod ↑ immigration
Number of patches (NP)	311	0.0000	↑ number of patches ↓ immigration
Distance between goldenrod patches (DIST)	126	0.0000	↑ distance ↓ immigration
PG*NP	83.4	0.0000	↑ goldenrod ↑ effect of NP
PG*DIST	19.6	0.0000	↑ goldenrod ↓ effect of DIST
NP*DIST	18.8	0.0000	↑ number of patches ↓ effect of DIST
PN*DIST	1.54	0.22	
Amount of netting (PN)	1.14	0.29	
PG*PN	0.80	0.37	
PN*NP	0.02	0.88	

b) Empirical results

Variable	<i>F</i>	<i>p</i> -level	Effect
Amount of goldenrod (PG)	1.77	0.19	↑ goldenrod ↑ immigration
Number of patches (NP)	4.26	0.045	↑ number of patches ↓ immigration
Distance between goldenrod patches (DIST)	15.5	0.0003	↑ distance ↓ immigration
PG*NP	0.14	0.71	↑ goldenrod ↓ effect of NP
PG*DIST	0.23	0.64	↑ goldenrod ↓ effect of DIST
NP*DIST	2.96	0.092	↑ number of patches ↓ effect of DIST
PN*DIST	0.08	0.78	
Amount of netting (PN)	1.77	0.19	
PG*PN	1.77	0.19	
PN*NP	0.144	0.71	

Table 4.13: Results of ANOVA (single factors and all 2-way interactions) for the influence of microlandscape structure (see Figure 4.3) on estimated cell immigration in a) simulated microlandscapes to prepare for field tests ($n = 320$) and b) field tests ($n = 64$). Effects for significant factors from either the simulation or the empirical results ($\alpha = 0.05$) are described.

a) Simulation results

Variable	<i>F</i>	<i>p</i> -level	Effect
Distance between goldenrod patches (DIST)	110	0.0000	↑ distance ↓ immigration
Number of patches (NP)	75.6	0.0000	↑ number of patches ↓ immigration
PG*DIST	6.63	0.011	↑ goldenrod ↓ effect of DIST
PG*NP	2.67	0.10	↑ goldenrod ↓ effect of NP
PN*DIST	2.65	0.10	
Amount of goldenrod (PG)	2.26	0.13	
Amount of netting (PN)	2.20	0.14	↑ netting ↓ immigration
PN*NP	0.20	0.66	
NP*DIST	0.07	0.79	
PG*PN	0.03	0.87	

b) Empirical results

Variable	<i>F</i>	<i>p</i> -level	Effect
Distance between goldenrod patches (dist)	3.42	0.071	↑ distance ↓ immigration
Number of patches (NP)	8.98	0.004	↑ number of patches ↓ immigration
PG*DIST	10.8	0.002	↑ goldenrod ↓ effect of DIST
PG*NP	21.1	0.0000	↑ goldenrod ↓ effect of NP
PN*DIST	0.14	0.708	
Amount of goldenrod (PG)	1.46	0.234	
Amount of netting (PN)	8.89	0.004	↑ netting ↓ immigration
PN*NP	1.50	0.280	
NP*DIST	1.38	0.246	
PG*PN	2.39	0.129	

Figure 4.1: Illustration of how habitat arrangement in the microlandscapes was manipulated for the habitat arrangement simulation experiment. Each panel shows how one of the aspects of the habitat arrangement was varied. The panel for amount of goldenrod is missing examples for 12, 20 and 28%. For the simulations all combinations of levels were created. The different microlandscape elements are ■ = goldenrod and □ = cut.

Figure 4.2: Illustration of how habitat and matrix arrangement in the microlandscapes was manipulated for the matrix arrangement simulation experiment. Each panel shows how one of the aspects of the habitat arrangement was varied. The panel for proportion of matrix in net is missing examples for 20, 40, 60 and 80%. For the simulations all combinations of levels were created. The different microlandscape elements are ■ = goldenrod, □ = camouflage netting, and □ = cut.

Figure 4.3: Illustration of the experimental design for the 5 x 5 m microlandscapes in which *T. borealis* were released (■ = goldenrod, □ = camouflage netting, □ = cut). Cut patches were randomly placed in the microlandscape.

Figure 4.4: Illustration of the tiled approach to dealing with movements in the landscape. By repeating the pattern of the focal landscape an infinitely large landscape is modelled but only movements in the focal landscape (black), and not the peripheral landscapes (grey) count towards landscape connectivity calculations.

Figure 4.5: Box-whisker plots of estimated patch immigration for the simulation results (left panel of each pair, $n = 320$) and field tests (right panel of each pair, $n = 64$). Plots have been classified by the four landscape structure parameters: a) amount of goldenrod in the landscape, b) if the matrix was predominately cut or netting, c) number of patches, and d) distance between patches. Whiskers represent the range, the boxes represent the interquartile range and the horizontal lines indicate the median value.

Figure 4.6: Scatterplot for connectivity measured as cell immigration vs. connectivity measured as patch immigration for the simulations investigating habitat arrangement.

Figure 4.7: Scatterplot for connectivity measured as cell visits vs. connectivity measured as cell immigration for the simulations investigating habitat arrangement. The amount of goldenrod in the microlandscape is indicated.

Figure 4.8: Scatterplot for connectivity measured as patch transition probability vs. connectivity measured as patch immigration for the simulations investigating habitat arrangement. The number of goldenrod patches in the microlandscape is indicated.

Chapter 5

GENERAL CONCLUSIONS

5.1 INTERCONNECTIONS BETWEEN MOVEMENT BEHAVIOUR, LANDSCAPE STRUCTURE, AND ECOLOGICAL PROCESSES

The traditional approach in ecology has been to look either at within-patch processes (e.g., birth and death rates) or at patch qualities (e.g., habitat quality, resource concentration) to predict population levels. More and more there has been a move toward at least incorporating, if not focusing on, processes occurring beyond the patch (e.g., dispersal and immigration) or qualities (e.g., surrounding matrix). In insect population ecology one of the leading contenders for a patch-based predictor of insect population levels has been the Resource Concentration Hypothesis (RCH). The meta-analysis that I conducted indicates that the concentration of resources in a patch rarely predicts the insect density attained. Furthermore, from an analysis of moderator variables, I was able to suggest some of the mechanisms influencing insect responses to resource concentration. These were heavily influenced by or dependent upon movement of the insects. Though demographic influences may be just as important, they were not over the time span of the studies in the literature (one to two years).

Animal movement has been traditionally studied in terms of maximizing fitness (Pyke 1984, Stephens & Krebs 1986). The influence of the environment may be just as important in determining organism movement behaviour. My tracking study of *T. borealis* individuals suggested that different patch types influence beetle movement

behaviour. Specifically, the presence of food and/or structural complexity influenced observed movement behaviour. Goldenrod patches were high in both structural complexity and food resources and engendered short bursts of slow, meandering movement interspersed with long periods of immobility. Cut patches were low in both food and structural complexity and engendered more sustained, directed movement interspersed with shorter periods of immobility. Netting patches were high in structural complexity and low in food resources and engendered short bursts of fast, meandering movements interspersed with short periods of immobility. Mark and release experiments suggested that *T. borealis* individuals do not respond to edges between the patch types, do not detect goldenrod patches from a distance, and do not display density-dependent emigration. If the patch environment an individual experiences can constrain movement behaviour, the spatial structuring of the different patches might influence the ability of individuals to move through a landscape. In other words, different landscape structures (composition and/or configuration) might influence landscape connectivity.

To test how landscape structure influences landscape connectivity I performed simulation and empirical experiments based on the observed movement behaviours of *T. borealis* (from Chapter 3). Since there is no generally accepted measure of landscape connectivity (see Table 1.1) I used six different potential measures of connectivity. These experiments suggested that changing the structure of the habitat (primarily inter-patch or inter-cell distance) could significantly influence landscape connectivity, and matrix elements (cut and netting patches) had little, if any, effect on landscape connectivity. Further, the six different measures of connectivity all behaved somewhat differently to changes in landscape structure, suggesting that landscape connectivity is still poorly

defined and comparisons between modelling and empirical situations and between different empirical systems will be difficult.

Logically, any connectivity metric should meet 2 criteria: i) it must be measurable in the field to allow for comparisons between simulation and empirical results and ii) it must respond intuitively to habitat fragmentation (decrease as fragmentation increases) and habitat loss (decrease as habitat amount decreases). It is imperative that simulation and empirical approaches to connectivity are easily comparable since simulation results are only useful if they are validated with empirical tests. Also, if connectivity metrics increase with increasing fragmentation or habitat loss then this leaves open the possibility of managers managing for connectivity by intentionally fragmenting and removing habitat. Habitat loss, and potentially fragmentation, are known to decrease population levels and increase extinction risks (Shaffer 1987, van Dorp & Opdam 1987, Robinson *et al.* 1992, Arnold *et al.* 1993, Kattan *et al.* 1994, Andrén 1994, Burkey 1995, Bender *et al.* 1998). None of the six measures I investigated completely met both criteria. The most likely candidates were patch and cell immigration but both would need to be modified to remove their non-intuitive responses to habitat loss (cell immigration) or fragmentation (patch immigration). I suggest that landscape connectivity is comparable to biodiversity. Both are influenced by complex processes and are not easily measured. There are many different metrics for biodiversity, which tend to respond to different aspects of changes in biodiversity (Magurran 1988), and the same could hold for connectivity metrics. It is worth noting that biodiversity research has advanced by utilizing a number of different metrics and investigating the inter-relationships amongst them.

It is important to note that this study has been limited to a single species. This has been beneficial in allowing me to investigate movement behaviour in some detail and then use that movement behaviour in the simulation models. This in turn allowed me to validate my simulation results through empirical experiments, which is rarely done in the connectivity literature. There has been a cost as well, in that the generality of my findings is still open to question. It is possible that other movement behaviours might have led to different conclusions regarding the relationships between landscape structure and connectivity. This problem is not unique to my study but is also a concern with studies that use simple movement algorithms (e.g., self-avoiding random walks) without assessing the dependency of the results upon movement parameter decisions.

5.2 IMPLICATIONS FOR APPLIED FIELDS

Notwithstanding the limitations mentioned above, I feel that this work has implications for a number of applied fields. I will illustrate this by briefly discussing three fields that could benefit from a better understanding of the relationship between movement behaviour, landscape structure, and connectivity, namely conservation biology, the study of invasive species, and pest management. Traditionally, conservation biologists have been more likely to think about connectivity and assess the impact of landscape structure on the success of individual movements. However, other fields could also benefit from understanding the forces that influence the ability of individuals to move through landscapes.

Conservation biology needs to understand population processes (including immigration and emigration) and must consider the real world location (including

landscape structure) of imperilled species. This naturally leads to some consideration of connectivity. Additionally, small populations, especially ones which are spread through a number of habitat fragments, are much more dependent upon movements to rescue local populations from extinction (Brown & Kodric-Brown 1977) and recolonize patches after local extinctions (Henderson *et al.* 1985) than large populations. Many of the studies in Table 1.1 either investigated a specific endangered or threatened species or used a more common species to draw implications for conservation.

Invasive species have become an increasingly important concern (Wilson & Graham 1983, Groves & Burdon 1986, Drake *et al.* 1989, diCatri *et al.* 1990, Pysek *et al.* 1995a). Much effort has been put into determining which species characteristics might be related to invasive ability (Caldwell *et al.* 1981, Newsome & Noble 1986, Roy 1990, Thompson *et al.* 1995, Pysek *et al.* 1995b, Rejmánek & Richardson 1996, Reichard & Hamilton 1997, Goodwin *et al.* 1999). A potentially important aspect that has received little attention is how landscape structure might aid or impede the invasion and spread of alien species. Finally, control of pest species (either invasive or otherwise) may be more effective if landscape connectivity is taken into account. This could occur in two ways: i) by understanding how to manipulate landscape structure to the detriment of the pest species it may be possible to depress population levels below acceptable thresholds (Bhar & Fahrig 1998), or ii) in the case of a biological control agent, it would be useful to maximize landscape connectivity for the control agent either by matching the control agent, in terms of movement behaviour, to the landscape or altering the landscape to match the control agent.

5.3 FUTURE DIRECTIONS

Despite the gains this study represents in terms of understanding how to measure connectivity and how landscape structure affects landscape connectivity, it is still necessary to determine how best to measure connectivity. My simulations suggest that patch or, more likely, cell immigration are promising leads but that problems with non-intuitive responses to habitat fragmentation and/or loss still need to be accounted for. This matter would best be pursued through further simulation studies confirmed through empirical experiments. The *T. borealis* system is a good vehicle for this endeavour. However, it is still imperative that the results, both of this study and any future studies, be assessed in terms of their sensitivity to the movement parameters employed. As mentioned in Chapter 4, this can be accomplished by either modelling a number of categories of species types regarding movement behaviour (e.g., Tischendorf & Fahrig 2000) or by a sensitivity analysis approach. The sensitivity analysis approach would require describing the movement behaviour with simple distributions that use as few parameters as possible. It would then be possible to vary those parameters over a wide range and see how the relationship between landscape structure and connectivity changes as movement behaviour changes. This approach would also allow other aspects of movement behaviour that were not present in the *T. borealis* system to be evaluated (e.g., edge crossing behaviour, detecting habitat from a distance, conspecific attraction, learning and navigation). Understanding the influence of particular movement behaviours will be necessary to establish how general the findings of both this and other studies are.

Similarly, it will be necessary to understand how comparable different connectivity metrics are. Many studies have already been conducted investigating the

influence of connectivity on other ecological processes, using many different measures of connectivity (Table 1.1). Also, different situations may call for the use of different metrics. To develop a general theory regarding connectivity we must be able to compare and synthesize studies. That will only be possible if we are able to both differentiate between and compare the different connectivity metrics.

Finally, it will be necessary to put the role of connectivity into perspective. That is, we need to be able to answer the question: relative to other ecological processes that impinge on a population, how important is landscape connectivity? This would be the next logical step for the modelling results reported here; the addition of demographic factors to the simulations would allow one to compare the importance of movement against the importance of survival and fecundity.

Appendix A

TABULATED DATA FOR THE RESOURCE CONCENTRATION HYPOTHESIS META-ANALYSIS

This appendix tabulates the correlations between herbivore density and resource concentration that were gathered from the literature and the associated moderator variables. The LS column reports the life stage of the insect censused (A = adult, L = larvae/nymph, E = egg). The Ph column reports the degree of specialization of the insect herbivore (S = species level, G = genus level, F = family level, B = broad). The FS column reports the feeding style of the insect (F = sap feeder, T = tissue feeder, S = seed feeder). The S column reports whether the test was performed in a natural (N) or experimental (E) setting. The I column reports the intensity of the resource concentration manipulation. A ? indicates the datum was not available. The *r* column reports the calculated Pearson product moment correlation (note that when resource concentration was measured as plant diversity the sign of the correlation was reversed). The appendix has been divided into 3 tables, one for each form (host-plant density, plant-diversity, patch size) of RCH.

INSECT	PLANT			LS	Ph	FS	S	I	r	REFERENCE
Curculionidae	<i>Ceutorhynchus quadridens</i>	Brassicaceae	<i>Brassica oleracea</i>	A	F	T	E	55.1	-0.677	(Finch & Skinner 1976)
	<i>Lissorhoptus oryzophilus</i>	Poaceae	<i>Oryza sativa</i>	E	F	T	E	83.5	-0.420	(Thompson & Quisenberry 1995)
	<i>Tychinae</i> sp.	Fabaceae	<i>Astragalus canadensis</i>	A	S	S	N	250.0	-0.991	(Platt <i>et al.</i> 1974)
DIPTERA										
Anthomyiidae	<i>Erioischia brassicae</i>	Brassicaceae	<i>Brassica oleracea</i>	L	F	T	E	55.1	-0.745	(Finch & Skinner 1976)
Chloropidae	<i>Oscinella frit</i>	Poaceae	<i>Maris oheron</i>	E	F	T	E	10.3	-0.870	(Adesiyun 1978)
	<i>Oscinella frit</i>		<i>Maris oheron</i>	L	F	T	E	10.3	-0.914	(Adesiyun 1978)
HEMIPTERA										
Lygaeidae	<i>Lygaeus kalmii</i>	Asclepiadaceae	<i>Asclepias viridis</i>	A	S	S	N	10.0	0.640	(Evans 1983)
HOMOPTERA										
Aphididae	<i>Aphis fabae</i>	Fabaceae	<i>Vicia fabae</i>	A	B	F	E	10.7	-0.900	(Way & Heathcote 1966)
	<i>Aphis fabae</i>		<i>Vicia fabae</i>	A	B	F	E	7.8	-0.960	(Way & Heathcote 1966)
	<i>Aphis fabae</i>		<i>Vicia fabae</i>	A	B	F	E	20.0	-0.630	(Way & Heathcote 1966)
	<i>Aphis fabae</i>		<i>Vicia fabae</i>	A	B	F	E	12.2	-0.910	(Way & Heathcote 1966)
	<i>Aphis craccivora</i>		<i>Arachis hypogaea</i>	A	F	F	E	2.0	-0.892	(Farrell 1976b)
Cicadellidae	<i>Dalbulus maidis</i>	Poaceae	<i>Zea mays</i>	A	G	F	E	2.0	-0.637	(Power 1987)

INSECT	PLANT	LS	Ph	FS	S	I	r	REFERENCE
	<i>Dalbulus maidis</i>							
								<i>Zea mays</i>
								A G F E 2.0 -0.883 (Power 1992)
LEPIDOPTERA								
Arctiidae	<i>Tyria jacobaeae</i>							
								Asteraceae
								<i>Senecio jacobaeae</i>
								A G T N 12.8 -0.715 (Crawley & Gilman 1989)
	<i>Tyria jacobaeae</i>							
								<i>Senecio jacobaeae</i>
								E G T N 12.8 -0.720 (Crawley & Gilman 1989)
Pyrilidae	<i>Etiella zinckenella</i>							
								Fabaceae
								<i>Crotalaria pallida</i>
								L F S E 4.0 -0.465 (Segarra-Carmona & Barbosa 1990)
Tortricidae	<i>Choristoneura fumiferana</i>							
								Pinaceae
								<i>Abies balsamea</i>
								L F T N 2.1 0.250 (Simmons <i>et al.</i> 1975)
Gelechiidae	<i>Frumenta nundinella</i>							
								Solanaceae
								<i>Solanum carolinense</i>
								L S S N 5.6 0.050 (Solomon 1981)
THYSANOPTERA								
Thripidae	<i>Frankliniella occidentalis</i>							
								Cucurbitaceae
								<i>Cucurbita pepo</i>
								A B T E 4.0 -0.402 (Letourneau 1990b)

Table A.2: Data that were used in the meta-analysis of the Resource Concentration Hypothesis when resource concentration was measured as plant diversity of the host-plant patch.

INSECT	PLANT		LS	Ph	FS	S	I	r	REFERENCE
COLEOPTERA									
Chrysomelidae	<i>Acalymma vittata</i>	Cucurbitaceae	<i>Cucumis sativus</i>	A	F	T	E	3.0	0.575 (Bach 1980a)
	<i>Acalymma vittata</i>		<i>Cucumis sativus</i>	A	F	T	E	3.0	0.645 (Bach 1980a)
	<i>Acalymma vittata</i>		<i>Cucumis sativus</i>	A	F	T	E	3.0	0.297 (Bach 1980a)
	<i>Acalymma vittata</i>		<i>Cucumis sativus</i>	A	F	T	E	2.0	0.207 (Bach 1981)
	<i>Acalymma vittata</i>		<i>Cucumis sativus</i>	A	F	T	E	2.0	0.585 (Bach 1981)
	<i>Colaspis brunnea</i>	Fabaceae	<i>Glycine max</i>	A	B	T	E	2.0	-0.720 (Tonhasca 1994)
	<i>Diabrotica</i> spp.	Poaceae	<i>Zea mays</i>	A	S	T	E	2.0	0.291 (Johnson <i>et al.</i> 1984)
	<i>Diabrotica</i> spp.		<i>Zea mays</i>	A	S	T	E	2.0	0.262 (Johnson <i>et al.</i> 1984)
	<i>Diabrotica</i> spp.		<i>Zea mays</i>	L	S	T	E	2.0	0.291 (Johnson <i>et al.</i> 1984)
	<i>Diabrotica virgifera virgifera</i>		<i>Zea mays</i>	A	S	T	E	2.0	-0.903 (Tonhasca & Stinner 1991)
	<i>Leptinotarsa decemlineata</i>	Solanaceae	<i>Solanum tuberosum</i>	L	F	T	E	3.0	0.569 (Horton & Capinera 1987)
	<i>Leptinotarsa decemlineata</i>		<i>Solanum tuberosum</i>	E	F	T	E	3.0	0.667 (Horton & Capinera 1987)
	<i>Leptinotarsa decemlineata</i>		<i>Solanum tuberosum</i>	A	F	T	E	3.0	0.606 (Horton & Capinera 1987)
	<i>Leptinotarsa decemlineata</i>		<i>Solanum tuberosum</i>	L	F	T	E	3.0	0.558 (Horton & Capinera 1987)

INSECT	PLANT	LS	Ph	FS	S	I	r	REFERENCE	
Coccinellidae	<i>Phyllotreta cruciferae</i>	Brassicaceae	<i>Brassica oleracea</i>	A	F	T	E	2.0	0.709 (Andow <i>et al.</i> 1986)
	<i>Phyllotreta cruciferae</i>		<i>Brassica oleracea</i>	A	F	T	E	30.0	0.977 (Cronartie 1975)
	<i>Phyllotreta cruciferae</i>		<i>Brassica oleracea</i>	A	F	T	E	30.0	0.546 (Kareiva 1985)
	<i>Phyllotreta cruciferae</i>		<i>Brassica oleracea</i>	A	F	T	E	30.0	0.314 (Kareiva 1985)
	<i>Phyllotreta cruciferae</i>		<i>Brassica rapa</i>	A	F	T	E	2.0	0.039 (Weiss <i>et al.</i> 1994)
	<i>Phyllotreta cruciferae</i>		<i>Brassica rapa</i>	A	F	T	E	2.0	0.289 (Weiss <i>et al.</i> 1994)
	<i>Phyllotreta cruciferae</i>		<i>Brassica rapa</i>	A	F	T	E	2.0	0.058 (Weiss <i>et al.</i> 1994)
	<i>Phyllotreta striolata</i>		<i>Brassica oleracea</i>	A	F	T	E	30.0	0.977 (Cronartie 1975)
	<i>Phyllotreta striolata</i>		<i>Brassica oleracea</i>	A	F	T	E	30.0	0.424 (Kareiva 1985)
	<i>Phyllotreta striolata</i>		<i>Brassica oleracea</i>	A	F	T	E	30.0	0.981 (Kareiva 1985)
Coccinellidae	<i>Epilachna varivestis</i>	Fabaceae	<i>Glycine max</i>	A	F	T	E	30.0	-0.033 (Kemp & Barrett 1989)
	<i>Epilachna varivestis</i>		<i>Glycine max</i>	A	F	T	E	30.0	-0.071 (Kemp & Barrett 1989)
	<i>Epilachna varivestis</i>		<i>Glycine max</i>	A	F	T	E	30.0	0.064 (Kemp & Barrett 1989)
	<i>Epilachna varivestis</i>		<i>Glycine max</i>	A	F	T	E	30.0	0.064 (Kemp & Barrett 1989)
Scarabaeidae	<i>Popillia japonica</i>	Fabaceae	<i>Glycine max</i>	A	B	T	E	2.0	-0.696 (Tonhasca 1994)

INSECT	PLANT			LS	Ph	FS	S	I	r	REFERENCE
DIPTERA										
Chloropidae	<i>Oscinella frit</i>	Poaceae	<i>Maris oleron</i>	E	F	T	E	2.0	0.582	(Adesiyun 1979)
HOMOPTERA										
Aphididae	<i>Brevicoryne brassicae</i>	Brassicaceae	<i>Brassica oleracea</i>	A	F	F	E	2.0	0.611	(Costello 1995)
	<i>Myzus persicae</i>		<i>Brassica oleracea</i>	A	B	F	E	2.0	0.737	(Costello 1995)
	<i>Rhopalosiphum oxyacanthae</i>	Poaceae	<i>Dactylis glomerata</i>	A	F	F	E	2.0	0.894	(A'Brook 1973)
	<i>Rhopalosiphum padi</i> (female)		<i>Dactylis glomerata</i>	A	F	F	E	2.0	0.042	(A'Brook 1973)
	<i>Rhopalosiphum padi</i> (male)		<i>Dactylis glomerata</i>	A	F	F	E	2.0	0.530	(A'Brook 1973)
Cicadellidae	<i>Dalbulus maidis</i>	Poaceae	<i>Zea mays</i>	A	G	F	E	30.0	-0.123	(Power 1987)
	<i>Empoasca abrupta</i> & <i>E. recurvata</i>	Cucurbitaceae	<i>Cucurbita pepo</i>	L	B	F	E	3.0	-0.918	(Letourneau 1990a)
	<i>Empoasca abrupta</i> & <i>E. recurvata</i>		<i>Cucurbita pepo</i>	A	B	F	E	3.0	0.878	(Letourneau 1990a)
	<i>Empoasca fabae</i>	Fabaceae	<i>Glycine max</i>	A	B	F	E	2.0	0.786	(Hammond & Jeffers 1990)
	<i>Empoasca fabae</i>		<i>Glycine max</i>	A	B	F	E	2.0	0.786	(Hammond & Jeffers 1990)
	<i>Empoasca fabae</i>		<i>Glycine max</i>	A	B	F	E	30.0	0.146	(Kemp & Barrett 1989)
	<i>Empoasca fabae</i>		<i>Glycine max</i>	A	B	F	E	30.0	0.181	(Kemp & Barrett 1989)

INSECT	PLANT		LS	Ph	FS	S	I	r	REFERENCE
	<i>Empoasca fabae</i>		A	B	F	E	30.0	0.000	(Kemp & Barrett 1989)
	<i>Empoasca fabae</i>		A	B	F	E	30.0	-0.027	(Kemp & Barrett 1989)
	<i>Empoasca fabae</i>		A	B	F	E	30.0	0.493	(Rodenhause <i>et al.</i> 1992)
	<i>Empoasca fabae</i>		A	B	F	E	30.0	0.730	(Rodenhause <i>et al.</i> 1992)
	<i>Empoasca fabae</i>		A	B	F	E	2.0	0.676	(Tonhasca 1994)
	<i>Empoasca fabae</i>		A	B	F	E	2.0	0.607	(Tonhasca 1994)
	<i>Empoasca fabae</i>		L	B	F	E	2.0	0.816	(Lamp 1991)
	<i>Empoasca fabae</i>		L	B	F	E	2.0	0.235	(Lamp 1991)
	<i>Empoasca fabae</i>		A	B	F	E	2.0	0.567	(Lamp 1991)
LEPIDOPTERA									
Lyoniitidae	<i>Leucopetra coffeella</i>	Rubiaceae	L	B	T	E	2.0	0.535	(Nestel <i>et al.</i> 1994)
Noctuidae	<i>Heliothis armigera</i>	Fabaceae	L	B	S	E	2.0	0.316	(Karel 1993)
	<i>Plathypena scabra</i>		L	B	T	E	30.0	0.203	(Kemp & Barrett 1989)
	<i>Plathypena scabra</i>		L	B	T	E	30.0	-0.097	(Kemp & Barrett 1989)
	<i>Plathypena scabra</i>		L	B	T	E	30.0	0.306	(Kemp & Barrett 1989)
	<i>Plathypena scabra</i>		L	B	T	E	30.0	0.000	(Kemp & Barrett 1989)
	<i>Plathypena scabra</i>		L	B	T	E	30.0	0.262	(Rodenhause <i>et al.</i> 1992)
	<i>Plathypena scabra</i>		L	B	T	E	30.0	-0.045	(Rodenhause <i>et al.</i> 1992)
	<i>Plathypena scabra</i>		L	B	T	E	2.0	-0.530	(Tonhasca 1994)
	<i>Plathypena scabra</i>		L	B	T	E	2.0	0.478	(Williams <i>et al.</i> 1995)

INSECT	PLANT	LS	Ph	FS	S	I	r	REFERENCE
Pieridae	<i>Pieris rapae</i>	Brassicaceae	<i>Brassica oleracea</i>	E	F	T	E	2.0 -0.048 (Andow <i>et al.</i> 1986)
	<i>Pieris rapae</i>		<i>Brassica oleracea</i>	L	F	T	E	2.0 -0.499 (Andow <i>et al.</i> 1986)
	<i>Pieris rapae</i>		<i>Brassica oleracea</i>	L	F	T	E	30.0 -0.977 (Cromartie 1975)
Plutellidae	<i>Plutella xylostella</i>	Brassicaceae	<i>Brassica oleracea</i>	L	F	T	E	2.0 0.048 (Bach & Tabashnik 1990)
Pyrilidae	<i>Diaphnia hyalinata</i>	Cucurbitaceae	<i>Cucurbita moschata</i>	E	F	T	E	3.0 0.890 (Letourneau 1986)
	<i>Diaphnia hyalinata</i>		<i>Cucurbita moschata</i>	L	F	T	E	3.0 0.772 (Letourneau 1986)
	<i>Maruca testulalis</i>	Fabaceae	<i>Phaseolus vulgaris</i>	L	F	S	E	2.0 0.659 (Karel 1993)
	<i>Ostrinia furnacalis</i>	Poaceae	<i>Zea mays</i>	L	F	S	E	2.0 0.411 (Litsinger <i>et al.</i> 1991)
THYSANOPTERA								
Phlaeothripidae	<i>Megalurothrips sjostedii</i>	Fabaceae	<i>Vigna unguiculata</i>	A	B	T	E	30.0 -0.368 (Ezueh & Amusan 1988)
Thripidae	<i>Frankliniella occidentalis</i>	Cucurbitaceae	<i>Cucurbita pepo</i>	A	B	T	E	3.0 0.822 (Letourneau 1990b)

Table A.3: Data that were used in the meta-analysis of the Resource Concentration Hypothesis when resource concentration was measured as host-plant patch size.

INSECT	PLANT		LS	Ph	FS	S	I	r	REFERENCE
COLEOPTERA									
Cerambycidae	<i>Tetraopes tetraophthalmus</i>	Asclepiadaceae	<i>Asclepias syriaca</i>	A	S	T	N	15.8	0.063 (Lawrence 1988)
Chrysomelidae	<i>Acalymma innubum</i>	Cucurbitaceae	<i>Cayaponia americana</i>	A	S	T	N	306.0	0.540 (Bach 1986)
	<i>Acalymma innubum</i>		<i>Cayaponia americana</i>	A	S	T	N	306.0	0.140 (Bach 1986)
	<i>Acalymma innubum</i>		<i>Cayaponia americana</i>	A	S	T	N	122.5	0.170 (Bach 1984)
	<i>Acalymma innubum</i>		<i>Cayaponia americana</i>	A	S	T	N	122.5	0.660 (Bach 1984)
Nitidulidae	<i>Meligethes aeneus</i>	Onagraceae	<i>Chamerion angustifolium</i>	A	?	?	N	28200.0	0.539 (MacGarvin 1982)
DIPTERA									
Agromyzidae	<i>Phytomyza ilicicola</i>	Aquifoliaceae	<i>Ilex opaca</i>	L	S	T	E	4.0	-0.087 (Marino & Cornell 1992)
Cecidomyiidae	<i>Dasineura kiefferiana</i>	Onagraceae	<i>Chamerion angustifolium</i>	A	S	?	N	28200.0	0.387 (MacGarvin 1982)
HEMIPTERA									
Tingidae	<i>Corythucha marmorata</i>	Asteraceae	<i>Solidago altissima</i>	A	F	F	E	9.0	-0.610 (Cappuccino & Root 1992)
	<i>Corythucha marmorata</i>		<i>Solidago altissima</i>	E	F	F	E	9.0	-0.351 (Cappuccino & Root 1992)
Pentatomidae	<i>Piezosternum subulatum</i>	Cucurbitaceae	<i>Cayaponia americana</i>	A	F	F	N	306.0	0.160 (Bach 1986)

INSECT	PLANT	LS	Ph	FS	S	I	r	REFERENCE
	<i>Piezosternum subulatum</i>	<i>Cayaponia americana</i>	A	F	F	N	306.0	-0.140 (Bach 1986)
	<i>Piezosternum subulatum</i>	<i>Cayaponia americana</i>	L	F	F	N	306.0	0.700 (Bach 1986)
	<i>Piezosternum subulatum</i>	<i>Cayaponia americana</i>	L	F	F	N	306.0	0.360 (Bach 1986)
HOMOPTERA								
Aphididae	<i>Aphis salicariae</i>	Onagraceae	A	B	?	N	28200.0	-0.316 (MacGarvin 1982)
	<i>Macrosiphum euphorbiae</i>		A	B	?	N	28200.0	-0.332 (MacGarvin 1982)
Cercopidae	<i>Philaneus spurnarius</i>	Onagraceae	A	B	?	N	28200.0	0.374 (MacGarvin 1982)
Cicadellidae	<i>Amplicephalus simplex</i>	Poaceae	A	S	F	N	20.0	0.336 (Raupp & Denno 1979)
	<i>Destria bisignata</i>		A	G	F	N	20.0	0.336 (Raupp & Denno 1979)
Delphacidae	<i>Delphacodes detecta</i>	Poaceae	A	S	F	N	20.0	0.336 (Raupp & Denno 1979)
	<i>Megamelus lobatus</i>		A	S	F	N	20.0	0.336 (Raupp & Denno 1979)
Issidae	<i>Aphelonema simplex</i>	Poaceae	A	S	F	N	20.0	0.336 (Raupp & Denno 1979)
Miridae	<i>Calocoris norvegicus</i>	Onagraceae	A	G	?	N	28200.0	0.224 (MacGarvin 1982)
Psyllidae	<i>Craspedolepta subpuncta</i>	Onagraceae	A	S	?	N	28200.0	0.557 (MacGarvin 1982)

INSECT	PLANT		LS	Ph	FS	S	I	r	REFERENCE
Tenthredinidae	<i>Tenthredo colon</i>	Onagraceae	A	B	?	N	28200.0	-0.412	(MacGarvin 1982)
LEPIDOPTERA									
Hesperiidae	<i>Pholisora catullus</i>	Chenopodiaceae	E	S	T	E	16.0	0.084	(Capman <i>et al.</i> 1990)
	<i>Pholisora catullus</i>		E	S	T	E	16.0	-0.282	(Capman <i>et al.</i> 1990)
	<i>Pholisora catullus</i>		E	S	T	E	16.0	-0.819	(Capman <i>et al.</i> 1990)
	<i>Pholisora catullus</i>		L	S	T	N	16.0	-0.100	(Capman <i>et al.</i> 1990)
	<i>Pholisora catullus</i>		L	S	T	E	16.0	-0.787	(Capman <i>et al.</i> 1990)
Lycanidae	<i>Glaucoopsyche lygdamus</i>	Fabaceae	E	F	T	N	9333.3	0.100	(Carey 1994)
Momphidae	<i>Mompha raschkiella</i>	Onagraceae	L	S	?	N	28200.0	0.361	(MacGarvin 1982)
Pieridae	<i>Pieris rapae</i>	Brassicaceae	E	F	T	E	16.0	-0.892	(Maguire 1983)
	<i>Pieris rapae</i>		L	F	T	E	16.0	-0.405	(Maguire 1983)
Plutellidae	<i>Plutella xylostella</i>	Brassicaceae	L	F	T	E	16.0	0.475	(Maguire 1983)
Pyralidae	<i>Ostrinia furnacalis</i>	Poaceae	E	F	T	E	34.7	0.787	(Litsinger <i>et al.</i> 1991)
THYSANOPTERA									
?	Thrips sp	Onagraceae	A	?	?	N	28200.0	0.557	(MacGarvin 1982)

*Chamerion angustifolium**Chenopodium album*

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