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Limits to butterfly movement in a successional landscape

by

Corina L. Brdar

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

in

Environmental Biology and Ecology
Department of Biological Sciences

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1523 Trowbridge Dr.
Oshawa, ON
L1G 7S3

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University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Limits to butterfly movement in a successional landscape** submitted by Corina L. Brdar in partial fulfillment of the requirements for the degree of Master of Science in Environmental Biology and Ecology.

Jens Roland

John Addicott

Eric Higgs

Fiona Schmiegelow

April 7, 2000.

Abstract

Unchecked forest succession is causing increased tree and shrub density in the patchy montane forests of Jasper National Park. I determined the interacting effects of forest density and butterfly life history attributes on the behaviour of two groups of montane butterflies: open area specialists, and habitat generalists.

Butterfly counts and vegetation surveys revealed that the abundance of open area specialist butterflies decreased sharply with increasing forest density, despite the presence of nectar plants and larval host plants in forests. Simpson's diversity index was highest in open, patchy forest. Both open area butterflies and forest-tolerant generalists were absent from dense forest, indicating a forest density threshold above which forest is non-habitat for butterflies. An increase in forest density also caused a decrease in the rate at which individuals crossed the meadow-forest boundary. This response was more pronounced for open area specialists. Within forest patches, butterflies preferred to move through open sections. Open area specialists moved through the forest more slowly. Both butterfly types tended to show rapid vertical flight, or "escape" behaviour, in dense forest.

This study is one of the first to compare individual butterfly movement behaviour among multiple species. These findings provide insight into the possible responses of butterflies to changing landscape structure, and the potential for managing fine-scale habitat structure for butterflies.

Acknowledgments

My supervisor Jens Roland deserves thanks for providing me with the opportunity to undertake such an enjoyable master's project and for teaching me about statistics, butterflies, and clear writing. I also thank my committee members, John Addicott, Eric Higgs, and Fiona Schmiegelow for their insights. My labmates provided much-appreciated and well-timed feedback, assistance, and supportive comments, and were good company at the many conferences we attended together. Chris Schmidt was the king of species identifications and the mysteries of butterfly biology.

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I survived many long hours on the 11th floor of the BioSci building with the good company of the others on this floor – I will miss our privileged 4:00 pm sunset view. Thanks also to Orville Redenbacher, Tim Horton, and el hombres del Buena Vista Social Club.

Above all, thanks to my parents for their support throughout my 2+ decades of education, and for providing me with the skills I required to excel.

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Chapter 1. General Introduction

"Species probably do not have binary perceptions of landscapes (*i.e.* presence or absence of resources) but instead respond to a gradient of resource quality" (With *et al.* 1997)

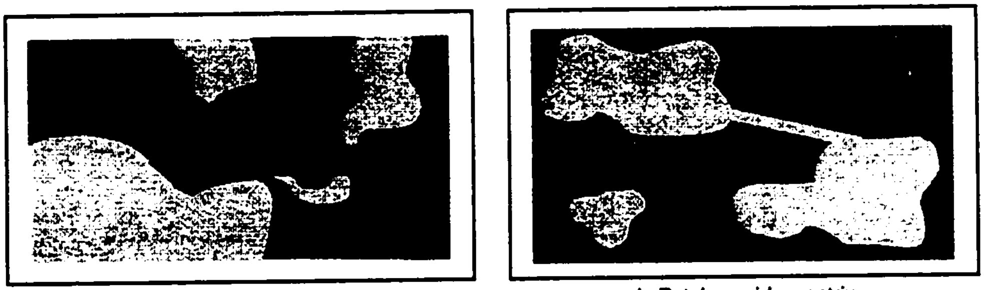
In this thesis I examine the use of a successional landscape by its butterfly community. Post-fire forest succession has produced a complex mosaic of forested and open patches in the Athabasca River Valley of Jasper National Park, Alberta, Canada. I assess butterfly diversity and abundance among these patches and relate these variables to tree density and larval host and nectar plant abundance. I then examine butterfly movement behaviour both at the meadow-forest boundary and within forest patches to determine how tree density and life history characteristics interact to influence individual movement, and ultimately species' distributions. In this chapter I provide the rationale for this research, introduce the terms that will be used throughout this thesis, and describe the study area and species.

Succession as landscape fragmentation

Most natural and modified landscapes are heterogeneous (Merriam 1991); that is, within these landscapes there is a certain degree of fragmentation of homogeneous areas at one or more spatial scales (Lord and Norton 1990, Fahrig and Merriam 1994). This patchiness may occur at the scale of individual resource patches, habitat patches, or entire landscapes. Many recent ecological studies have focussed on large-scale fragmentation caused by anthropogenic factors that produce discrete patches of habitat within a uniform matrix of non-habitat (Saunders *et al.* 1991). In such systems, the issues that have been of greatest interest to ecologists are patterns of patch occupancy and movement between patches, and the relationships between these patterns and patch area or isolation (*e.g.* Wilcox *et al.* 1986, Saunders *et al.* 1991, Hanski and Thomas 1994, Åberg *et al.* 1995, Dennis and Eales 1999). These studies generally assume internal homogeneity of habitat patches and the non-habitat area surrounding them in terms of both structure and quality (Addicott *et al.* 1987, Andrén *et al.* 1997).

Forest succession is another agent of landscape fragmentation, which produces isolated patches of meadows or open forests. These open areas are important habitat for some organisms, including butterflies. Through succession, trees gradually encroach upon early successional areas, increasing their canopy cover and isolating open meadows. For example, in Jasper National Park the amount of forest with less than 15% crown closure decreased by 73% between 1915 and 1997, while forests with greater than 70% crown closure increased by 25% (Rhemtulla 1999).

Unlike other forms of fragmentation, the intervening areas between early seral stage patches are modified versions of the original habitat, and as such they are not pure "non-habitat" (McIntyre & Barrett 1992). Landscapes in which succession is occurring are complex mosaics, resembling a "heterogeneous undivided" landscape pattern (Addicott *et al.* 1987; Figure 1-1a) rather than the traditional "patch-corridor-matrix" model (Forman 1997; Figure 1-1b). In systems fragmented by succession, questions of patch occupancy and movement become more difficult to answer because what constitutes a habitat patch versus matrix cannot be defined as clearly as in the fragmented landscapes usually examined.



a Heterogeneous undivided

b Patch-corridor-matrix

Figure 1-1. Two models of landscape fragmentation (modified from Addicott *et al.* 1987). Light grey areas represent optimal habitat patches.

Landscape concepts: patch-corridor-matrix, or continuum of varying suitability?

The traditional view of heterogeneous or fragmented landscapes (Figure 1-1b) is modified from island biogeography theory (Saunders *et al.* 1991, Åberg *et al.* 1995, Sisk *et al.* 1997) and treats habitat patches as "terrestrial archipelagos" (Thomas *et al.* 1992). Functionally, landscape mosaics are often defined as binary (*i.e.* habitat/non-habitat) conglomerations of background matrix, in which habitat patches connected by corridors are embedded (With and Crist 1995, Forman 1997). Habitat patches are delineated as areas where resources are abundant (*e.g.* Harrison *et al.* 1988, Thomas *et al.* 1992, Sutcliffe and Thomas 1996, Grundel *et al.* 1998, Moilanen and Hanski 1998).

The matrix is often assumed to lack resources and to be either neutral (Wiens *et al.* 1993, 1997) or hostile to the organisms in question (McIntyre and Barrett 1992, Andrén *et al.* 1997). Habitat patches may differ in quality, but the matrix is assumed to be homogeneous (Addicott *et al.* 1987). Corridors are usually linear strips of habitat connecting two patches, and are often anthropogenic, such as fencerows or roadsides (*e.g.* Sutcliffe and Thomas 1996, Haddad and Baum 1999). While these definitions are appropriate for some systems, such as the serpentine grasslands of the southwest U.S. (Harrison *et al.* 1988, Harrison 1989) or the alpine meadows of the Rocky Mountains (Roland *et al.* 2000), most fragmented systems are not composed of discrete patches embedded in a uniform matrix (Gustafson and Gardner 1996). It is difficult to apply these definitions to the complex patterns produced by succession.

Non-binary systems, such as successional landscapes, require less rigid definitions of their components. The landscape elements in these complex systems represent a continuum or mosaic of varying habitat suitability (McIntyre and Barrett 1992, Wiens 1992), rather than islands of habitat in a sea of non-habitat. Both patches of habitat and intervening areas may be internally heterogeneous (Fahrig and Merriam 1994, Gustafson and Gardner 1996). Individuals moving through these landscapes encounter boundaries differing in permeability, and landscape elements differing in resistance to movement (Wiens *et al.* 1997). The differences perceived by organisms determine their rate of transit through the landscape (With and Crist 1995). The interaction between animal movement and landscape element characteristics is a major determinant of the distribution of organisms (With and Crist 1995, Wiens *et al.* 1997).

Responses to landscape fragmentation occur at the level of individuals

Landscape components are functionally defined by the way that individuals use them (Addicott *et al.* 1987, Fahrig and Merriam 1994, Ingham and Samways 1996). The response to different landscape elements, and thus to fragmentation, depends on several life-history characteristics of an organism (With *et al.* 1997). Types of movement behaviour, vagility, habitat requirements, and degree of habitat specialization are some of the major factors that determine how and if a species will move through the "peaks and valleys of habitat suitability" (Wiens *et al.* 1993, With *et al.* 1997) that are present in heterogeneous landscapes. These characteristics can also determine whether the organism will perceive its environment as fragmented (With and Crist 1995, Andrén *et al.* 1997). Areas that are used as dispersal routes by vagile species may act as barriers to less mobile species (Fahrig and Merriam 1994, Ims 1995, Sutcliffe and Thomas 1996). As a result, a landscape that is perceived as fragmented by a poor disperser may be viewed as continuous by a good disperser (Andrén *et al.* 1997). Behavioural decisions made at an individual level can influence processes at the population level (Jonsen and Taylor 2000). Therefore, it is these individual-level mechanisms that produce patterns of distribution in mosaic landscapes (Johnson *et al.* 1992, Wiens *et al.* 1993, Lima and Zollner 1996, Roitberg and Mangel 1997, With *et al.* 1997).

Butterflies as model systems

Butterflies are well-suited for studies examining individual behavioural responses to fragmentation because their biology is relatively well known, and they are day-active and are easy to observe (Pollard and Yates 1993, New 1997, Haddad 1999). Some of the fundamental research on movement through fragmented systems was initiated by metapopulation studies using butterflies (*e.g.* Harrison *et al.* 1988, Harrison 1989, Hanski *et al.* 1994) and therefore it is possible to build on their findings using related organisms. Butterflies respond quickly to environmental change, due to their mobility (Erhardt 1985) and their short generation times. They are representative organisms found in early-successional habitat types and are sensitive indicators of habitat change, due to their narrow range of resource requirements (Ehrlich and Raven 1974).

Additionally, the abundance and visibility of butterflies in several systems make them easy to census and their behaviour easy to observe. Multi-species butterfly behavioural studies are relatively easy to conduct due to the diversity of butterflies in most systems (*e.g.* Haddad 1999, Haddad and Baum 1999), in terms of both species richness and life history traits. Because responses to landscape structure are species-specific, single species studies can be limited in their generality (New 1997) and are often too impractical to repeat spatially or temporally (McIntyre and Barrett 1992). By examining organisms whose movement behaviour occurs at easily observable spatial scales, it is possible to determine the influence of movement behaviour on population-level patterns and gain insight into similar systems at broader scales (Wiens and Milne 1989, Wiens *et al.* 1993).

The effect of tree density of butterfly abundance and movement

In order to determine the potential influence of the mosaic structure of a successional landscape on its butterfly community, I compare abundance and individual behavioural responses of butterflies in patches of differing tree density. Many potential variables influence butterfly distribution and movement in heterogeneous landscapes (Ims 1995); therefore, it is instructive to managers to identify key variables that are easily evaluated. Most butterflies require sunlight for thermoregulation and nectar plants at some point in their daily activities (Bird *et al.* 1995, Layberry *et al.* 1998). Tree density directly affects both of these resources: trees create shade, decreasing the amount of sunlight available, and nectar plants are often negatively correlated with shade (Warren 1985). Additionally, increase in canopy cover is a prominent effect of forest succession (Grundel *et al.* 1998, Rhemtulla 1999). In this study I therefore explore the effects of tree density on butterflies, independent of landscape variables such as area and isolation of habitat patches.

While patch area and isolation are important in determining occupancy of, and rates of movement between habitat patches, the nature of intervening areas or matrix is recognized as being an equally important – but poorly understood – determinant of responses to fragmentation (*e.g.* Gustafson and Gardner 1996, Hanski and Moilanen 1998, Law and Dickman 1998, Dennis and Eales 1999). Tree density may influence the *viscosity* (Wiens *et al.* 1997), or resistance to butterfly movement, of the areas between open habitat patches. Tree density also affects resource availability in inter-habitat patches, and therefore patch quality.

In this thesis I assess the effect of tree density on three of the species-specific responses to landscape structure defined by With *et al.* (1997): affinity of butterflies for certain habitats, butterfly response to boundaries, and butterfly movement behaviour within landscape elements. In Chapter 2 I relate the abundance of butterflies and their resource plants to tree density, which is a direct measurement of butterfly habitat affinity and their assessment of habitat quality. This information provides baseline data for the following chapters. In Chapter 3 I determine butterfly responses to several meadow-forest boundaries that differ in boundary hardness. In Chapter 4 I quantify several aspects of butterfly movement behaviour that reflect the degree to which patches of different tree density facilitate or inhibit movement through them. By looking at these butterfly responses to landscape structure, I am able to determine how increased tree density may affect the probability of movement by butterflies between patches of open habitat. I am also able to determine the threshold at which the forest is too dense to allow butterflies to move into and through the forest.

General methods

Study area

This study was conducted in the Henry House and Jackladder grasslands located in the Athabasca River Valley of Jasper National Park, Alberta, Canada (118° 04' W, 53° 14' N; Figure 1-2). This area is a unique system of patchy forests and open grasslands. As in many parts of the Northern Hemisphere, the montane ecoregion of the Canadian National Parks in the Rocky Mountains is experiencing unchecked forest succession due to the disruption of historical fire regimes (Erhardt 1985, Grundel *et al.* 1998, Schultz 1998). Over the past 80 years, the reduced frequency of both anthropogenic and natural fires has caused a dramatic shift towards late successional vegetation types (Achuff *et al.* 1996, Rhemtulla 1999). Open forests and some grasslands are becoming closed canopy coniferous forests in the study area.

To increase the amount of early-successional habitat in montane forests, Parks Canada has introduced a policy of prescribed burning (Achuff *et al.* 1996). In the Henry House and Jackladder areas three small burns (approximately 16, 7, and 5 ha.) were made in 1989, 1998, and 1999 respectively. I established a total of seven sites: two in meadow, three in intact forest, and two in burned forest areas in 1998. In 1999 I added two more intact forest sites and one more burned forest site. I measured tree density in each site in one of two ways (Table 1-1), depending upon what aspects of this thesis the sites were used for. In all intact forest sites, excluding the densest (F5), I counted the absolute number of trees within the site, and calculated number of trees per

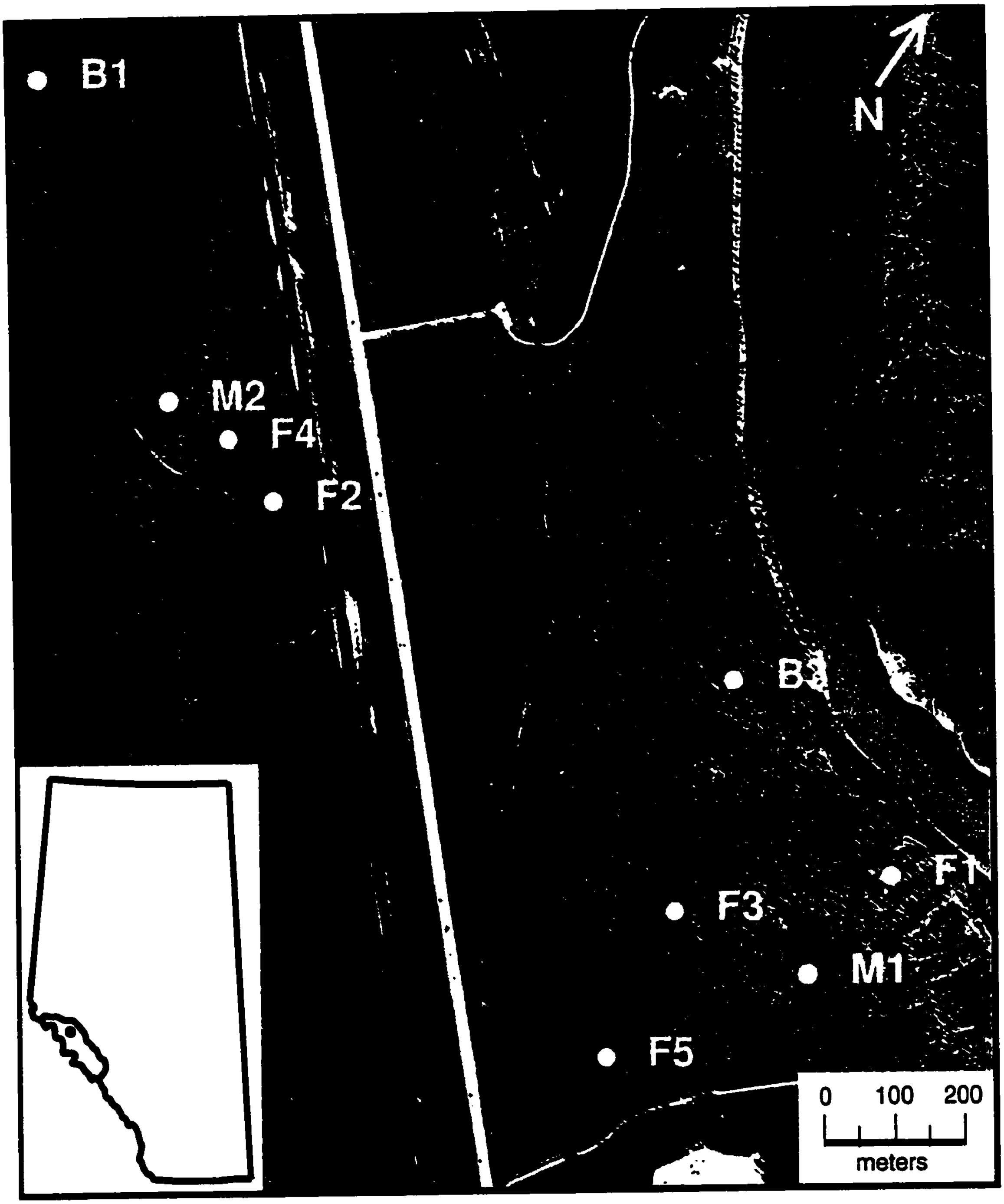


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Figure 1-2. Aerial photograph of the study area, located within Jasper National Park, Alberta, Canada (118° 04' W, 53° 14' N). The 1999 burn (B3) occurred after this photograph was taken. The 1998 burn (B2) is located approximately 1.4 km. SSE of site F5.

m^2. Small trees (height < 3.5 m) and shrubs were weighted at 0.5, as they produce less shade and are assumed to present smaller barriers to dispersing butterflies than do mature trees. In the dense forest site F5, and in the burned sites, I used the point-quarter method (Krebs 1989) to estimate tree density, again weighting small trees and shrubs as 0.5. Although the point-quarter method provides a less precise estimate of tree density, it is more time-efficient, and so was used in sites where estimates of density, rather than absolute values, were sufficient. Sites F1 to F4 were patchy, with variable sizes and numbers of open sunny patches, while the dense forest site F5 was completely closed. Almost all large trees in the burned sites were standing dead.

Table 1-1. Study sites used in this thesis. Checks indicate which year(s) the sites were used. Sites increased in tree density from F1 to F5. Tree density was measured as total number of trees/m^2. Asterisks indicate sites where the point-quarter method was used to estimate tree density. "Chapters" lists the parts of this thesis for which the sites were used.

1998	1999	site	type	tree density	chapters
✓	✓	M1	meadow	0	2,4
✓	✓	M2	meadow	<0.005	2,4
✓	✓	F1	forest (low density)	0.0400	2,3,4
	✓	F2	forest (low density)	0.0855	2,3,4
✓	✓	F3	forest (medium density)	0.1125	2,3,4
	✓	F4	forest (medium density)	0.1325	2,3,4
✓	✓	F5	forest (high density)	0.1525*	2,3,4
✓	✓	B1	burn (1989)	0.0345*	2
✓	✓	B2	burn (1998)	0.0535*	2
	✓	B3	burn (1999)	0.0460*	2

Due to the mosaic pattern and unique nature of this landscape in Jasper National Park, I was not able to replicate the forest densities. This is a common problem in large-scale studies (Hurlburt 1984). However, my objective was to identify general trends and relationships connected to tree density.

Study species

Butterflies are abundant in this region, and there are no butterfly species at risk in Jasper National Park. Common butterfly species in this mixed meadow-forest system are listed in Table 1-2 according to their habitat preferences. I was most interested in species that prefer grassy open areas or forest edges and openings, and I concentrate on these species throughout this thesis. I refer to butterflies typically classified in most guides (Bird *et al.* 1995, Layberry *et al.* 1998) as open area species as "meadow" butterflies, and those using forest openings and edges as "forest" butterflies (Pollard and

Yates 1993). I expected both groups to be affected by increasing tree density, but to different extents. The broad classifications of "meadow" and "forest" do not take into account the fine-scale behaviours that determine butterfly distribution within coarsely defined patch types (*i.e.* meadow *vs.* forest). Therefore, it is important to determine whether both groups use forested areas, if they respond to tree density differently, and at what tree density meadow and forest butterflies are absent.

Table 1-2. Butterfly species present in the study area (Bird *et al.* 1995, C. Brdar & B. Schmidt, *pers. observation*).

Habitat preference	Species
Grassy, open areas	Pieridae: *Colias christina, Colias philodice, Euchloe creusa, Pieris occidentalis* Satyridae: *Coenonympha inornata, Erebia discoidales, Erebia epipsodea*
Forest edges and openings	Nymphalidae (fritillaries): *Boloria bellona, Boloria freija, Speyeria atlantis, Speyeria electa, Speyeria mormonia*
Mixed deciduous forest	Nymphalidae: *Nymphalis antiopa, Nymphalis milberti, Nymphalis vaualbum j-album, Polygonia spp.* Papilionidae: *Papilio canadensis*
Ubiquitous	Lycaenidae: *Celastrina ladon, Everes amyntula, Glaucopsyche lygdamus, Incisalia spp., Lycaeides idas, Plebejus icarioides* Nymphalidae: *Phyciodes cocyta, Phyciodes tharos*

Literature Cited

Åberg, J., G. Jansson, J.E. Swenson, and P. Angelstam. 1995. The effect of matrix on the occurrence of hazel grouse (*Bonasa bonasai*) in isolated habitat fragments. Oecologia 103: 265 – 269.

Achuff, P.L., I. Pengelly, and J. Wierzchowski. 1996. Vegetation: cumulative effects and ecological futures outlook. *In* Greens, J., C. Pacas, L. Cornwell, and S. Bayley, editors. Ecological Outlooks Project. A cumulative effects assessment and futures outlook of the Banff Bow Valley. Prepared for the Banff Bow Valley Study. Department of Canadian Heritage, Ottawa, ON.

Addicott, J.F., J.M. Aho, M.F. Antolin, D.K. Padilla, J.S. Richardson, and D.A. Soluk. 1987. Ecological neighbourhoods: scaling environmental patterns. Oikos 49: 340 – 346.

Andrén, H., A. Delin, and A. Seiler. 1997. Population response to landscape changes depends on specialization to different landscape elements. Oikos 80: 193 – 196.

Bird, C.D., G.J. Hilchie, N.G. Kondla, E.M. Pike, and F.A.H. Sperling. 1995. Alberta butterflies. The Provincial Museum of Alberta, Edmonton, Alberta.

Dennis, R.L.H. and H.T. Eales. 1999. Probability of site occupancy in the large heath butterfly *Coenonympha tullia* determined from geographic and ecological data. Biological Conservation 87: 295 – 301.

Erhardt, A. 1985. Diurnal Lepidoptera: sensitive indicators of cultivated and abandoned grassland. Journal of Applied Ecology 22: 849 – 861.

Ehrlich, P.R. and P.H. Raven 1974. Butterflies and plants. Scientific American 216: 104 – 113.

Fahrig, L. and G. Merriam. 1994. Conservation of fragmented populations. Conservation Biology 8: 50 – 59.

Forman, R.T.T. 1997. Land mosaics: the ecology of landscapes and regions. Cambridge University Press, New York, USA.

Grundel, R., N.B. Pavlovic, and C.L. Sulzman. 1998. Habitat use by the endangered Karner blue butterfly in oak woodlands: the influence of canopy cover. Biological Conservation 85: 47 – 53.

Gustafson, E.J. and R.H. Gardner. 1996. The effect of landscape heterogeneity on the probability of patch colonization. Ecology 77: 94 – 107.

Haddad, N.M. 1999. Corridor and distance effects on interpatch movements: a landscape experiment with butterflies. Ecological Applications 9: 612 – 622.

Haddad, N.M. and K.A. Baum. 1999. An experimental test of corridor effects on butterfly densities. Ecological Applications 9: 623 – 633.

Hanski, I. and C. Thomas. 1994. Metapopulation dynamics and conservation: a spatially explicit model applied to butterflies. Biological Conservation 68: 167 – 180.

Harrison, S. 1989. Long-distance dispersal and colonization in the bay checkerspot butterfly, *Euphydryas editha bayensis*. Ecology 70: 1236 – 1243.

Harrison, S., D.D. Murphy, and P.R. Ehrlich. 1988. Distribution of the bay checkerspot butterfly, *Euphydryas editha bayensis*: evidence for a metapopulation model. The American Naturalist 132: 360 – 382.

Ingham, D.S. and M.J. Samways. 1996. Application of fragmentation and variegation models to epigaeic invertebrates in South Africa. Conservation Biology 10: 1353 – 1358.

Johnson, A.R., J.A. Wiens, B.T. Milne, and T.O. Crist. 1992. Animal movements and population dynamics in heterogeneous landscapes. Landscape Ecology 7: 63 – 75.

Jonsen, I.D. and P.D. Taylor. 2000. Fine-scale movement behaviours of Calopterygid damselflies are influenced by landscape structure: An experimental manipulation. Oikos 88: 553 – 562.

Krebs, C. J. 1989. Ecological methodology. Harper Collins Publishers, New York, NY, USA.

Law, B.S. and C.R. Dickman. 1998. The use of habitat mosaics by terrestrial vertebrate fauna: implications for conservation and management. Biodiversity and Conservation 7: 323 – 333.

Layberry, R.A., P.W. Hall, and J.D. Lafontaine. 1998. The butterflies of Canada. University of Toronto Press, Toronto, Canada.

Lima, S.L. and P.A. Zollner. 1996. Towards a behavioural ecology of ecological landscapes. Trends in Ecology and Evolution 11: 131 – 135.

Lord, J.M. and D. A. Norton. 1990. Scale and the spatial concept of fragmentation. Conservation Biology 4: 197 – 202.

McIntyre, S. and G.W. Barrett. 1992. Habitat variegation, an alternative to fragmentation. Conservation Biology 6: 146 – 147.

Merriam, G. 1991. Corridors and connectivity: animal populations in heterogeneous environments. Pages 133 – 142 *in* Saunders, D.A. and R.J. Hobbs, editors. Nature Conservation 2: the role of corridors. Surrey Beatty & Sons.

Moilanen, A. and I. Hanski. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. Ecology 79: 2503 – 2515.

New, T.R. 1997. Are Lepidoptera an effective "umbrella group" for biodiversity conservation? Journal of Insect Conservation 1: 5 – 12.

Pollard, E. and T.J. Yates. 1993. Monitoring butterflies for ecology and conservation. Chapman and Hall, London.

Rhemtulla, J.M. 1999. Eighty years of change: the montane vegetation of Jasper National Park. M.Sc. Thesis. University of Alberta.

Roland, J., N. Keyghobadi, and S. Fownes. 2000. Alpine *Parnassius* butterfly dispersal: effects of landscape and population size. Ecology (in press)

Roitberg, B.D., and M. Mangel. 1997. Individuals on the landscape: behaviour can mitigate landscape differences among habitats. Oikos 80: 234 – 240.

Saunders, D.A., R.J. Hobbs, and C.R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5: 18 – 32.

Sisk, T.D., N.M. Haddad and P.R. Ehrlich. 1997. Bird assemblages in patchy woodlands: modeling the effects of edge and matrix habitats. Ecological Applications 7: 1170 – 1180.

Sutcliffe, O.L. and C.D. Thomas. 1996. Open corridors appear to facilitate dispersal by ringlet butterflies (*Aphantopus hyperantus*) between woodland clearings. Conservation Biology 10: 1359 – 1365.

Thomas, C.D., J.A. Thomas, and M.S. Warren. 1992. Distributions of occupied and vacant butterfly habitats in fragmented landscapes. Oecologia 92: 563 – 567.

Warren, M.S. 1985. The influence of shade on butterfly numbers in woodland rides, with special reference to the wood white *Leptidea sinapsis*. Biological Conservation 33: 147 – 164.

Wiens, J.A. 1992. Ecological flows across landscape boundaries: a conceptual overview. Pages 217 – 235 *in* Armand, A.O. *et al.*, editors. Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows. New York: Springer-Verlag.

Wiens, J.A. and B.T. Milne. 1989. Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective. Landscape Ecology 3: 87 – 96.

Wiens, J.A., N.C. Stenseth, B. Van Horne, and R.A. Ims. 1993. Ecological mechanisms and landscape ecology. Oikos 66: 369 – 380.

Wilcox, B.A., D.D. Murphy, P.R. Ehrlich, and G.T. Austin. 1986. Insular biogeography of the montane butterfly faunas in the Great Basin: comparison with birds and mammals.

With, K.A. and T.O. Crist. 1995. Critical thresholds in species' responses to landscape structure. Ecology 76: 2446 – 2459.

With, K.A., R.H. Gardner, and M.G. Turner. 1997. Landscape connectivity and population distributions in heterogeneous environments. Oikos 78: 151 – 169.

Chapter 2. The effect of tree density on butterfly diversity and abundance in a successional landscape

> **"Woodland management policies that do not promote opening of canopies often negatively affect butterflies exploiting seral stages within the successional progression from grassland to woodland"**
> **(Grundel *et al.* 1998)**

Introduction

Landscape change is an unavoidable consequence of human presence in natural areas. Most ecologists studying the effects of landscape change are concerned with the fragmentation of habitat resulting from logging, farming, or urban expansion (*e.g.* Fahrig and Merriam 1994, Nève *et al.* 1996, Schultz 1998, Haddad and Baum 1999). Another consequence of human activity is the disturbance of the natural fire cycles that thin forest and maintain landscape heterogeneity. Even in protected areas, such as national parks, the policy of fire prevention encourages forest succession. The result is more extensive, dense, and homogeneous forests, and reduced landscape heterogeneity (Achuff *et al.* 1996, Rhemtulla 1999). The homogenization of forests decreases the amount of early-successional open and patchy areas. For the organisms occupying such areas, the likely outcome of forest succession is a scenario of habitat fragmentation where remnants of meadows and open forests are surrounded by an impassable matrix of dense "non-habitat" forest.

There are few tools currently available to park managers to monitor the ecological effects of such changes. The only indicators of habitat integrity used to date are elk and other large mammals (Achuff *et al.* 1996, G. Mercer *personal communication*). However, an organism's response to fragmentation is dependent upon both the scale at which it interacts with its environment (Lord and Norton 1990, Doak *et al.* 1992) and its life history (With 1994, Andrén *et al.* 1997). It is unlikely that the scale to which large mammals respond to succession represents the responses of the entire montane animal community. Fragmentation at a scale imperceptible to vertebrates may seriously influence invertebrates (Murphy and Wilcox 1986).

Butterflies are one group of organisms that rely upon these disappearing open areas. Butterflies are tightly linked to open, sunny areas, as they require solar radiation to raise body temperature for flight (Pollard and Yates 1993). Additionally, larval host plants and adults nectar plants are often found in open, early-successional habitats (Warren 1985, Loertscher *et al.* 1995). Even those species whose larval hosts are forest-dwelling plants must use open areas to obtain nectar or to locate mates (Warren 1985). As a result of their strict habitat requirements, butterflies are more sensitive to loss of early-successional habitat than other groups typically used as indicators (Murphy and Wilcox 1986, Wilcox *et al.* 1986, New 1997).

Generally, butterflies are more diverse and abundant in open areas or early-successional stages and decrease rapidly with increases in shrubs and trees (Erhardt 1985, Warren 1985). In the Great Lakes region of North America, fire suppression and the subsequent increase in canopy cover influenced the behaviour of the endangered Karner blue butterfly (*Lycaeides melissa samuelis*) enough to contribute to its decline (Grundel *et al.* 1998). Greatorex-Davies *et al.* (1993) predict that unchecked forest succession will cause marked declines in butterfly abundance, especially those species with very low shade tolerance.

In order to understand how the disappearance of open areas may affect the resident butterfly community of the montane ecoregion in Jasper National Park, I established baseline data on the current distribution of those species that are most likely to be influenced by increasing tree density. My main objective was to identify what determines their distribution in this mosaic landscape, and what may be the outcome of increased tree density and the resultant decreased landscape heterogeneity. I asked three main questions: 1) what are the patterns of butterfly abundance and diversity among sites differing in tree density? 2) do these patterns reflect the distribution of butterfly resource plants? 3) do burned areas represent "new" suitable butterfly habitat? I expected to find species-specific decreases in butterflies and their resource plants with increasing tree density. Forests may become so dense that they support few or no butterflies. By comparing butterfly abundance among sites that differ in tree density and resource plant abundance, I determined if such patterns exist for a variety of butterflies, or only those that are most reliant on open meadows. I also surveyed burned areas for butterflies and their resource plants. Later in this thesis I explore specific behavioural responses to tree density and the possible mechanisms contributing to the patterns of distribution found here.

Methods

Study area

I conducted repeated butterfly counts and vegetation surveys in all 10 study sites (Table 1-1). Seven of these sites were used in 1998, and all ten were used in 1999.

Study species

I collected abundance data for all butterfly species that were present, but focussed on 5 main genera that were common in this system for further analyses: *Coenonympha* spp., *Erebia* spp., *Colias* spp., *Boloria* spp., and *Speyeria* spp. (Table 2-1). I will use the genus names of these groups and refer to them as "species" throughout this thesis. All require open meadows or open sunny patches in the forest, but the habitats of their larval host plants differ. The larval host plants of "meadow" butterflies (*Coenonympha*, *Erebia*, and *Colias*) are found in meadows and forest. The larval host plant of "forest" butterflies (*Boloria* and *Speyeria*) is found almost exclusively in forest. Two of the meadow butterflies, *Coenonympha* and *Erebia*, are reported as not feeding on nectar (Bird *et al.* 1995). However, I have observed several nectar-feeding events by *Coenonympha*.

Table 2-1. Main study species and their larval host plants (Bird *et al.* 1995).

Genus	Included species	Larval host plant
Boloria	*bellona**	*Viola* spp.
Colias	*christina, philodoce*	*Astragalus* spp.
Coenonympha	*inornata*	grasses
Erebia	*discoidalis, epipsodea*	grasses
Speyeria	*atlantis, electa, mormonia*	*Viola* spp.

*Some individuals of *Boloria freija* were counted early in the season, but were not included in the abundance regression analyses as their larval host plant differs from that of *B. bellona*.

1998 counts

During the summer of 1998, I conducted preliminary butterfly counts in seven of the sites (Table 1 -1) at regular intervals between June 5 and August 14. Sites were surveyed every week when possible, during the peak of butterfly activity (1000 – 1600) on warm, sunny, low-wind days. Using the transect method of Pollard and Yates (1993), two observers walked a predetermined circular transect in opposite directions at a pace of approximately 66m/min, recording all individuals that crossed within a 76 m^2 (approximately 18 m. long and 5 m. wide) detection area in front of them. The circular transects were 314 m. long at each forested site. At the meadow sites we followed the perimeter of the meadow, approximately five meters from its edge. Therefore, at sites M1 and M2 the transects were 1122 m. and 528 m. in circumference, respectively (Figure 2-1). In order to standardize the lengths of these counts between sites, I used the numbers of butterflies observed per minute, rather than absolute number of butterflies, as a measure of abundance.

Most identifications were done to species or genus, but sometimes only to subfamily. In 1998 we did not distinguish between *Speyeria* spp. and *Boloria* spp., and refer to them collectively as fritillaries. Due to the relative difficulty of distinguishing Lycaenids on the wing, they were grouped into one category ("blues").

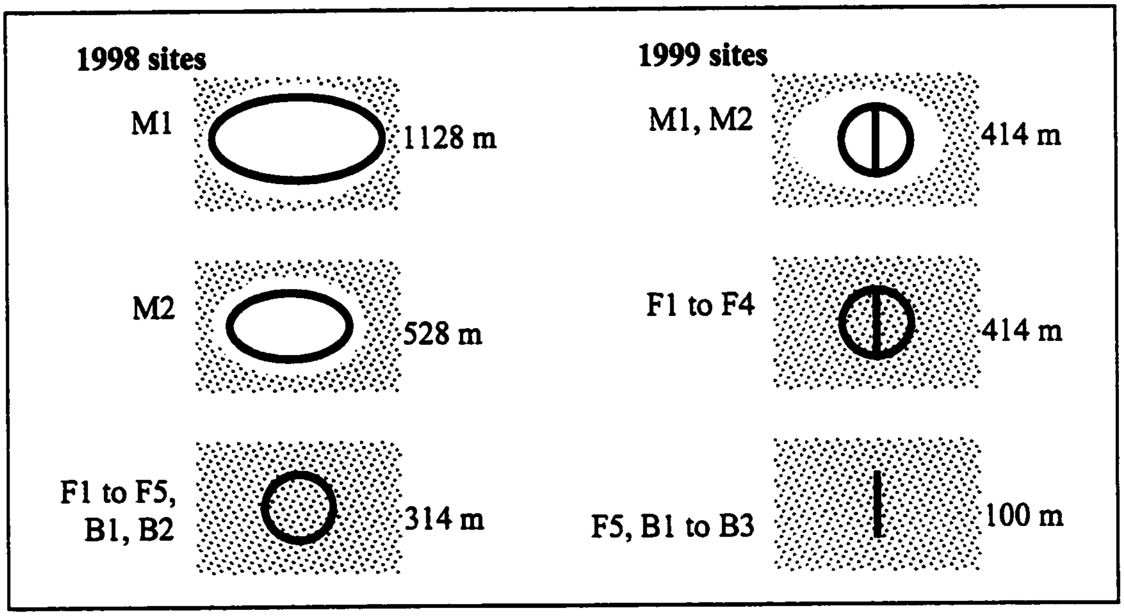

Figure 2-1. Transects used for butterfly counts. Shaded areas represent forest; open areas represent meadow.

1999 counts

In 1999, counts were expanded to include a total of 10 sites with the addition of two forest sites, F2, F4, and one burn site, B3 (Table 1 -1). The count transects were modified in order to concentrate sampling effort in the sites that were also used in other aspects of this thesis. I used the same circular transects in sites F1 and F3 as in 1998, and ran similar transects in sites F2 and F4, adding a 100 m section through the middle of the circle in these four forest sites (Figure 2-1). In the dense forest site F5 and in the burned sites B1, B2, and B3, I marked new linear transects 100 m long. In the two meadow sites, I used 314 m circular transects with a 100 m section through the middle, consistent with those at sites F1 through F4. The counts were conducted in the same fashion as in 1998, except that we walked at a pace of 40 m/min. and decreased our detection area to 11 m^2 (approximately 5 m by 3 m) in order to improve our species recognition and count accuracy between observers.

Host and nectar plant abundance

I conducted vegetation surveys for host plants and flowers used as nectar resources by adults three times during the summer of 1999. Larval host plants surveyed were grasses (*Coenonympha* and *Erebia*), *Astragalus* spp. (*Colias*), and *Viola* spp. (*Boloria* and *Speyeria*). I estimated abundance of the following nectar plants, upon which adult butterflies of at least one, and in many cases all, genera had been observed feeding: *Agoseris* spp., rockcresses (*Arabis* spp.), hawksbeard (*Crepis tectorum*), fleabanes (*Erigeron spp.*), mustard (*Erysimum cheiranthoides*), brown-eyed susan (*Gaillardia aristata*), bedstraw (*Galium boreale*), groundsel (*Senecio* spp.), and goldenrod (*Solidago multiradiata*).

In order to quantify host and nectar plant abundance, I established 20 circular quadrats, 3 m in diameter, randomly throughout sites M1, M2, F1, F2, F3, and F4. In sites B1, B2, B3, and F5, six such quadrats were placed along the 100 m count transect. Individual clumps of *Viola* were counted early in the season before they were hidden beneath other herbaceous vegetation. Percent cover of *Astragalus* and dried grasses were estimated on a scale of 0 – 5, where 0 = none, 1 = < 5%, 2 = < 20%, 3 = 20 – 40%, 4 = 40 – 60%, and 5 = > 60%. Warren (1985) found that such abundance indices correlated well with more objective but time-consuming methods. Individual stems of flowering nectar plants were counted in June, July, and August, as the species in flower changed over the course of the summer. In the burned sites, I scored host and nectar plants as either present or absent.

Data analyses

Observer effect

I tested for differences in observation rates between the two observers using a Wilcoxon signed ranks test to determine if data from both observers could be combined. This test was conducted using counts of the most abundant "groups" (*i.e.* genera, subfamilies, or families) of butterflies from both years. Replicates were individual butterfly group counts, which were paired by date and site. Only counts where at least 10 butterflies of a particular group were seen were used.

Tree density effects on butterfly community composition

To determine which site(s) were potential habitat for the largest number of butterflies, I assessed butterfly group richness and abundance in all sites. Using the count data from both years, I calculated the inverse of Simpson's index of diversity for all sites. This diversity measure places more emphasis on common groups (Krebs 1989). I used mean rates of observation in terms of number of individuals of each group observed per survey minute, which I refer to as "abundance". These values are based on counts over the course of the entire summer, so species with short flight periods and low numbers were weighted less. I excluded all Lycaenids from these analyses due to their extreme abundance and ubiquity relative to other groups.

In 1999 we recorded all incidental butterfly observations outside of counts as I had repeatedly noted the presence of some species that were not observed in formal counts. I compiled these data and combined them with count data from both years to score presence of each butterfly species or subfamily in each site. I then calculated Jaccard (S3) similarity coefficients among sites. This measure compares presence-absence data and ranges from 1 for sites with identical species presence to 0 for completely dissimilar sites (Krebs 1989).

Tree density effects on butterfly abundance

Abundance of *Colias*, *Coenonympha*, *Erebia*, *Boloria*, and *Speyeria* was calculated in each site as the mean number of butterflies seen per survey minute during each species' flight period in 1999. In order to determine possible relationships among habitat variables and butterfly abundance, I plotted butterfly abundance against tree density, and host and nectar plant abundance. After examining these scatterplots, I performed linear and non-linear regression analyses to find the best-fitting relationship. I also determined if relationships existed between each plant resource and tree density in order to obtain an approximation of habitat suitability. Although count data are often Poisson-distributed, the use of parametric regression is not prohibited for the purpose of examining trends and calculating regression statistics (Zar 1996). Outliers and other influential data points (Sokal and Rohlf 1998) were not excluded from analyses due to lack of replication; rather, I considered the biological reasons for the patterns they produced.

Butterfly response to site patchiness

In 1998 more butterflies were observed in the open sunny sections of forest sites than in the closed, shaded sections of the same sites, indicating a possible reaction to fine-scale variation in tree density or patchiness. In order to test this pattern statistically in 1999, I divided sites M1, M2, and F1 through F4 into ten equal sectors and recorded butterfly numbers separately for each sector. Numbers of butterflies seen in each sector over the course of the summer were compared within sites using G tests for heterogeneity. I performed this test separately for meadow butterflies (*Coenonympha*, *Erebia*, and *Colias*) and forest butterflies (*Boloria* and *Speyeria*). Differences were related to the level of sun versus shade, which was categorized visually into three levels: > 75% sun, 25 – 75% sun, and < 25% sun. I also performed this test for the two meadow sites to determine if heterogeneity in butterfly abundance existed without the effect of variability in tree density.

Results

Observer effect

In 1998, butterfly numbers were high, allowing me to test for differences in observation rates for three groups of butterflies: "blues" (Lycaenidae), *Colias* and fritillaries (*Boloria* and *Speyeria*). In 1999 butterflies were far less abundant, precluding the use of this test on most groups. The only group abundant enough to be compared between observers in 1999 was blues.

The only significant observer effect was for blues in 1998 ($Z = -0.263$, $df = 2,10$, $P = 0.024$). I suspect the significant difference was due to the 1998 sampling method, which was less precise than the 1999 sampling method, especially for small, difficult to see butterflies (see methods). Blues were not included in any analyses. Counts of all other groups by both observers were combined for the following analyses.

Tree density effects on butterfly community composition

In 1998 we conducted a total of 46 counts, for an average of 7 counts per site. In 1999, our total number of counts was 149, for an average of 17 counts at sites M1, M2, and F1 through F4, and 12 counts at F5 and the burn sites. In 1998 numbers decreased over the course of the sampling period due to an unusually early spring – it is likely that we missed the beginning of the flight season in that year. In 1999 the entire flight period occurred within our sampling timeframe. Butterfly numbers were lower in 1999, likely due to cool and wet weather. Despite the modified count technique and the decrease in butterfly numbers from 1998 to 1999, Simpson's index of diversity was similar between years for sites evaluated in 1998 and 1999. Nonetheless, I limit interpretations to the more frequent and precise 1999 counts. Diversity values were similar among the two meadow sites in both years, and among the four low and medium density forest sites in 1999 (Figure 2-2). The meadow sites were less diverse than all forest sites but the most dense. This was undoubtedly due to the dominance of *Colias* and *Coenonympha* in the meadows, and the presence of forest-dwelling butterflies whose larvae feed on tree foliage in the forest sites, such as *Papilio canadensis* and Nymphalid species (Table 1-2).

The 1989 and 1999 burns had low butterfly diversity, while the 1998 burn was similar in diversity to the intact forest sites (Figure 2-2). Of the burned sites, the 1998 burn B2 had the most butterfly resources (Table 2-2). All plants except a small amount of grass and *Astragalus* were absent from the most recent burn, B3.

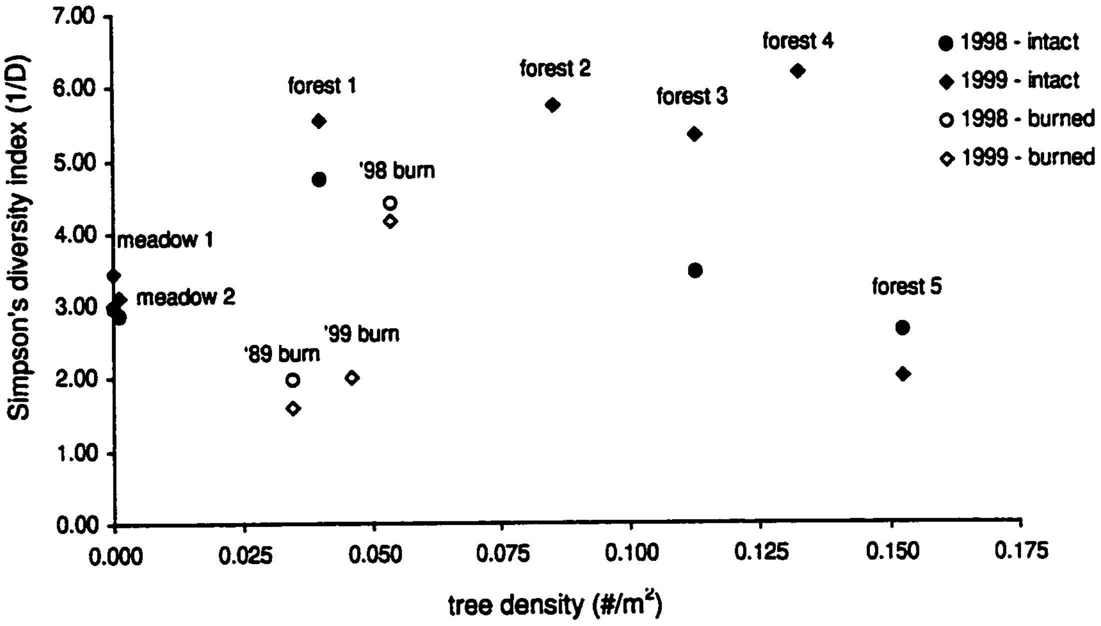

Figure 2-2. Simpson's diversity index (1/D) for all sites surveyed in both years. Calculations based on mean number of butterflies of each group seen per minute in each site.

Table 2-2. Presence and absence of butterfly resource plants in the three burned sites.

plant	Burn1 (1989)	Burn2 (1998)	Burn3 (1999)
Viola	present*	present	absent
Astragalus	present	present	present
Nectar plants (June)	present	present	absent
Nectar plants (July)	present	present	absent
Nectar plants (August)	present	present	absent

*One quadrat out of six had approximately 14 violets; the remainder had 0.

In terms of species presence, tree density does not appear to be the only factor that influenced community similarity. Sites M1, F1, and F3, which were located in close proximity to each other, were highly correlated to one another (Table 2-3). Similarly, highly correlated pairs F2 and F4 were adjacent to one another. Both M2 and B1, which were also correlated to one another, were both located on a slight rise that was more xeric than the other sites. If tree density was the main factor determining butterfly species composition, sites M1 and M2 would be highly correlated, as would sites F1 and F2, F3 and F4, F4 and F5. Sites B3 and F5, which were depauperate relative to the other sites, showed little correlation with any other sites.

Table 2-3. Jaccard coefficients (S3) among sites in 1999. A value of 1.00 indicates a perfect correlation between sites. Coefficients are calculated based on presence-absence data from both years for eleven groups of butterflies. Bold values indicate the highest S3 value for each site listed along the top of the table. Sites labeled M are meadow sites; those labeled F are forest sites; those labeled B are burn sites.

	M1	M2	F1	F2	F3	F4	F5	B1	B2	B3
M1		**0.78**	0.90	0.80	0.82	0.80	0.40	0.56	**0.78**	0.33
M2	0.78		0.70	0.78	0.64	0.78	0.33	**0.71**	0.75	0.43
F1	**0.90**	0.70		0.90	**0.91**	0.90	0.50	0.50	0.70	0.30
F2	0.80	**0.78**	0.90		0.82	**1.00**	**0.56**	0.56	**0.78**	0.33
F3	0.82	0.64	**0.91**	0.82		0.82	0.46	0.46	0.64	0.27
F4	0.80	**0.78**	0.90	**1.00**	0.82		**0.56**	0.56	**0.78**	0.33
F5	0.40	0.33	0.50	0.56	0.46	0.56		0.43	0.50	0.33
B1	0.56	0.71	0.50	0.56	0.46	0.56	0.43		0.71	**0.60**
B2	0.78	0.75	0.70	0.78	0.64	0.78	0.50	**0.71**		0.43
B3	0.33	0.43	0.30	0.33	0.27	0.33	0.33	0.60	0.43	

These descriptive metrics indicate that the butterfly communities of patchy forests and meadows overlapped, although the forests supported a somewhat more diverse community. Tree density did not influence diversity (Figure 2-2) or species composition (Table 2-3) in terms of presence/absence except at the threshold density seen at F5. The burned areas also supported butterfly communities, although in the 1989 burn and the 1999 burn these communities were less diverse than intact forest sites of similar tree density. The 1998 burn was similar to the patchy forest sites in both butterfly diversity and composition.

Tree density effects on butterfly abundance

Three of the four butterfly resource plants showed trends relative to tree density, (Table 2-4). Dried grass (larval host plant for *Coenonympha* and *Erebia*) was the one plant resource that showed no clear relationship to tree density (Figure 2-3 a). However, the proportion of quadrats with *Astragalus* present and the number of violets per quadrat were related to tree density (Figure 2-3 b and c.), with no violets present in the samples from meadows. Violets were noted as present in low numbers in sites M1 and F1, but were totally absent from M2. The abundance and species of nectar plants in flower changed through the summer. In June and August, there were no differences among sites, although meadow site M2 had high numbers of nectar plants. By midsummer, the difference between M1 and M2 had decreased, and nectar plants abundance generally decreased with tree density (Figure 2-3d).

Table 2-4. Linear and non-linear regression statistics for the effect of tree density of the abundance of each plant group (Systat 8.0 1999). Coefficient letters in brackets denote linear (l) or quadratic (q) functions.

Plant	Regression coefficients	r^2	p
dried grass	--	--	ns
Astragalus	b1=8.07, b2=-60.24 (q)	0.98	<0.001
Viola	b1=44.19, b2=-137.16 (q)	0.91	<0.05
nectar (June)	--	--	ns
nectar (July)	-30.67 (l)	0.77	<0.05
nectar (August)	--	--	ns

The date of peak abundance for each butterfly species differed slightly between sites (Table 2-5), although this may be due more to random variation (sampling frequency, weather conditions, and lack of replication) than differences in phenology. The three species associated with open meadow habitat - *Coenonympha*, *Erebia*, and

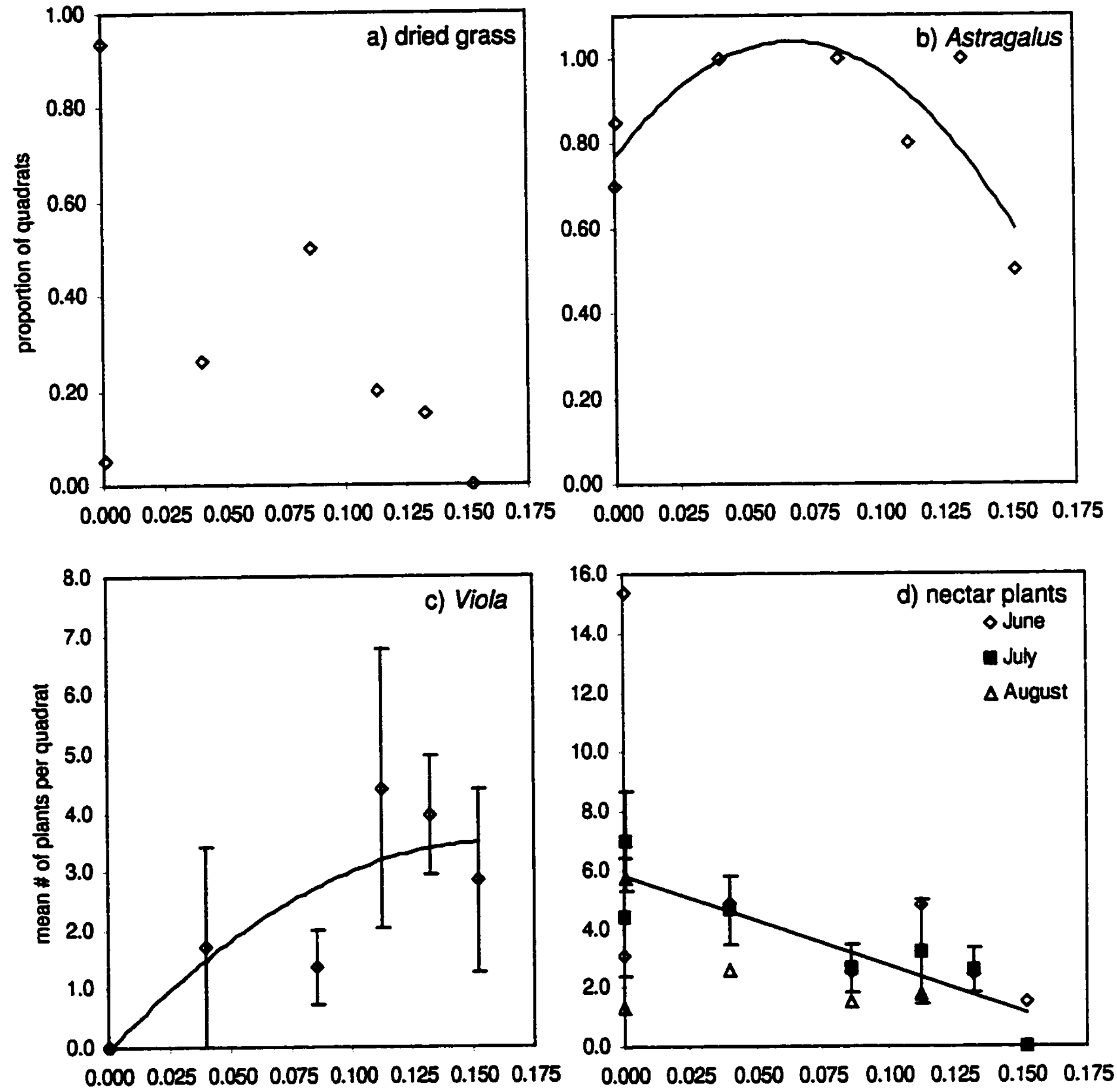

Figure 2-3. Abundance of butterfly resource plants in sites differing in tree density in 1999. Grass and *Astragalus* were measured in terms of the proportion of quadrats with a minimum density of plants; *Viola* and nectar plants were measured in terms of absolute number of plants. Trendlines indicate significant relationships. In d), the trendline corresponds to July values of nectar plant abundance only.

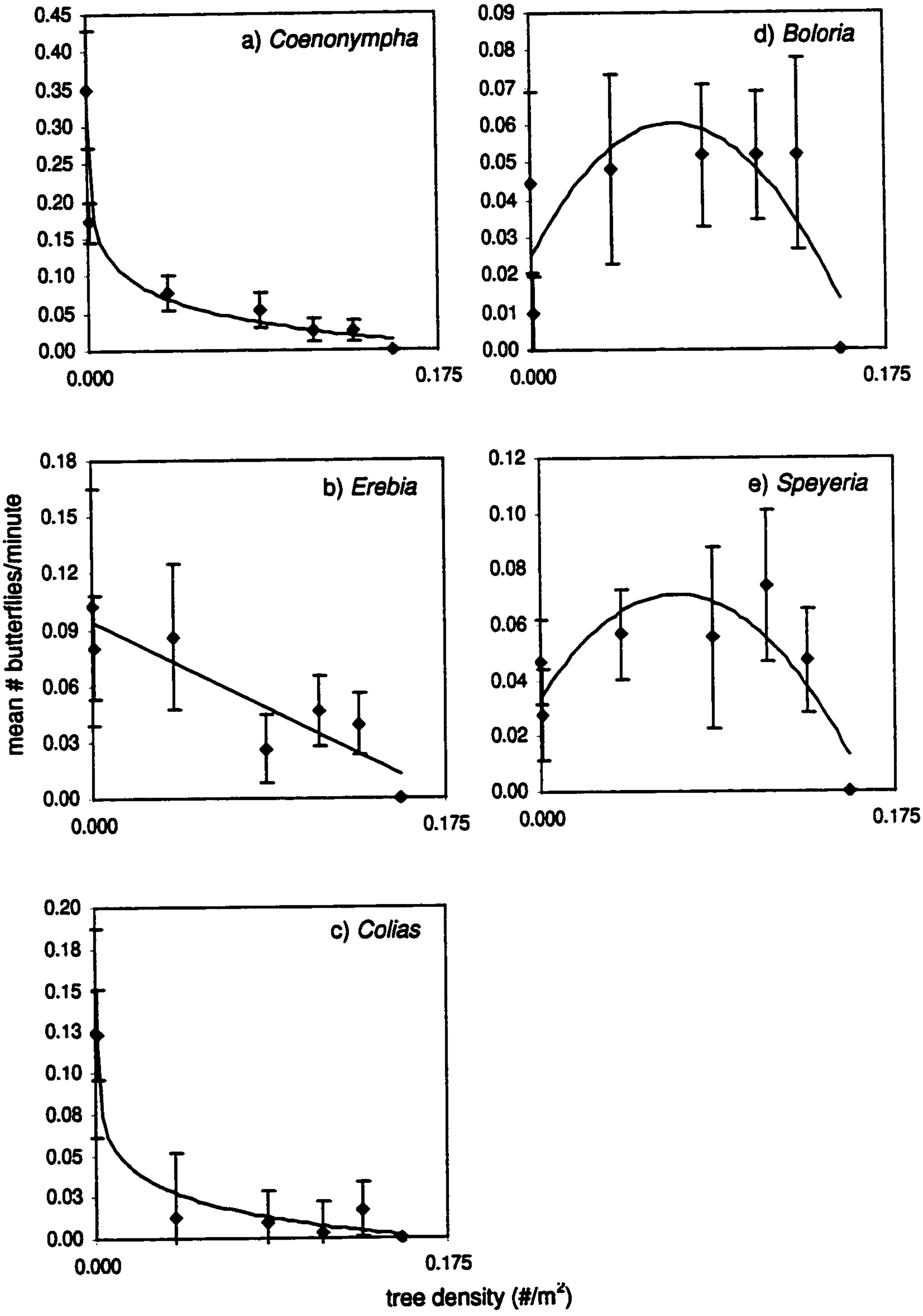

Figure 2-4. Mean number of butterflies seen per minute in 1999 at sites differing in tree density. Trendlines indicate significant relationships.

Colias - all declined with increasing tree density (Figures 2-4 a, b, and c, respectively), although the shape and strength of the relationship differed between species (Table 2-6). The abundance of forest butterflies *Boloria* and *Speyeria* showed significant relationships with tree density, with both species being most abundant in medium density forest (Figure 2-4 c and d). All five species of butterfly are absent at F5, indicating a likely tree density threshold.

Table 2-5. Flight periods and date of maximum abundance of each species in 1999.

Species	Flight period	M1	M2	F1	F2	F3	F4
Coenonympha	15 June – 21 July	4 Jul	9 Jul	16 Jul	4 Jul	30 Jn	10 Jul
Erebia	20 May – 6 July	16 Jn	12 Jn	16 Jn	12 Jn	26 Jn	12 Jn
Colias	24 May – 7 Aug	6 Jul	6 Aug	3 Jn	12 Jn	16 Jul	11 Jn
Boloria	6 June – 9 July	16 Jn	12 Jn	3 Jn	7 Jn		14 Jn
Speyeria	3 June – 7 Aug	3 Aug	6 Aug	13 Jul	31 Jul	29 Jul	31 Jul

It is possible that the shapes of these curves were influenced by butterfly responses to host and/or nectar plant densities in each site, rather than tree density *per se*. *Coenonympha* increased significantly, but weakly, with increasing grass cover (Figure 2-5 a). Site M1 had the most grass and *Coenonympha* and clearly drove this relationship (leverage = 0.907, Cook distance = 7.818). Conversely, *Erebia* abundance was not related to dried grass abundance (Figure 2-5 b), despite grass being its host plant. *Colias*, *Boloria*, and *Speyeria* did not show clear relationships with the abundance of their respective host plants (Figure 2-5 c, d, and e).

None of the nectar-feeding species were more abundant at sites with high nectar plant density (Figures 2-6 a-d). *Coenonympha* responded to nectar as it did to dried grass – it is quite high in both meadow sites, regardless of resource density (Figure 2-5 a and 2-6 a). It is possible that the high abundance of grass in M1 and the high abundance of nectar plants in M2 counteracted the low abundance of the complementary plant resource in both sites.

Response to site patchiness

Although there were differences in butterfly abundance among sectors within most sites, these patterns do not reflect the levels of sun in these sectors (Table 2-7, column A). Interestingly, of the sites that showed significant differences in butterfly numbers among sectors, two were the meadow sites. For each forest site I combined sectors with similar levels of sun and repeated the analyses on these larger groups, but again found no significant differences related to sun (Table 2-7, column B).

Table 2-6. Linear and non-linear regression statistics for the relationship between the abundance of each butterfly species and three different factors. Non-linear coefficient letters in brackets denote exponential (e), logarithmic (l), or quadratic (q) functions

Species	Factor	Linear Coefficient	r^2	p	Non-linear Coefficients	r^2	p
Coenonympha	tree density	-1.665	0.71	<0.05	-0.042 (l)	0.98	<0.001
	dried grass	0.091	0.57	<0.05	--	--	--
	nectar (June)	--	--	ns	--	--	--
Erebia	tree density	-0.531	0.82	<0.005	--	--	--
	dried grass	--	--	ns	--	--	--
Colias	tree density	-0.759	0.70	<0.05	-0.019 (l)	0.96	<0.001
	Astragalus	--	--	ns	--	--	--
	nectar (July)	0.019	0.52	<0.10	0.40(e)	0.73	ns
Boloria	tree density	--	--	ns	$b_1=0.10$, $b_2=-7.04$(q)	0.76	<0.01
	Viola	--	--	ns	--	--	--
	nectar (June)	--	--	ns	--	--	--
Speyeria	tree density	--	--	ns	$b_1=1.08$, $b_2=-8.01$(q)	0.93	<0.05
	Viola	--	--	ns	--	--	--
	nectar (July)	--	--	ns	--	--	--

Table 2-7. G values and significance for differences in meadow and forest butterfly abundance. In column A, differences between individual sections were compared (df = 9). In column B, differences between sunny and shady areas were compared (df = 1). Values marked with an asterisk denote G-tests with 2 df. This site had sunny, shady, and sunless sections.

site	butterfly type	n	A G-test (sections)	B G-test (sun level)
M1	meadow	123	29.51, $p< 0.005$	N/A
	forest	17	7.96, ns	
M2	meadow	65	7.88, ns	N/A
	forest	8	17.43, $p< 0.05$	
F1	meadow	36	3.28, ns	0.021, ns
	forest	21	9.75, ns	0.005, ns
F2	meadow	16	14.92, ns	0.019, ns
	forest	25	17.64, $p< 0.05$	0.000, ns
F3	meadow	17	11.78, ns	0.052, ns
	forest	31	20.15, $p< 0.025$	0.018, ns
F4	meadow	18	15.25, ns	5.01, $p< 0.10$*
	forest	20	13.32, ns	2.73, ns*

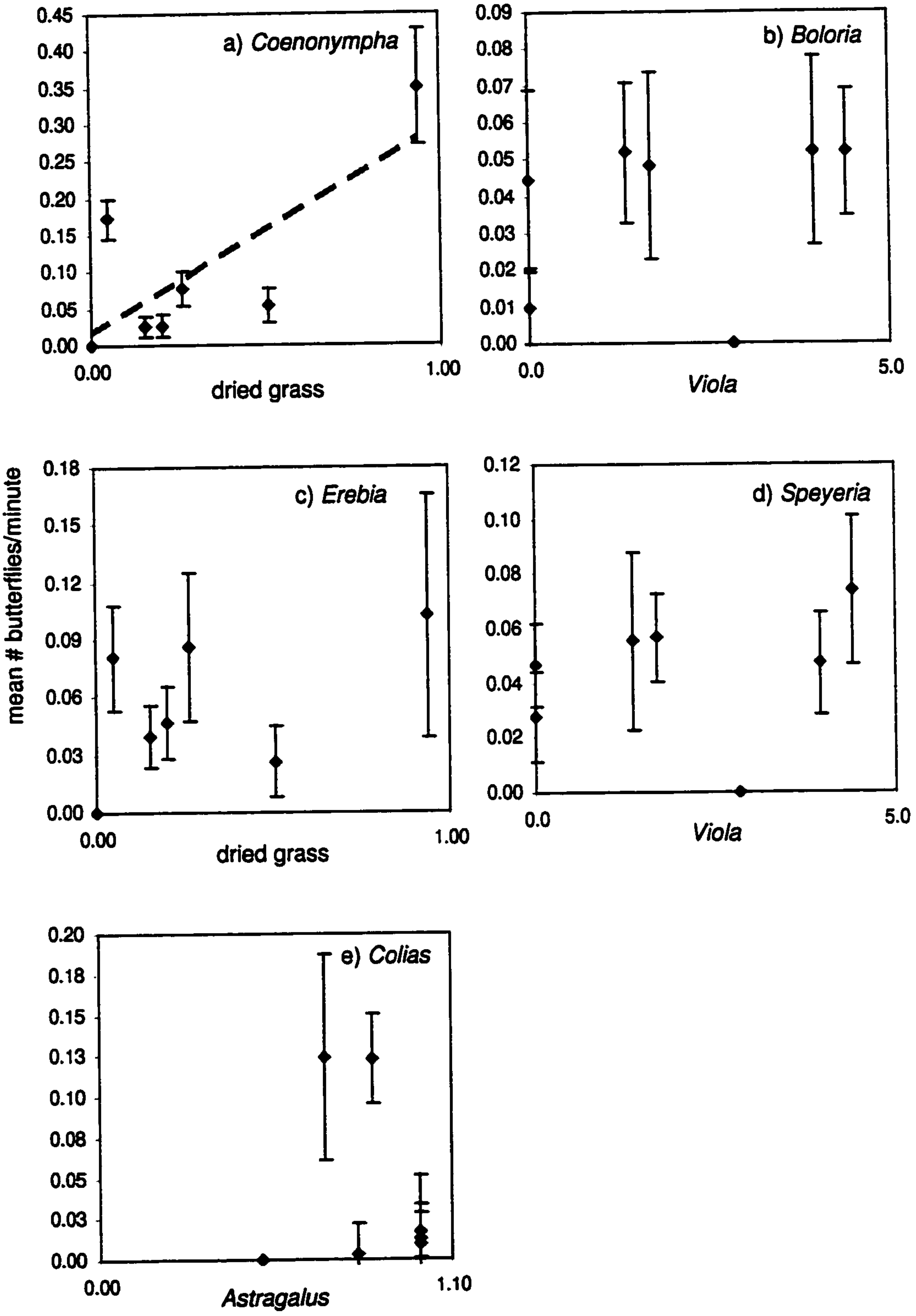

Figure 2-5. Relationships between butterfly abundance and abundance of their respective larval host plants. Larval host plant units are the same as in Figure 2-3.

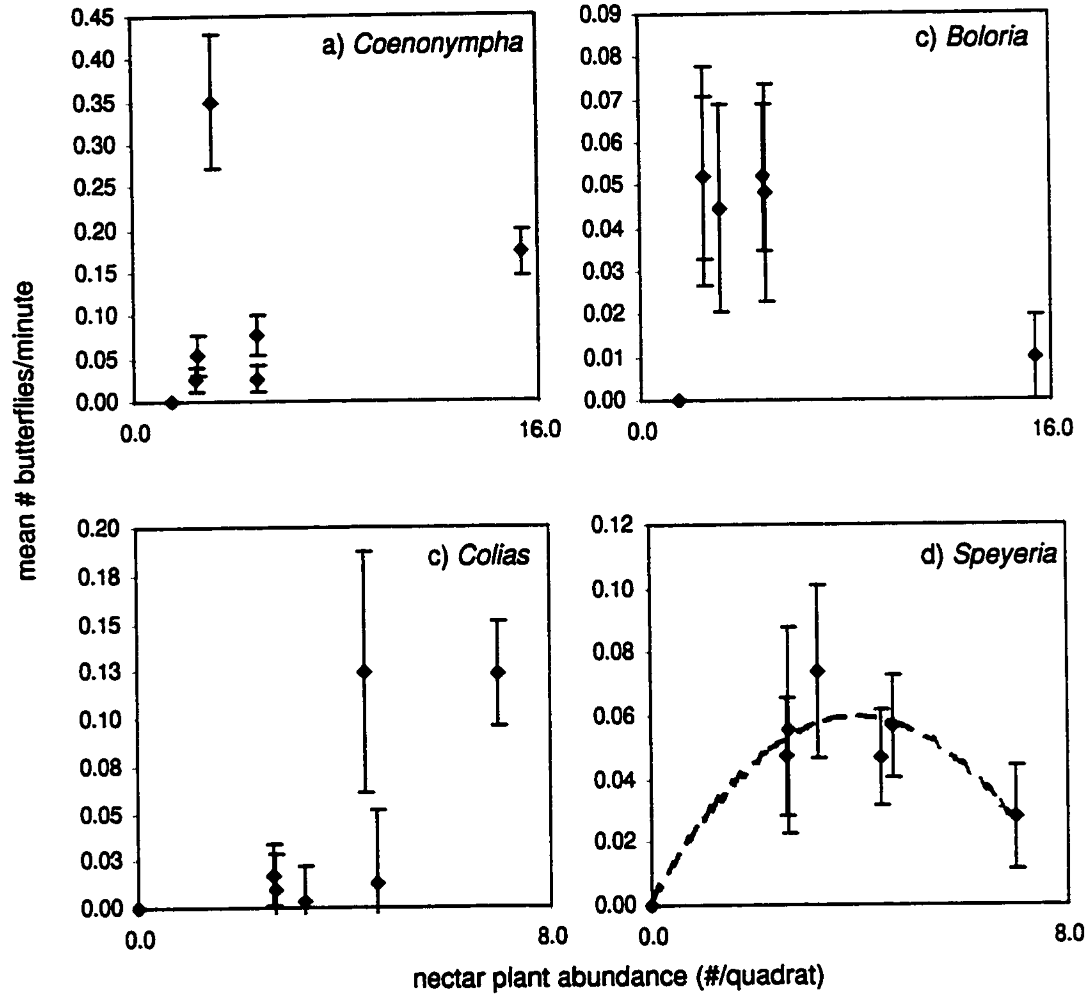

Figure 2-6. Relationships between butterfly abundance and nectar plant abundance for species that nectar-feed. *Coenonympha* and *Boloria* are related to nectar plants abundance in June 1999; *Colias* and *Speyeria* are related to nectar plant abundance in July 1999.

Discussion

This study demonstrated a small-scale, species-specific effect of tree density on the abundance of butterflies and their larval and adult food resources. Butterflies used both open meadows and patchy forests, suggesting that the meadows are not strictly habitat "islands", and that forests are not strictly "hostile matrix". However, a limit to the abundance and diversity of all butterflies was detected at the highest tree density examined, suggesting that there is a tree density threshold that is either impenetrable or unsuitable for these butterflies. The effects of tree density on butterfly movement and behaviour are examined in the following two chapters.

Low and medium density forests are clearly valuable butterfly habitat in this system. All five focal species were present in the patchy forest sites, as were their resource plants. The high levels of butterfly community correlation between some meadow and forest sites indicate that butterflies readily move among these landscape elements, and that butterflies view this system as heterogeneously undivided (Addicott *et al.* 1987) to some extent. Contrary to Warren's finding (1985) that the most sunny and open areas had the most diverse butterfly communities in British woodlands, I found that the low and medium density forests were the most diverse (Figure 2-2). Sites at either end of the tree density spectrum had reduced butterfly diversity. This pattern was predicted by With and Crist (1995) in the context of fragmentation in large landscapes. Here at the scale of individual patches, we see that the most homogeneous patches (*i.e.* meadows and dense forest) are dominated by species specializing in such areas. As heterogeneity increases (*i.e.* patchy forests), there is a mixture of meadow and forest-opening species. With and Crist (1995) labeled this the "double-threshold effect", where a decrease in diversity is seen at the highest levels of homogeneity. In this case, this occurs at the lowest and highest levels of tree density.

In addition to supporting diverse butterfly communities, the low and medium density forests supported high numbers of fritillaries, *Boloria* and *Speyeria*. Fritillaries are normally associated with forest openings and edges (Bird *et al.* 1995). Their abundance in patchy forest suggests that they are probably responding to the small sunny patches that were not quantified in this study. Tree density is an indirect measure of the amount of sunny patches in the forest – at high tree densities, there are fewer sunny patches. Although a response to patchiness of sun and shade was not detected in this study (Table 2-7), I found that butterflies oriented towards open areas within the forest in other aspects of this study that were specifically designed to detect such a response (Chapter 4).

Both *Boloria* and *Speyeria* were absent from the high density forest despite the presence of their host plant *Viola*. Absence of these species was therefore likely due to the paucity of sunny patches and nectar plants in this forest. Nectar-feeding butterflies tend to avoid areas where nectar plants are absent, such as dense forest (Figure 2-3 d), even if these areas are rich in larval host plants (Grossmueller and Lederhouse 1987). Conversely, fritillary abundance in areas lacking violets but rich in nectar plants was similar to their abundance in patchy forests. Due to their vagility (Wiklund 1977) and their abundance throughout most sites, it is likely that the habitat requirements of fritillaries are partitioned among several patch types (Brakefield 1982, Andrén *et al.* 1997, Schwarzwälder *et al.* 1997, Law and Dickman 1998). Habitat partitioning by fritillaries may be related to canopy cover (Grundel *et al.* 1988), with shady, violet-rich areas used for oviposition, and open areas used for nectar-feeding. These patterns suggest that the juxtaposition of landscape elements, as well as the ability to move between landscape elements, may be crucial to butterfly abundance.

While forest species made use of the low and medium density forests, the strong response to tree density of meadow butterflies indicates their clear preference for meadows. It seems that meadow species are responding to sun, rather than larval host plants or nectar availability. However, nectar plants and amount of sun are often correlated (Warren 1985, Haddad and Baum 1999) and the correlation among these factors and tree density produced complex relationships between butterfly abundance and plant resources. Ingham and Samways (1996) found that few butterfly species' distributions mirrored that of the vegetation they relied upon. A field experiment manipulating plant resources would help tease apart the separate effects.

Both meadow butterflies and nectar plants were less abundant at high tree densities, yet I failed to find a clear relationship between butterfly and nectar plant abundance. This was surprising given that *Colias* are known to nectar-feed frequently

(Boggs 1987) and that other studies have found correlations between butterfly and nectar plant distributions and abundance (Murphy 1983, Munguira and Thomas 1992, Loertscher *et al.* 1995, Haddad and Baum 1999). The main reason I did not observe this relationship was the disproportionately high butterfly abundance in M1 relative to nectar plants. Similarly, F1 had high numbers of nectar plants but not butterflies. The fact that all three butterfly species decreased markedly with tree density (which is tightly correlated with amount of sunlight), but had less obvious relationships with their resource plants, suggests that sunlight is the most important resource in this system determining fine-scale patterns of butterfly abundance. It is also possible that these species prefer to navigate through open areas, either in order to maintain their body temperature, or perhaps because they are looking for mates. All three species employ a patrolling mating strategy (Bird *et al.* 1995) – a method that is probably most effective in areas with high visibility, such as meadows. Mate-finding behaviour (Loertscher *et al.* 1995) and female avoidance of male harassment (Odendaal *et al.* 1989) are also known to disrupt correlations between plant and butterfly distributions.

Habitat selection by butterflies is based on a wide variety of factors (Warren 1985, Haddad 1999), and I have only measured three. Topography and aspect (Harrison *et al.* 1988), as well as wind (Dover *et al.* 1997), influence habitat quality. The differences between and within the two meadow sites in terms of plant and butterfly abundance are evidence of the importance of factors such as microclimatic conditions, which can influence butterflies directly by facilitating thermoregulation, or indirectly through host plant suitability (Bourn and Thomas 1993). However, as the results of this study suggest, tree density may be a critical factor determining the distribution of butterfly species (Warren 1985) at fine scales, partially due to its influence on other factors.

Although meadow butterflies decreased with tree density, they were present in the forest sites, and later in this thesis I show that they use the resources available in forest sites (Chapter 4). Others have shown that because butterflies will nectar-feed opportunistically, passing butterflies can be drawn into otherwise suboptimal areas (Sharp *et al.* 1974, Warren 1985, Nève et al 1996). Although not optimal habitat for meadow butterflies, forests are important refuges providing shade on very hot days

(Pollard and Yates 1993) or shelter on windy days (Dover *et al.* 1997). All butterflies, however, require some open patches when using forests (Warren 1985). Additionally, the varied microclimates within forests cause variation in the quality of any larval host or nectar plants present. For example, meadow-specialist *Aricia agestis* butterflies prefer larval host plants growing in or near forests, due to their higher quality (Bourn and Thomas 1993). The homogenization of forests through succession would prevent the use of forests by both meadow and forest species.

Are prescribed burns a feasible way to maintain open and patchy forests? Two of the burned sites I surveyed supported butterfly communities and the plants that they depend upon. The 1998 burn, in particular, appeared to be similar to comparable intact forest sites in terms of butterfly habitat quality. Most butterflies present in the burns were fritillaries, which are habitat "generalists" (Figures 2-4 d and e). Swengel (1996) also reported high abundance of habitat generalists in burned grassland sites. Timing of burns is likely to influence the response of butterflies in the first few summers following the burn. It is not surprising that the 1999 burn had so few butterflies and plants as it was still smoldering at the beginning of my sample period, while the 1998 burn, which took place earlier in the year, was experiencing regrowth when I began sampling it. By applying the methods used and knowledge gained in this study to several forested areas pre- and post-burn, it would be possible to make definitive statements regarding the ability of prescribed burning to open up new early-successional butterfly habitat. It is likely that the historical fire regime in this area maintained forest heterogeneity through frequent fine-scale burns within forest patches (*i.e.* individual trees), with occasional stand-replacing fires (Rhemtulla 1999). By attempting to mimic such patterns and creating heterogeneity within dense stands, prescribed fires would reduce forest homogeneity, increasing the amount and extent of potential butterfly habitat.

This preliminary survey indicates that tree density is an important determinant of butterfly distribution. The transect count method, despite its variability (Frazer 1973), is an easy way to assess butterfly presence and relative abundance. At a larger scale, with several replicated sites, these methods could be used in conjunction with multiple regression analysis to clarify the relationships between plant abundance, environmental variables, and butterfly abundance. Some authors have suggested using butterflies as surrogates for other groups, such as vertebrates (Murphy and Wilcox 1986, Blair 1999, Swengel and Swengel 1999) and plants (Launer and Murphy 1994). Correlations in abundance between butterflies and these other groups have been documented, despite possible differences in the scale at which each group responds to its environment (Swengel and Swengel 1999). Although responses to fragmentation are species-specific due to both the scale at which organisms respond to the landscape and their life history, it may be demonstrative to use easily censused groups such as butterflies as "bioassays" of habitat heterogeneity.

Conclusion

It is clear that a heterogeneous landscape, composed of meadows, open forest, and older forest, would support the greatest diversity and abundance of montane butterflies. Both meadow and forest butterflies use open and patchy forests, indicating that these areas provide at least part of their habitat requirements. In Chapters 3 and 4 I explore how movement between patches of optimal habitat is facilitated by open and patchy forest.

It is unlikely that even butterflies specializing in meadow habitat view this system as a discrete series of meadow "islands". Rather, the results I have obtained indicate that the montane region is a "continuum of varying suitability" (McIntyre and Barrett 1992), and that each forest patch supports its own mixed butterfly community. Further increases in forest homogeneity in the Athabasca River Valley of Jasper National Park would affect the abundance of the resident butterfly species. Other studies have suggested that preserving a variety of habitat types maintains the greatest number of species, both in butterfly communities (Warren 1985, Schwarzwälder *et al.* 1997) and other groups (Erhardt 1985, Freemark and Merriam 1986, McIntyre and Barrett 1992). Grasslands are of limited extent in the Rocky Mountain parks, yet many animals are at least somewhat reliant on them (Achuff *et al.* 1996). In order to monitor the integrity of the unique open areas in the valley bottom, it is important to observe groups like butterflies that are so closely tied to them.

Literature Cited

Achuff, P.L., I. Pengelly, and J. Wierzchowski. 1996. Vegetation: cumulative effects and ecological futures outlook. *In* Greens, J., C. Pacas, L. Cornwell, and S. Bayley, editors. Ecological Outlooks Project. A cumulative effects assessment and futures outlook of the Banff Bow Valley. Prepared for the Banff Bow Valley Study. Department of Canadian Heritage, Ottawa, ON. 47 pp.

Addicott, J.F., J.M. Aho, M.F. Antolin, D.K. Padilla, J.S. Richardson, and D.A. Soluk. 1987. Ecological neighbourhoods: scaling environmental patterns. Oikos 49: 340 – 346.

Andrén, H., A. Delin, and A. Seiler. 1997. Population response to landscape changes depends on specialization to different landscape elements. Oikos 80: 193 – 196.

Bird, C.D., G.J. Hilchie, N.G. Kondla, E.M. Pike, and F.A.H. Sperling. 1995. Alberta butterflies. The Provincial Museum of Alberta, Edmonton, Alberta.

Blair, R.B. 1999. Birds and butterflies along an urban gradient: surrogate taxa for assessing biodiversity? Ecological Applications 9: 164 – 170.

Boggs, C. 1987. Ecology of nectar and pollen feeding in Lepidoptera. Pages 370 – 391 *in* Slansky, F. and J.G. Rodriguez, editors. Nutritional ecology of insects, mites, spiders, and related invertebrates. John Wiley and Sons, Toronto.

Bourn, N.A.D. and J.A. Thomas. 1993. The ecology and conservation of the brown argus butterfly *Aricia agestis* in Britain. Biological Conservation 63: 67 – 74.

Brakefield, P.M. 1982. Ecological studies on the butterfly *Maniola jurtina* in Britain. I. Adult behaviour, microdistribution, and dispersal. Journal of Animal Ecology. 51: 713 – 726.

Doak, D.F., P.C. Marino, and P.M. Kareiva. 1992. Spatial scale mediates the influence of habitat fragmentation on dispersal success: implications for conservation. Theoretical Population Biology 41: 315 – 316.

Dover, J.W., T.H. Sparks, and J.N. Greatorex-Davies. 1997. The importance of shelter for butterflies in open landscapes. Journal of Insect Conservation 1: 89 – 97.

Erhardt, A. 1985. Diurnal Lepidoptera: sensitive indicators of cultivated and abandoned grassland. Journal of Applied Ecology 22: 849 – 861.

Fahrig, L. and G. Merriam. 1994. Conservation of fragmented populations. Conservation Biology 8: 50 – 59.

Frazer, J.F.D. 1973. Estimating butterfly numbers. Biological Conservation 5: 271 – 276.

Freemark, K.E. and H.G. Merriam. 1986. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. Biological Conservation 36: 115 – 141.

Greatorex-Davies, J.N., T.H. Sparks, M.L. Hall, and R.H. Marrs. 1993. The influence of shade on butterflies in rides of coniferised lowland woods in southern England and implications for conservation management. Biological Conservation 63: 31 – 41.

Grossmueller, D.W. and R.C. Lederhouse. 1987. The role of nectar source distribution in habitat use and oviposition by the tiger swallowtail butterfly. Journal of the Lepidopterists' Society 41: 159 – 165.

Grundel, R., N.B. Pavlovic, and C.L. Sulzman. 1998. Habitat use by the endangered Karner blue butterfly in oak woodlands: the influence of canopy cover. Biological Conservation 85: 47 – 53.

Haddad, N.M. 1999. Corridor and distance effects on interpatch movements: a landscape experiment with butterflies. Ecological Applications 9: 612 –622.

Haddad, N.M and K.A. Baum. 1999. An experimental test of corridor effects on butterfly densities. Ecological Applications 9: 623 – 633.

Harrison, S., D.D. Murphy, and P.R. Ehrlich. 1988. Distribution of the bay checkerspot butterfly, *Euphydryas editha bayensis*: evidence for a metapopulation model. The American Naturalist 132: 360 – 382.

Ingham, D.S. and M.J. Samways. 1996. Application of fragmentation and variegation models to epigaeic invertebrates in South Africa. Conservation Biology 10: 1353 – 1358.

Krebs, C. J. 1989. Ecological methodology. Harper Collins Publishers, New York, NY, USA.

Launer, A.E. and D.D. Murphy. 1994. Umbrella species and the conservation of habitat fragments: a case of a threatened butterfly and a vanishing grassland ecosystem. Biological Conservation 69: 145 – 153.

Law, B.S. and C.R. Dickman. 1998. The use of habitat mosaics by terrestrial vertebrate fauna: implications for conservation and management. Biodiversity and Conservation 7: 323 – 333.

Loertscher, M., A. Erhardt, and J. Zettel. 1995. Microdistribution of butterflies in a mosaic-like habitat: the role of nectar sources. Ecography 18: 15 – 26.

Lord, J.M. and D.A. Norton. 1990. Scale and the spatial concept of fragmentation. Conservation Biology 4: 197 – 202.

McIntyre, S. and G.W. Barrett. 1992. Habitat variegation, an alternative to fragmentation. Conservation Biology 6: 146 – 147.

Munguira, M.L. and J.A. Thomas. 1992. Use of road verges by butterfly and burnet populations, and the effect of roads on adult dispersal and mortality. Journal of Applied Ecology 29: 316 – 329.

Murphy, D.D. 1983. Nectar sources as constraints on the distribution of egg masses by the checkerspot butterfly, *Euphydryas chalcedona* (Lepidoptera: Nymphalidae). Environmental Entomology 12: 463 – 466.

Murphy, D.D., and B.A. Wilcox. 1986. Butterfly diversity in natural habitat fragments: a test of the validity of vertebrate-based management. Pages 287 – 292 *in* Verner, J., M.L. Morrison, and C.J. Ralph, editors. Wildlife 2000, modeling habitat relationships of terrestrial vertebrates.

New, T.R. 1997. Are Lepidoptera an effective "umbrella group" for biodiversity conservation? Journal of Insect Conservation 1: 5 – 12.

Nève, G., B. Barascud, R. Hughes, J. Aubert, H. Descimon, P. Lebrun, and M. Baguette. 1996. Dispersal, colonization power and metapopulation structure in the vulnerable butterfly *Proclossiana eunomia* (Lepidoptera: Nymphalidae). Journal of Applied Ecology 33: 14 – 22.

Odendaal, F.J., P. Turchin, and F.R. Stermitz. 1989. Influence of host-plant density and male harassment on the distribution of female *Euphydryas anicia* (Nymphalidae). Oecologia 78: 283 – 288.

Pollard, E. and T.J. Yates. 1993. Monitoring butterflies for ecology and conservation. Chapman and Hall, London.

Rhemtulla, J.M. 1999. Eighty years of change: the montane vegetation of Jasper National Park. M.Sc. Thesis. University of Alberta.

Schultz, C. 1998. Dispersal behaviour and its implications for reserve design in a rare oregon butterfly. Conservation Biology 12: 284 – 292.

Schwartzwälder, B., M. Lörtscher, A. Erhardt, and J. Zettel. 1997. Habitat utilization by the heath fritillary butterfly, *Mellicta athalia* ssp. *celadussa* in montane grasslands of different management. Biological Conservation 82: 157 – 165.

Sharp, M.A., D.R. Parks, and P.R. Ehrlich. 1974. Plant resources and butterfly habitat selection. Ecology 55: 870 – 875.

Sokal, R.R. and F.J. Rohlf. 1998. Biometry. W.H. Freeman and Company, N.Y. USA.

Swengel, A.B. 1996. Effects of fire and hay management on abundance of prairie butterflies. Biological Conservation 76: 73 – 85.

Swengel, S.R. and A.B. Swengel. 1999. Correlations in abundance of grassland songbirds and prairie butterflies. Biological Conservation 90: 1 – 11.

Warren, M.S. 1985. The influence of shade on butterfly numbers in woodland rides, with special reference to the wood white *Leptidea sinapsis*. Biological Conservation 33: 147 – 164.

Wiklund, C. 1977. Oviposition, feeding, and spatial separation of breeding and foraging habitats in a population of *Leptidea sinapsis* (Lepidoptera). Oikos 28: 56 – 68.

Wilcox, B.A., D.D. Murphy, P.R. Ehrlich, and G.T. Austin. 1986. Insular biogeography of the montane butterfly faunas in the Great Basin: comparison with birds and mammals.

With, K.A. 1994. Using fractal analysis to assess how species perceive landscape structure. Landscape Ecology 9: 25 – 36.

With, K.A. and T.O. Crist. 1995. Critical thresholds in species' response to landscape structure. Ecology 76: 2446 – 2459.

Zar, J.H. 1996. Biostatistical analysis, 3rd edition. Prentice Hall, Upper Saddle River, USA.

Chapter 3. Barriers to movement: butterfly behaviour at the meadow-forest boundary

"...in order to begin to understand landscape-level patterns and processes, we must know the details of boundary dynamics..." (Wiens *et al.* 1985)

Introduction

Animal movement across different landscape elements links habitat patches and partially determines large-scale patterns of species' distribution and abundance (Wiens *et al.* 1985, Wiens 1992, Stamps *et al.* 1997). The metric used to describe the effect of this phenomenon across landscapes is connectivity (Merriam 1984, Taylor *et al.* 1993), also referred to as behavioural or functional connectivity (Forman 1997). Connectivity is defined as "the degree to which landscape facilitates or impedes movement among resource patches" and is a major component of landscape structure (Taylor *et al.* 1993, Fahrig and Merriam 1994). Since it was first introduced into the landscape literature, connectivity has become a key issue in understanding the ecological effects of landscape heterogeneity on animal populations (*e.g.* Fahrig and Merriam 1994, Sutcliffe and Thomas 1996, With *et al.* 1997, Bjornstad *et al.* 1998, Pither and Taylor 1998).

Connectivity is determined by an organism's response to patches of differing type as it moves through its environment. These responses often take place at the boundaries that define the transitions between patches (Wiens *et al.* 1985, Wiens 1992), and the amount of movement across these boundaries is one way to quantify connectivity (Taylor *et al.* 1993). A boundary is the intersection between patch types, often characterized by a change in vegetation structure (Gosz 1991, Wiens 1992, Lidicker 1999), and its characteristics are important attributes of habitat fragments (Lord and Norton 1990). Several authors have pointed out the importance of boundaries to ecological processes in heterogeneous landscapes (Wiens *et al.* 1985, Stamps *et al.* 1987, Dunning *et al.* 1992, Hansen and di Castri 1992, Fagan *et al.* 1999). For example, boundaries can affect the rate of movement or flow between patches, causing low abundance of individuals in some areas, and high abundance in others (Wiens *et al.* 1985, Dunning *et al.* 1992, Wiens 1992). This effect is due to biases in turning behaviour, whereby more turns are made back into the source patch at boundaries than into the surrounding matrix (Stamps *et al.* 1997, Haddad 1999). By looking at simple behaviours at the boundaries between patches, we can understand how boundary attributes may influence movement across them (Wiens *et al.* 1993, Tischendorf and Wissel 1997, Haddad 1999) and therefore how the resulting patterns of distribution and abundance are produced.

The impact of landscape structure on individual behaviour is a primary mechanism determining the distribution of populations within patchy landscapes (Stamps *et al.* 1987, Johnson *et al.* 1992, Wiens *et al.* 1993, Lima and Zollner 1996, Haddad and Baum 1999), and many authors have decried the lack of empirical studies at this scale (Lima and Zollner 1996, Fagan *et al.* 1999). Indeed, few researchers have examined the way in which boundaries affect rates of movement in the field, although this subject has received attention in both conceptual (*e.g.* Stamps *et al.* 1987, Wiens 1992) and modeling papers (*e.g.* Tischendorf and Wissel 1997, With et. al. 1997, Fagan *et al.* 1999). This study aims to address the lack of empirical research. Many studies have looked at individual behaviours within patches (*e.g.* Stanton 1982, Karieva and Shigesada 1983, Fahrig and Paloheimo 1987, Wiens *et al.* 1993b, Grundel *et al.* 1998), or have looked at movement between patches indirectly through mark-recapture (*e.g.* Kuussaari *et al.* 1996, Nève *et al.* 1996, Mousson *et al.* 1999, Roland *et al.* 2000). In order to synthesize these two methods into techniques that are useful for investigating the mechanisms by which boundaries may affect movement, researchers have just begun to examine individual behaviour at habitat boundaries (Schultz 1998, Haddad 1999, Jonsen and Taylor 2000).

Here I compare the behaviour of several species of butterfly at different meadow-forest boundaries within a patchy landscape caused by forest succession following fire. These butterflies all require open areas for at least some of their resources, including larval host plants, nectar plants, and sunlight. Therefore, I am interested in determining how these organisms respond to the interface between meadow and forest in their daily movements, and how this response is affected by tree density. By observing individual behaviour at the meadow-forest boundary, I am able to quantify the effect of both boundary and butterfly attributes on the amount of movement occurring across these boundaries, and predict the effects on butterfly distributions.

The components of movement across boundaries

Several factors determine the amount of movement across a boundary, including features of both the boundary and the organism (Wiens *et al.* 1985, Stamps *et al.* 1987, Fahrig and Merriam 1994). A key boundary characteristic is hardness; that is, the degree of contrast between adjacent patches in a landscape (Stamps *et al.* 1987, Wiens 1992). In this study, I define hardness as the density of trees at the meadow/forest interface, where low-density forests produce a "soft" edge, and high-density forests produce a "hard" edge. I compared butterfly movement among boundaries differing in hardness. In the landscape that I examined, forest succession is allowing patches of forest to become denser, possibly limiting the movement of butterflies. Boundaries between meadow and forest at my study sites are probably maintained through grazing by elk (P. Achuff, *personal communication*), while trees and shrubs are recruited inside the forest edge, thus increasing the overall hardness of forest boundaries.

Connectivity also depends on an animal's perception of the landscape and its dispersal abilities (With and Crist 1995, Sutcliffe and Thomas 1996, With *et al.* 1997, Gosz 1991, Pither and Taylor 1998, Haddad 1999). I looked at the behaviour of two groups of butterflies that differed in their propensity to fly into forest areas and to use available resources. For each butterfly type I assessed the influence of boundary hardness on three factors that are likely to determine the probability of movement across boundaries: 1) response distance, 2) reaction to boundary, and 3) boundary permeability (Stamps *et al.* 1987, Wiens *et al.* 1985, Wiens 1992, Jonsen and Taylor 1999).

Response distance is the distance at which an individual responds to a boundary by turning away from it (Lima and Zollner 1996), which may indicate where and if an organism perceives a boundary (Wiens 1992). There are very few studies of perceptual ranges of animals, or from what distance they can distinguish habitat vs. non-habitat, although it is a major determinant of dispersal success between habitat patches (Zollner and Lima 1997). At what point an animal perceives a boundary influences the probability that it will cross that boundary (Wiens 1992), and is likely to be species-specific (Lidicker 1999).

The *reaction to the boundary* is the type of behaviour that occurs when an animal detects and responds to the boundary. The type of movement used by animals reacting to boundaries affects overall emigration patterns by influencing rates of encounter with landscape elements and dispersal patterns. Animals that turn back into the source patch will remain concentrated in that patch, while individuals that fly along boundaries are more likely to encounter novel barriers or habitat patches (Stamps *et al.* 1987, Tischendorf and Wissel 1997). The reaction behaviour should differ between organisms, depending upon their sensitivity to the boundary and their degree of habitat specialization (Lidicker 1999).

Finally, *permeability* has been defined as the degree to which a boundary deflects the movement of organisms (Wiens *et al.* 1985). A simple quantitative measure of permeability is the proportion of individuals that actually reach the boundary and then cross it (Stamps *et al.* 1987). This tendency to inhibit or facilitate the movement of organisms reflects the suitability of the forest relative to meadow – if the matrix is suitable habitat, its boundary will be more permeable (Lidicker 1999).

In this study I examine the effect of boundary hardness on each of the above factors in order to discover how dense the forest may become before it disrupts landscape connectivity. I do this for two butterfly types that differ in their habitat preference. I determine how these factors culminate in overall movement across the boundaries, allowing me to identify underlying behavioural mechanisms determining the connectivity of this landscape for butterflies. I expect that species whose resources are partially found in the forest will be more likely to cross boundaries; however, it is possible that some boundaries are too hard for any species to cross them. Overall, I expect to see fewer individuals flying into the forest as boundaries increase in hardness. By relating the effects to life-history characteristics, results may permit extrapolation to other butterfly species.

Methods

Study site

This study was conducted at five forest-meadow boundaries within the Henry House Flats study area in the Athabasca River Valley, Jasper National Park. Each boundary differed in hardness, which I defined in terms of absolute tree and shrub density within the first three meters of forest from the edge (Table 3-1). Shrubs and small trees (< 3.5 m. height) were weighted as 0.50, as large trees were assumed to be at least twice as much of a barrier to movement.

Table 3-1. Tree densities (number/m^2), and small tree and shrub densities (0.5*number/m^2) for each study arena. Boundary hardness increases from site F1 to site F5.

site	trees	small trees	shrubs	total = hardness
F1	0.067	0.0000	0.0135	0.0800
F2	0.080	0.0135	0.0000	0.0935
F3	0.027	0.0200	0.0665	0.1135
F4	0.093	0.0135	0.0200	0.1295
F5	0.200	0.0000	0.0335	0.2335

At each of these five boundaries I located a 25 m. section along the forest edge that represented a distinct boundary between the forest and open meadow. The adjacent meadows were approximately 1 ha. in area at sites F2 and F4, and 0.25 ha. at sites F1, F3, and F5. All five adjacent meadows were linked to larger meadows by open corridors.

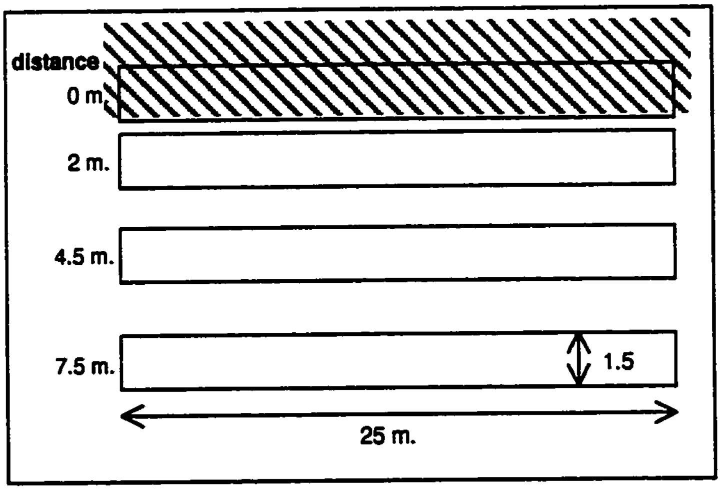

Figure 3-1. Schematic representation of study arena layout. The shaded area represents forest, while the remainder of the area is meadow. Numbers at left indicate how far the bottom edge of each transect was from the meadow-forest boundary.

Four 1.5 m. transects, marked by stakes and twine, were laid out parallel to the forest edge at increasing distances from the edge: 0 m., 2 m., 4.5 m., and 7.5 m. (Figure 3-1). "Sampling" of butterfly behaviour was most concentrated close to the forest edge, where I expected to see more fine-scale decisions occurring. I will refer to these transects and the areas they encompass as study arenas.

Study species

I looked at two groups of butterflies that differed in their abundance in forested areas and the location of their host plants (Table 3-2). Generally, forest is considered to be matrix or non-habitat for butterflies and is assumed to act as an absolute barrier (Wood and Samways 1991, Sutcliffe and Thomas 1996). However, some species depend on the forest as a source of larval host plants, while using open meadows for sunlight and nectar foraging. These butterflies tend to be habitat generalists, in that they move between meadow and forest in their daily activities (Schwarzwälder *et al.* 1997). Many of these butterflies are also strong flyers (Bird *et al.* 1995, C. Brdar *personal observation*). I will refer to these as "forest" butterflies. All required resources of "meadow" butterflies are found in open areas. These butterflies prefer meadows and tend to avoid forest, but will enter it on occasion (Chapter 2).

Table 3-2. Forest and meadow butterfly species used in this study. Forest butterflies must use the forest to oviposit, and all except *Boloria* spp. tend to be more vagile than meadow species.

Forest	Meadow
Aglais milberti	*Colias christina*
Boloria bellona	*Colias philodice*
Boloria freija	*Coenonympha inornata*
Nymphalis antiopa	*Erebia epipsodea*
Speyeria atlantis,	*Euchloe creusa*
electa, and *mormonia*	

Field methods

At each site, two or three people stood outside the transects and observed every butterfly that passed through the study arena. We identified each butterfly to genus and categorized and recorded individual butterfly behaviour in each transect that they flew through, as well as the direction from which they entered the study arena (*e.g.* meadow side of 7.5 m. transect). We also recorded what direction they flew through each transect relative to the forest edge, and where they exited the study arena. If an individual re-entered the study arena soon after its initial exit we did not record its behaviour, in order to maintain independence between sampling units. There is no reason to believe that our presence influenced butterfly behaviour, as the butterflies that came within close proximity to us appeared to show no reaction compared to the other butterflies we observed.

Observations were made from 3 June and 9 August 1999, between 1030 – 1330 for NE facing sites (sites 1,3, and 4) and between 1300 – 1645 for SW facing sites (sites 2 and 5). These times coincide with the peak of butterfly activity in this region. Observations were made only when tree shadows did not fall on the study arenas.

Data Analyses

Movement across boundaries

To determine the overall movement across the boundaries, I examined the total number of butterflies that entered the study arenas and crossed the boundaries. Of all butterflies that entered each study arena, I compared the proportion that entered the forest to those that exited the study arena on the meadow side of the boundary, using a G test with site, butterfly type, and whether or not the butterfly crossed the boundary as explanatory factors.

Response distance

Response distance is one component of the overall movement across a boundary. To assess the effect of boundary hardness on the response distance at the boundary of both butterfly types, I determined in which transect each butterfly stopped moving towards the forest, by turning around, or by making a right-angle turn and flying parallel to the forest edge along the length of the transect. For this particular analysis I used only individuals that entered the study arena at the 7.5 m. transect with the assumption that these individuals had not yet responded to the boundary when they first entered the study arena. I excluded individuals that flew into the forest since they did not show a turning response to the boundary. The response variable used for analysis was the number of butterflies turning in each transect at each site. Turning distance, site, and butterfly type were used as explanatory factors in a G test.

Boundary reaction

To compare the responses to boundaries of both types of butterflies, I examined behaviour at the point where each individual turned away from the boundary. I classified butterfly reaction to the forest edge into three categories: turn around, parallel, or away (Figure 3-2). I pooled the data for all sites and transects, as the factor of interest was butterfly type. I tested for differences in the frequency of these responses between meadow and forest opening butterflies by performing a two-way G test, with response type and butterfly type as variables.

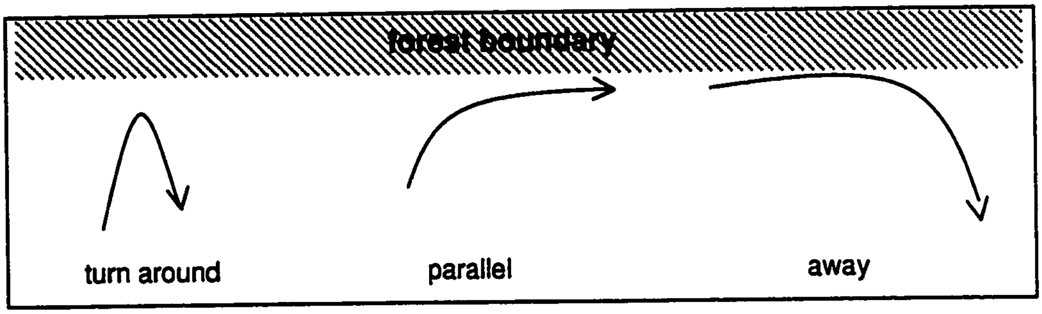

Figure 3-2. Behaviour categories for butterfly responses to meadow-forest boundary.

Permeability

It is impossible to be certain when and if a butterfly has "encountered" or perceived the forest boundary if it chooses to cross that boundary. In order to estimate boundary permeability I assumed that all butterflies that reached the 0 m. transect had already perceived the boundary and made the decision to attempt to cross it. I then calculated the proportion of butterflies that successful reached the edge and then crossed it versus those that turned and flew back into the meadow. As in the overall movement analysis, boundary hardness, butterfly type, and whether or not each butterfly crossed the boundary were used as explanatory factors in a G test.

Results

Over the course of the 1999 season we observed a total of 675 individuals. Approximately one third of these individuals entered the experimental study area from the forest. These butterflies were excluded from the behaviour analyses, as these individuals would have encountered and responded to the forest edge outside of the study arena. The remainder of the individuals observed were used in the following analyses (Table 3-3).

Table 3-3. Numbers of individuals used in analyses for each boundary hardness and butterfly type. Sites increase in boundary hardness from F1 to F5

site	forest butterflies	meadow butterflies	total
F1	32	36	68
F2	35	46	81
F3	57	49	106
F4	40	36	76
F5	69	65	134
total	233	232	465

Movement across boundaries

Both boundary hardness and butterfly type had a significant effect on the overall number of individuals entering the study arena and crossing the boundary, although there was no interaction between these two factors (Figure 3-3). As boundary hardness increased, fewer butterflies of both types crossed the boundary ($G = 34.72$, $df = 4$, $n = 465$, $p < 0.001$). Fewer meadow butterflies crossed the forest/meadow boundary at all five sites than forest butterflies ($G = 24.60$, $df = 1$, $p < 0.001$). These results suggest that both boundary hardness and butterfly type influence the amount of movement occurring across boundaries. In this circumstance, only 37.5 % of all the individuals that entered the study arena at site F1, the softest boundary, actually crossed the boundary. This number decreased to 12.5% at site F5, the hardest boundary.

Response distance

Response distances differed among boundary hardnesses ($G = 27.72$, $df = 12$, $n = 364$, $p < 0.01$). A post-hoc comparison between boundary hardness revealed that more butterflies turned around in the 0 m. transect (*i.e.* right at the edge) at site F5, which had the hardest boundary, than at any of the other sites (STP: $G = 25.60$, $df = 4$, $p < 0.001$, Figure 3-4 a and b). Seventy-nine percent of these individuals were forest butterflies. Detection distances also differed between butterfly types ($G = 12.04$, $df = 3$,

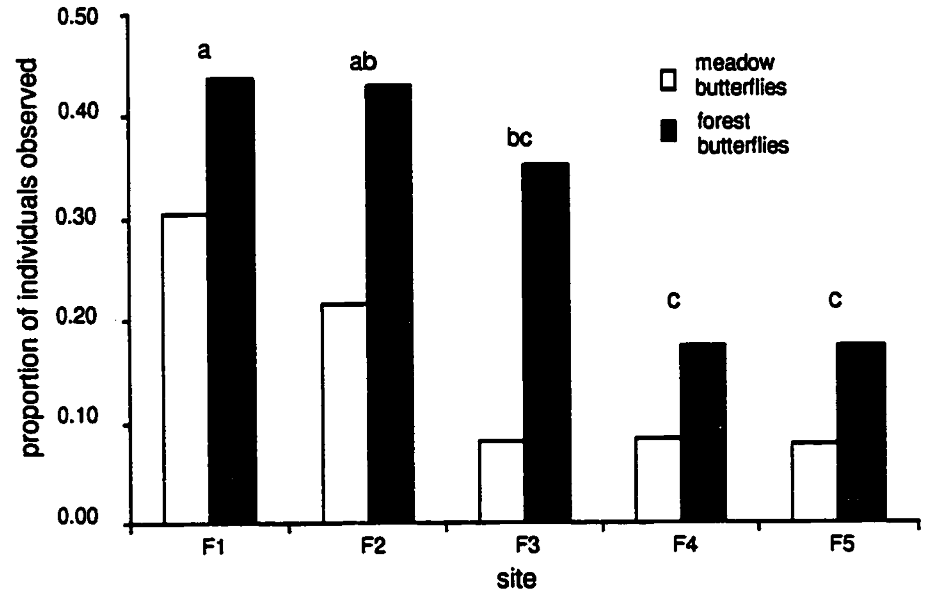

Figure 3-3. Proportion of butterflies that entered the study arena and subsequently crossed the boundary at each site. Both boundary hardness and butterfly type significantly influenced the amount of movement occurring across boundary ($p < 0.001$). Letters identify homogeneous subsets of sites from a post-hoc comparison among sites.

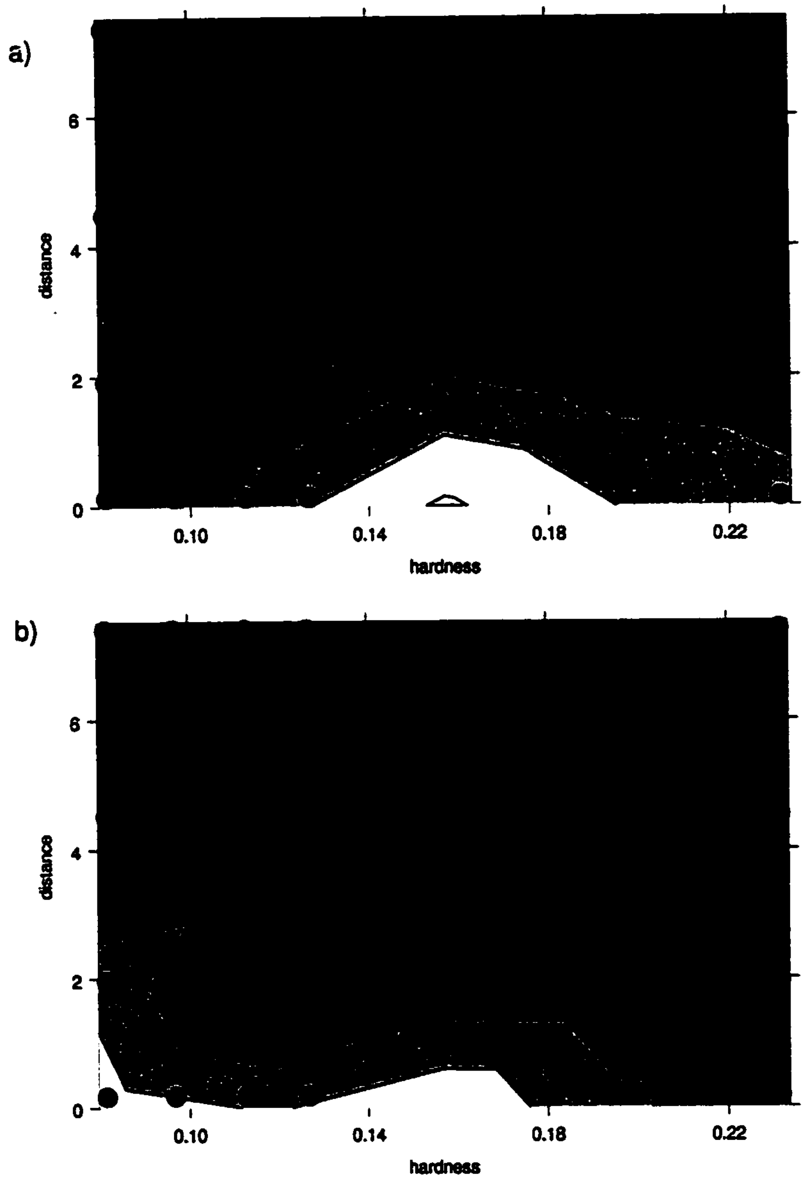

Figure 3-4. Contour plots of response distances at different boundary hardnesses for **a)** meadow butterflies and **b)** forest butterflies. Black dots represent actual data points (*i.e.* proportion of butterflies turning at a given distance for a particular boundary hardness) from which contours were extrapolated (MathSoft Inc.1998). Contours represent proportions of butterflies turning around at each distance for each boundary hardness. Values increase with contour darkness.

$p < 0.01$). Forest butterflies turned around more often in the 0 m. than meadow butterflies (STP: $G = 11.6$, $df = 3$, $p < 0.01$), suggesting that meadow butterflies respond to the forest at a greater distance forest butterflies.

Although the interaction between boundary hardness and butterfly type was not significant, most meadow butterflies responded to boundaries at a distance of 4.5 m. or more (Figure 3-4 a), while forest butterflies were more likely to fly right up to the edge (Figure 3-4 b). The difference in response distance between the two butterfly types was most pronounced at the hardest boundary, F5.

Boundary reaction

Butterfly type did not affect whether butterflies turned around, flew parallel, or turned away from the boundary ($G = 1.099$, $df = 2$, $n = 361$, $p = 0.58$).

Permeability

Less than 32 individuals entered the 0 m. transect at each site, and of these, more than 50% were forest butterflies at each site. Despite the small sample size, site had a significant effect on the number of butterflies crossing the boundary ($G = 24.64$, $df = 8$, $n = 136$, $p < 0.001$). Site F5, which had the hardest boundary, was less permeable than were the other four sites; that is, fewer individuals who reached this boundary crossed it (Figure 3-5). The forest boundaries at sites F1-4 only filtered out 6 – 30% of the butterflies that reached them, while site F5 filtered out 50%.

Discussion

I used a novel study design to measure the impact of disperser and boundary attributes on movement across boundaries at a scale relevant to daily activity decisions. I expected increasing boundary hardness to cause decreased butterfly movement into the forest through its effects on boundary response distance and boundary permeability. Similarly, I predicted that butterflies whose larval host plants were restricted to forests would show a greater rate of movement across boundaries than would butterflies that prefer meadows. These predictions were generally supported by the experimental results. I found an overall decrease in the number of butterflies moving across

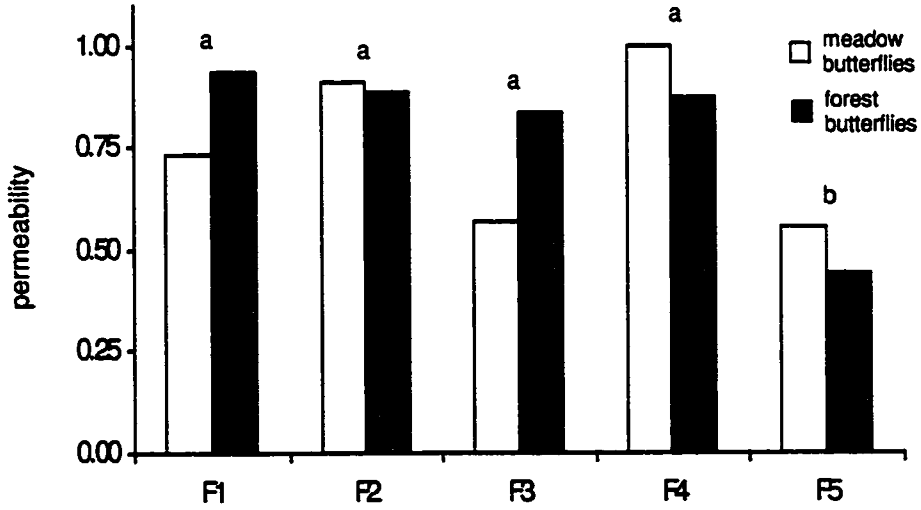

Figure 3-5. Boundary permeability of study sites with increasing boundary hardness. Permeability is the proportion of individuals at the meadow-forest boundary that cross into the forest. Boundary hardness significantly influenced permeability ($p < 0.001$). Letters identify homogeneous subgroups in a comparison of permeability between sites.

boundaries as the density of trees and shrubs at the boundary increased. This effect was stronger for meadow butterflies than for forest butterflies, supporting the view that the response to boundaries is species-specific (Ims 1995, Lidicker 1999) and related to habitat preference (Jonsen and Taylor 1999).

It appears that decreased movement across boundaries is caused by differences in both detection distance and boundary permeability. Meadow butterflies tended to turn around more often at a distance of 4.5 m. or greater from the edge of the forest, especially as boundary hardness increased. Such behaviour reduces their probability of interacting with and potentially moving across the boundary (Wiens 1992). Forest butterflies approached the forest more closely before turning away.

It is interesting to note that as boundary hardness increased, more forest opening butterflies flew directly up to the forest edge before turning away. These butterflies may actually view forest edges as ecotones, with their own emergent properties: *i.e.* rather than just being a discontinuity on the landscape, meadow-forest boundaries may form a unique habitat type (Lidicker 1999). Some butterflies actually follow linear features of the landscape as corridors (Dover *et al.* 1997), especially those species whose preferred habitat is forest openings and edges. Forest butterflies may react to the boundaries used in this study as habitat in their own right, rather than merely landscape filters. Alternatively, this behaviour shown by forest butterflies may be a result of their limited ability to detect habitat patches (Fahrig and Paloheimo 1987, Zollner and Lima 1997). It may be that forest butterflies, which are capable of using some types of forest habitat (Chapter 2), could not assess the habitat unsuitability of site F5 from a distance. Studies specifically designed to address the question of detection distance and perceptual range would provide useful information for understanding how perceptual range affects movement across boundaries.

The behavioural reaction to boundaries can influence the distance moved by a dispersing individual (Tischendorf and Wissel 1997). I did not detect differences in the specific butterfly boundary response behaviour, but the behaviour categories I chose may not have been biologically relevant. It is likely that some of the behaviours I observed within the study arenas were not reactions to the boundary, but routine movements. While other studies have recorded many butterflies flying over forest boundaries (Brakefield 1982, Wood and Samways 1991, Sutcliffe and Thomas 1996, Haddad 1999), I only observed this behaviour once out of over 600 observations. Flying over forest barriers in search of habitat patches does not appear to be a strategy for the butterfly species used in this study. The amount of impermeable boundary and sizes of unsuitable patches should then be very important in determining connectivity for butterflies in this landscape, as butterflies must pass through the boundaries directly, rather than flying over inhospitable patches (Stamps *et al.* 1987, Tischendorf and Wissel 1997).

The actual filtering function, or permeability of the boundary itself, also partially determines the amount of movement occurring across the boundary. Although it is difficult to separate permeability (Wiens *et al.* 1985) from overall movement, I did observe that butterflies that approached boundaries were less successful in crossing the boundary at site F5, the hardest boundary. Permeability as I have defined it did not differ between butterfly types, although the sample sizes I used were small. I would expect boundaries to be more permeable to forest butterflies, as these butterflies are adapted to navigating through forests.

These life history-specific responses can lead to the overall differences in butterfly distribution seen among landscape elements in patchy landscapes (Andrén *et al.* 1997). Meadow butterfly abundance in forest sites decreases with tree density, as does their propensity to cross meadow-forest boundaries (Chapter 2).

Habitat preference, life history, and behaviour characteristics can influence sensitivity to boundaries (Jonsen and Taylor 1999, Haddad 1999). The degree of fragmentation perceived by habitat generalists and good dispersers (*i.e.* forest butterflies) is less than that perceived by specialists or poor dispersers (*i.e.* meadow butterflies) (Lord and Norton 1990, Hansson 1991, With and Crist 1995). The same edge may be treated as an ecotonal area for some species and a discrete boundary between habitat and non-habitat by others (Lidicker 1999). In this case, forest opening butterflies might view the boundaries as ecotones and the overall successional landscape as "pseudocontinuous usable" (Lord and Norton 1990, With and Crist 1995), while meadow butterflies probably perceive this landscape as discontinuous.

Recent movement models include attributes of the landscape elements separating high quality habitat patches, especially in systems where populations do inhabit discrete patches (Moilanen and Hanski 1998, Roland *et al.* 2000). The methods used in this study would greatly improve the resolution of such models when intervening patches are of varying quality.

Overall, the connectivity of this section of the Athabasca River valley appears to be compromised by fire suppression and subsequent forest succession. Boundaries are increasing in hardness throughout the mountain parks as forests increase in tree density and trees are recruited within the forest edge (Achuff *et al.* 1996, Rhemtulla 1999). The results of this study suggest that increased forest closure will lead to reduced movement between habitat patches, especially by those species that prefer meadow habitat.

Conclusion

It is clear that several factors mediate the response of organisms to habitat boundaries. Behavioural studies such as this one provide a better mechanistic understanding of how aspects of landscape structure, such as the nature of boundaries, affect animal movement across heterogeneous landscapes. I found evidence for the concept of the landscape as a filter, rather than a series of discrete patches (Ingham and Samways 1996), as there was flow occurring across all five boundaries. This suggests that butterflies are not strictly limited to their habitat (Schultz 1998), and movement through what is traditionally considered non-habitat may be important for dispersal or resource supplementation (Dunning *et al.* 1992, Chapter 4). Forest barriers appear to be a coarse filter for forest butterflies and a finer filter for meadow butterflies. While most studies depend on indirect methods to discern these effects (*e.g.* Munguira and Thomas 1992), this study demonstrates some of the mechanisms responsible for the responses to boundaries of forest and meadow butterflies.

Literature Cited

Achuff, P.L., I. Pengelly, and J. Wierzchowski. 1996. Vegetation: cumulative effects and ecological futures outlook. *In* Greens, J., C. Pacas, L. Cornwell, and S. Bayley, editors. Ecological Outlooks Project. A cumulative effects assessment and futures outlook of the Banff Bow Valley. Prepared for the Banff Bow Valley Study. Department of Canadian Heritage, Ottawa, ON.

Andrén, H., A. Delin, and A. Seiler. 1997. Population response to landscape changes depends on specialization to different landscape elements. Oikos 80: 193 – 196.

Björnstad, O., H.P. Andreassen, and R.A. Ims. 1998. Effects of habitat patchiness and connectivity on the spatial ecology of the root vole *Microtus oeconomus*. Journal of Animal Ecology 67: 127 – 147.

Brakefield, P.M. 1982. Ecological studies on the butterfly *Maniola jurtina* in Britain. I. Adult behaviour, microdistribution, and dispersal. Journal of Animal Ecology. 51: 713 – 726.

Dover, J.W., T.H. Sparks, and J.N. Greatorex-Davies. 1997. The importance of shelter for butterflies in open landscapes. Journal of Insect Conservation 1: 89 – 97.

Dunning, J.B., B.J. Danielson, and H.R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65: 169 – 175.

Fagan, W.F., R. S. Cantrell, and C. Cosner. 1999. How habitat edges change species interactions. The American Naturalist 153: 165 – 182.

Fahrig, L. and G. Merriam. 1994. Conservation of fragmented populations. Conservation Biology 8: 50 – 59.

Fahrig, L. and J.E. Paloheimo. 1987. Interpatch dispersal of the cabbage butterfly. Canadian Journal of Zoology 65: 616 – 622.

Forman, R.T.T. 1997. Land mosaics: the ecology of landscapes and regions. Cambridge University Press, New York, USA.

Gosz, J.R. 1991. Fundamental ecological characteristics of landscape boundaries. *In* Holland, M.M., P.G. Risser, and R.J. Naiman, editors. Ecotones: the role of landscape boundaries in the management and restoration of changing environments. Chapman and Hall, New York.

Grundel, R., N.B. Pavlovic, and C.L. Sulzman. 1998. Habitat use by the endangered Karner blue butterfly in oak woodlands: the influence of canopy cover. Biological Conservation 85: 47 – 53.

Haddad, N.M. 1999. Corridor use predicted from behaviours at habitat boundaries. The American Naturalist 153: 215 – 227.

Haddad, N.M. and K.A. Baum. 1999. An experimental test of corridor effects on butterfly densities. Ecological Applications 9: 623 – 633.

Hansen, A.J. and diCastri, F., editors. 1992. Landscape boundaries: consequences for biotic diversity and ecological flows. Springer-Verlag, New York, USA.

Hansson, L. 1991. Dispersal and connectivity in metapopulations. Biological Journal of the Linnean Society 42: 89 – 103.

Ims, R.A. 1995. Movement patterns related to spatial structures. Pages 85 - 109 *in* Hansson, L., L. Fahrig, and G. Merriam, editors. Mosaic landscapes and ecological processes. Chapman and Hall, London, England.

Ingham, D.S. and M.J. Samways. 1996. Application of fragmentation and variegation models to epigaeic invertebrates in South Africa. Conservation Biology 10: 1353 – 1358.

Johnson, A.R., J.A. Wiens, B.T. Milne, and T.O. Crist. 1992. Animal movements and population dynamics in heterogeneous landscapes. Landscape Ecology 7: 63 – 75.

Jonsen, I.D. and P.D. Taylor. 2000. Fine-scale movement behaviours of Calopterygid damselflies are influenced by landscape structure: An experimental manipulation. Oikos 88: 553 – 562.

Kareiva, P.M. and N. Shigesada. 1983. Analyzing insect movement as a correlated random walk. Oecologia 56: 234 – 238.

Kuussaari, M., M. Nieminen, and I. Hanski. 1996. An experimental study of migration in the Glanville fritillary butterfly *Melitaea cinxia*. Journal of Animal Ecology 65: 791 – 801.

Lidicker, W.Z. Jr. 1999. Responses of mammals to habitat edges: an overview. Landscape Ecology 14: 333 – 343.

Lima, S.L. and P.A. Zollner. 1996. Towards a behavioural ecology of ecological landscapes. Trends in Ecology and Evolution 11: 131 – 135.

Lord, J.M. and D. A. Norton. 1990. Scale and the spatial concept of fragmentation. Conservation Biology 4: 197 – 202.

Merriam, G. 1984. Connectivity: a fundamental ecological characteristic of landscape pattern. Pages 5 – 15 *in* Brandt, J. and P. Agger, editors. Proceedings of the first international seminar on methodology in landscape ecological research and planning. International Association for Landscape Ecology, Roskilde University, Roskilde.

Moilanen, A. and I. Hanski. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. Ecology 79: 2503 – 2515.

Mousson, L., G. Nève, and M. Baguette. 1999. Metapopulation structure and conservation of the cranberry fritillary *Boloria aquilonaris* (Lepidoptera, Nymphalidae) in Belgium. Biological Conservation 87: 285 – 293.

Munguira, M.L. and J.A. Thomas. 1992. Use of road verges by butterfly and burnet populations, and the effect of roads on adult dispersal and mortality. Journal of Applied Ecology 29: 316 – 329.

Nève, G., B. Barascud, R. Hughes, J. Aubert, H. Descimon, P. Lebrun, and M. Baguette. 1996. Dispersal, colonization power and metapopulation structure in the vulnerable butterfly *Proclossiana eunomia* (Lepidoptera: Nymphalidae). Journal of Applied Ecology 33: 14 – 22.

Pither, J. and P.D. Taylor. 1998. An experimental assessment of landscape connectivity. Oikos 83: 166 – 174.

Rhemtulla, J.M. 1999. Eighty years of change: the montane vegetation of Jasper National Park. M.Sc. Thesis. University of Alberta.

Roland, J., N. Keyghobadi, and S. Fownes. 2000. Alpine *Parnassius* butterfly dispersal: effects of landscape and population size. Ecology (in press)

Schultz, C. 1998. Dispersal behaviour and its implications for reserve design in a rare oregon butterfly. Conservation Biology 12: 284 – 292.

Stamps, J.A., M. Buechner, and V.V. Krishnan. 1987. The effects of edge permeability and habitat geometry on emigration from patches of habitat. The American Naturalist. 129: 533 – 552.

Stanton, M.L. 1982. Searching in a patchy environment: foodplant selection by *Colias p. eriphyle* butterflies. Ecology 63: 839 – 853.

Sutcliffe, O.L. and C.D. Thomas. 1996. Open corridors appear to facilitate dispersal by ringlet butterflies (*Aphantopus hyperantus*) between woodland clearings. Conservation Biology 10: 1359 – 1365.

Taylor, P.D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. Oikos 68: 571 – 573.

Tischendorf, L. and C. Wissel. 1997. Corridors as conduits for small animals: attainable distances depending on movement pattern, boundary reaction and corridor width. Oikos 79: 603 – 611.

Wiens, J.A. 1992. Ecological flows across landscape boundaries: a conceptual overview. Pages 217 - 235 *in* Armand, A.O. *et. al.*, editors. Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows. Springer-Verlag, New York, USA.

Wiens, J.A., C.S. Crawford, and J.R. Gosz. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. Oikos 45: 421 – 427.

Wiens, J.A., T.O. Crist and B.T. Milne. 1993a. On quantifying insect movements. Environmental Entomology 22: 709 – 715.

Wiens, J.A., N.C. Stenseth, B. Van Horne, and R.A. Ims. 1993b. Ecological mechanisms and landscape ecology. Oikos 66: 369 – 380.

With, K.A. and T.O. Crist. 1995. Critical thresholds in species' responses to landscape structure. Ecology 76: 2446 – 2459.

With, K.A., R.H. Gardner, and M.G. Turner. 1997. Landscape connectivity and population distributions in heterogeneous environments. Oikos 78: 151 – 169.

Wood, P.A. and M.J. Samways. 1991. Landscape element pattern and continuity of butterfly flight paths in an ecologically landscaped botanic garden, Natal, South Africa. Biological Conservation 58: 149 – 166.

Zollner, P.A. and S.L. Lima. 1997. Landscape-level perceptual abilities in white-footed mice: perceptual range and the detection of forested habitat. Oikos 80: 51 – 60.

Chapter 4. The influence of tree density on butterfly movement within landscape elements

"...whether or not a landscape is fragmented depends upon how species are able to utilize and move through elements of the landscape" (With *et al.* 1997)

Introduction

The spatial distribution of animal populations is partially determined by the interaction between the movement of individuals and the mosaic structure of the landscape (Wiens *et al.* 1993, Wiens *et al.* 1997). Consequently, in heterogeneous landscapes, the degree of fragmentation perceived by an organism depends upon differences among landscape elements in terms of the ease with which organisms can use and move among them (With *et al.* 1997). The nature of suboptimal habitat areas, which dominate most fragmented landscapes, determines the amount of movement that can occur between optimal habitat patches (Fahrig and Merriam 1994, Åberg *et al.* 1995, Tischendorf and Wissel 1997, Bowne *et al.* 1999, Szacki 1999). Therefore, a mechanistic understanding of how movement patterns are influenced by both habitat and non-habitat landscape elements can provide insight into the effects of fragmentation on populations (Ims 1995, With *et al.* 1997, Law and Dickman 1998, Pither and Taylor 1998).

The amount of movement occurring through non-habitat landscape elements depends upon the *viscosity* of those areas. Viscosity is a measure of the degree of resistance to animal movement (Wiens *et al.* 1997) and is related to the internal structure and hostility of the patch (Jonsen and Taylor 1999). The movement speed and the path taken by organisms are indications of patch viscosity. Organisms move more slowly and tortuously through landscape elements with high viscosity, and more quickly and directly through those with low viscosity (Wiens *et al.* 1997). Patch viscosity directly influences how organisms respond to habitat fragmentation through its effect on movement behaviour within various patches (Lord and Norton 1990, With and Crist 1995, Lidicker 1999).

A thorough understanding of the viscosity of landscape elements and its effect on connectivity of landscapes requires empirical studies that estimate habitat-specific movement capabilities and rates (Åberg *et al.* 1995, Pither and Taylor 1998). Despite the direct relationship between connectivity and animal behaviour in non-habitat landscape elements (Merriam 1991, Fahrig and Merriam 1994), few empirical studies describe animal movement through these areas (Shreeve 1995, Pither and Taylor 1998). Recent movement models have begun to include parameters describing the quality of the areas between habitat patches (*e.g.* Gustafson and Gardner 1996, Moilanen and Hanski 1998, Roland *et al.* 2000). A measure of interhabitat patch viscosity may refine such models or make them applicable to a greater variety of landscapes.

Of primary interest in my study is how patch viscosity, or the rate and tortuosity of butterfly movement occurring in different patches, is related to tree density in those patches. Although butterflies have some resource requirements that are met only in open sunny patches, they leave these areas at observable rates and are capable of moving through forest between unconnected open patches (Sutcliffe and Thomas 1996, Schultz 1998, Haddad 1999b, Mousson *et al.* 1999, Roland *et al.* 2000). In successional landscapes, the areas between patches of optimal habitat represent a gradient of tree density and hostility to butterflies. Dense forest is assumed to be relatively hostile to butterflies due to its lack of resources, and open forest and meadows are assumed to be suitable due to the availability of nectar flowers and sunlight (Chapter 2). There are two possible effects of tree density on viscosity for butterflies: A) Dense forest (*i.e.* hostile patches) could have high viscosity by making navigation difficult and thus stopping or slowing butterfly movement; in contrast, open areas (*i.e.* utilizable patches) could have low viscosity, by allowing butterflies to move freely B) Dense forest could have low viscosity because butterflies attempt to leave these patches rapidly and disperse to more favourable habitat; conversely, utilizable patches provide resources, increasing butterfly residence time and patch viscosity.

As both butterfly navigational ability and habitat suitability may affect viscosity, I expect that these two scenarios are not mutually exclusive. Additionally, landscape elements are species-specific filters (With *et al.* 1997, Bowne *et al.* 1999), and their effects on movement are related to the degree of habitat specialization and the vagility of the organisms moving through them (With and Crist 1995, With *et al.* 1997). Organisms that are specialized for a particular habitat type, such as "meadow" butterflies (Chapters 1, 2, and 3), are often more affected by fine scales of fragmentation than habitat generalists (Lord and Norton 1990). Therefore, I expect the effect of tree density on the viscosity of landscape elements to be species-specific.

Quantifying landscape element viscosity

Observation of individual behaviour is an effective method for determining the mechanisms producing population responses to landscape structure (Turchin *et al.* 1991, Wiens *et al.* 1993a, Andrén *et al.* 1997). Movement is an important mechanism influencing population-level responses. The use of simple behaviours to predict patterns of movement is less intensive than is the mark-release-recapture method, and allows a more direct interpretation of results (Haddad 1999a). Simple behavioural observations can allow rapid assessment of the effects of landscape changes like succession on several species differing in life-history characteristics, such as degree of habitat specialization (Haddad 1999a).

In order to understand the interacting effects of forest density and butterfly habitat specialization on within-patch movement, I observed the behaviour of individual butterflies released in several sites that differed in tree density at a scale relative to that involved in daily foraging activities. I determined the relative ability of open area specialist butterflies and forest-tolerant generalist butterflies to move through and use areas of different tree densities by evaluating four aspects of their behaviour:

1) *Movement rates* – I compared movement rates, or the time it took individuals to move through patches, among sites of differing tree density for both butterfly types. Previous studies have found that individuals search more thoroughly in hospitable patches, and disperse more quickly from hostile patches (Tischendorf and Wissel 1997, Schultz 1998) (scenario B). Additionally, habitat specialists are often assumed to be less vagile than are generalists, because they are adapted to remaining within habitat patches (Lord and Norton 1990). Therefore, I predicted that movement rates would increase with tree density, and decrease with habitat specialization.

2) *Flight behaviour* – Movement rate is a function of flight tortuosity: straight flights result in more rapid displacement than irregular flights. I compared the tortuosity of flight behaviour between butterfly types and among sites differing in tree density. I expected to see more straight flights through inhospitable sites (*i.e.* high tree density),

again, because butterflies should fly straight to find new habitats when flying through inhospitable areas, and search more thoroughly in good habitat (Odendaal *et al.* 1989, Zollner and Lima 1999). This would indicate that these sites have low viscosity (scenario B).

3). *Resource use* – Landscape elements with high viscosity should be those in which butterflies forage more, according to scenario B. To test this, I determined foraging probabilities for each butterfly type as a function of tree density.

4.) *Flight direction* - In patchy forests, movement may be constrained by discontinuities within the patches (Wiens 1992). To discover how butterflies respond to the internal heterogeneity of forest patches, I determined if relatively more butterflies fly through the open sections within each forest site. The viscosity of landscape elements should be influenced by the ability of butterflies to navigate through open sections of otherwise hostile patches (Fahrig and Merriam 1994).

The results of this study, along with those of Chapter 3, provide insights into how individual movement behaviour, and therefore overall landscape connectivity for butterflies, would be affected by increased forest density through succession. Additionally, I am able to identify the reduction in tree density necessary to promote butterfly movement.

Methods

Study area and species

The study sites and species used for this experiment are described in detail in Chapter 1. I used two meadow sites and five intact forest sites with varying tree densities (Table 1-1). In 1998, we released butterflies in sites M1, F1, F3, and F5. In 1999, we also used sites M1, F2, and F4, but excluded the dense forest site F5 due to the difficulty of following individuals in this site.

For the analysis, I categorized *Coenonympha*, *Erebia*, and *Colias* as open area specialist or "meadow" butterflies and *Boloria* and *Speyeria* as forest opening generalist or "forest" butterflies. Rationale for the assignment of these two groups is described in

Chapters 1 and 2. For both groups, meadows contain required resources: sunlight and nectar flowers. Meadow butterflies may use forests opportunistically to locate host or nectar plants. Forest butterflies require forests for their larval host plant, *Viola* spp. (Chapter 2). Closely related species, such as *Coenonympha* and *Erebia* or *Boloria* and *Speyeria* have similar flight behaviours (Scott 1975). Although *Colias* is not related to the satyrids *Coenonympha* and *Erebia,* all three genera are similar in their degree of habitat specialization (Chapter 2). Small sample sizes prevented meaningful analysis for individual species.

Field methods

Butterflies were collected from two meadows that were not included in the rest of the overall study. Individual female butterflies were netted between 1000 and 1300, placed in glassine envelopes, and stored in a cooler until their release. Storing butterflies at low temperatures reduces capture trauma and decreases the likelihood of atypical or escape behaviour upon release (Watt *et al.* 1977, Schultz 1998). We limited our collections to females in order to decrease the intraspecific variability in flight and foraging behaviour that is observed between sexes (Ims 1995). Additionally, females are responsible for colonizing new or isolated patches (Scott 1975); therefore, their movement patterns are the most relevant for determining the effects of habitat fragmentation on butterfly populations.

Butterflies were released one at a time in the center of one of the circular study sites. Individual butterflies were gently dropped from the glassine envelope onto the vegetation in a sunny patch to allow solar orientation for recovery from being stored at cold temperature (Watt *et al.* 1977, Schultz 1998). Releases took place on warm, sunny, low wind days between 8 July and 28 July 1998, and 26 May and 4 August 1999.

We observed the behaviour of each released individual until it reached the edge of the study site, which was 50 m. from the release point. Observers remained at least 2 m. away from butterflies to avoid influencing their behaviour. If an individual stayed within the study site for more than 30 minutes without reaching the edge, we terminated observations and recorded this result. We also terminated observations if an individual remained stationary for more than 15 minutes. We noted the following behaviours: number of stops, plants used for foraging or oviposition, general flight pattern (straight, erratic, or "escape" response), section of the study site exited from, and time taken to reach the edge of the site. Butterflies that showed "escape" responses (Haddad 1999b) were excluded from all of the following analyses, except the analysis of flight behaviour. Escape responses are characterized by rapid vertical flight (3 or more meters above the ground), which allows the wind currents to move them to a new location (Fahrig and Paloheimo 1987).

Data analyses

Tree density effects on movement rates

To evaluate differences in movement rates between sites, I calculated the amount of time it took individuals to leave the site, excluding the initial "warm-up" period. Time was used as a response variable in a generalized linear model with Poisson error (MathSoft Inc. 1998). Independent variables included tree density, butterfly type, number of stops made, and all interactions between these terms. All significant explanatory variables ($p(\chi^2) < 0.05$) were retained in the final model. I used data from butterflies released in both 1998 and 1999 in this analysis. We did not record flight behaviour in 1998; therefore, I was not able to include flight behaviour as an explanatory variable in the model.

Tree density effects on flight behaviour

I characterized the flight patterns of released butterflies as they moved through the sites as straight, erratic, or "escape" response. I noticed a trend of more individuals showing an escape response with increasing tree density; therefore, I examined the effect of tree density and butterfly type on the proportion of butterflies showing an escape response using logistic regression. I compared the proportion of butterflies with straight flights versus erratic flights among sites for both butterfly types using a G test, excluding those butterflies that showed an escape response. In these analyses I included data from butterflies that were eventually lost, or that moved through the site for 30 minutes without leaving the site, along with those that were successfully followed to the edge of the site.

Tree density effects on nectar and larval host plant use

Several butterflies stopped to forage or oviposit after they were released in both 1998 and 1999. To determine the effect of forest density on the probability of individuals using the nectar plants available in each site, I compared the proportion of foraging individuals among sites and between butterfly types using a G test. *Erebia* were excluded from this analysis, as they do not nectar-feed.

I performed a similar analysis on the proportion of *Colias* butterflies that landed on their larval host plant, *Astragalus* spp. I assumed that by landing on *Astragalus*, *Colias* females had perceived the plant and were investigating it as a possible oviposition location. Again, I included data from "lost" butterflies and those that did not leave the site within 30 minutes.

Response to within-site heterogeneity

In order to examine butterfly responses to within-site heterogeneity, I divided each study site into eight equal sectors (Figure 4-1). In each section, I quantified the absolute density of trees and shrubs, as well as the amount of open meadow visible from the edge of the study site. I used these values and the interactions of tree density and meadow visible with butterfly type as predictors of numbers of butterflies leaving the study site from each section in a generalized linear model with Poisson error. This analysis was repeated for each site separately.

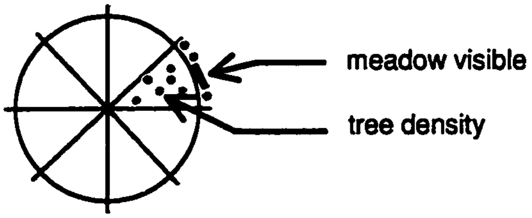

Figure 4-1. Schematic representation of treatment of study sites for analysis of response to within-site heterogeneity. Grey dots represent trees.

Results

We successfully released a total of 374 butterflies in 1998 and 1999 (Table 4-1). Sixty-seven of these individuals were lost from sight before the observations were complete. Not surprisingly, the greatest proportion of butterflies (50%) were lost in the densest site, F5, relative to the proportion of released butterflies lost in the other sites.

Table 4-1. Numbers of butterflies released in each study site in 1998 and 1999. Numbers in brackets indicate forest density in terms of number of trees per m^2. Releases were done in F5 in 1998 only, and in M2, F2, and F4 in 1999 only.

butterfly type	M1 (0.00)	M2 (0.005)	F1 (0.04)	F2 (0.086)	F3 (0.113)	F4 (0.133)	F5 (0.153)
meadow	38	27	69	48	56	45	6
forest	11	10	23	11	19	7	4

Tree density effects on movement rate

Movement rates were dependent upon the number of stops made by each butterfly, butterfly type, tree density, and the interactions among these terms. While the number of stops was associated with the greatest change in deviance, the effects of butterfly type and forest density were also significant (Table 4-2). Generally, meadow butterflies took longer to fly through all sites than did forest butterflies (Figure 4-2 a). Time taken to leave a site shows a non-linear trend with tree density (Figure 4-2 a), which peaks at medium tree densities, due to the interaction with number of stops made. Meadow butterflies generally stopped most often in the three least dense forest sites (F1, F2, and F3), while forest butterflies stopped most often in the medium density forest site, F3 (Figure 4-2 b).

Table 4-2. Statistics for all significant variables retained in Poisson generalized linear model (MathSoft. Inc. 1998) of time taken by butterflies to move through study sites. The r^2 for the model was 0.35, and n = 250.

Term	Coefficient (SE)	df	Change in deviance	$p(\chi^2)$
Null		249	1558.9	
stops	0.17 (0.03)	1	424.7	0.000
type	0.87 (0.13)	1	24.6	0.000
density	8.18 (1.31)	1	24.5	0.000
stops x type	-0.12 (0.03)	1	38.7	0.000
type x density	-5.8 (1.31)	1	16.6	0.000
density x stops	-0.96 (0.26)	1	5.0	0.025
stops x type x density	0.84 (0.26)	1	9.6	0.020

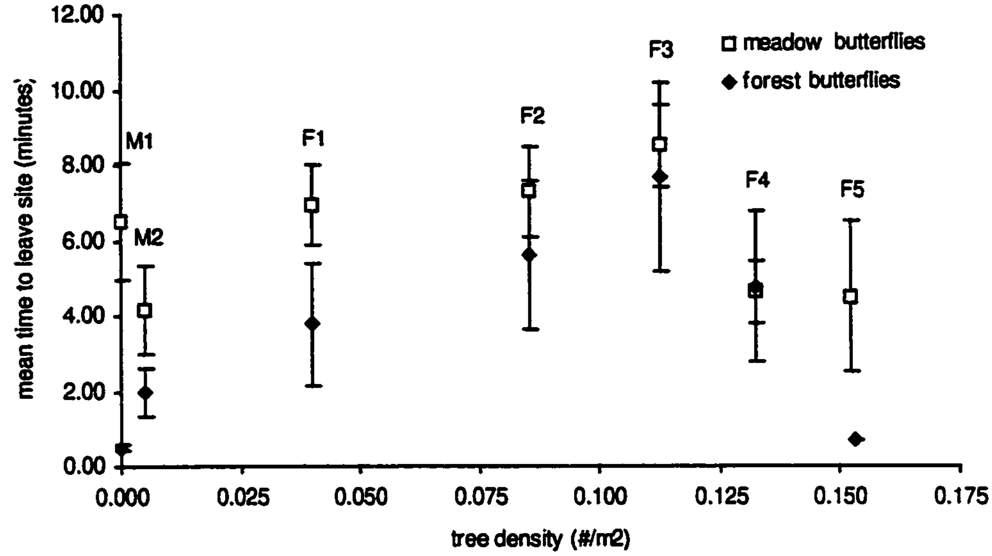

Figure 4-2a. Mean time taken by meadow and forest butterflies to leave study sites. The interaction between butterfly type and forest density was a significant term in the GLM explaining time taken to leave sites ($\chi^2 = 16.6$, df = 1, n = 250, $p < 0.001$)

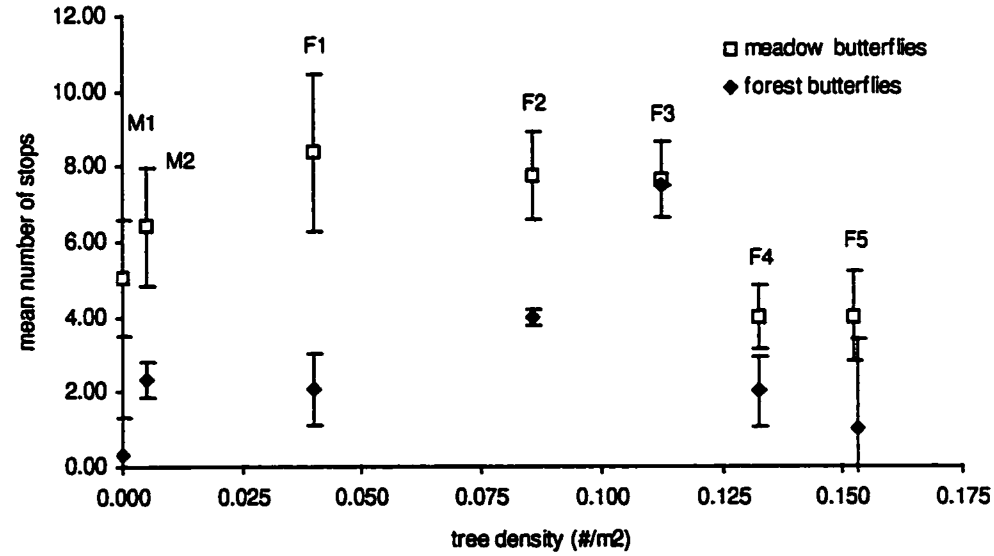

Figure 4-2b. Mean number of stops made by meadow and forest butterflies as leaving study sites. The interaction between number of stops, forest density, and butterfly type was a significant term in the GLM explaining time taken to leave sites ($\chi^2 = 5.0$, df = 1, n = 250, $p < 0.05$).

Tree density effects on flight behaviour

The proportion of butterflies showing an escape response was not significantly related to tree density or butterfly type. There was a trend, however, for more butterflies exhibiting an escape response in the densest forest sites (Figure 4-3). Fifty percent of all butterflies released in the dense forest site F5 showed an escape response, although fewer butterflies were released in this site ($n = 10$, Table 4-1). In the patchy forests and meadow sites, the proportion of all butterflies showing an escape response varied from 8% in the low density site F2 to 19% in the medium density site F4. Due to the difficulty of successfully observing butterflies in the dense forest and the time-intensive nature of this experiment, we concentrated our effort in the other sites. Therefore, site F5 was excluded from all subsequent analyses.

Butterfly type and site significantly affected the proportion of butterflies flying straight, rather than erratically ($G = 14.70$, $df = 5$, $n = 225$, $p < 0.05$). Meadow butterflies flew straight more often in site F4, which was the densest site used in this analysis. Forest butterflies flew straight more often in the meadow M1 (Figure 4-4).

Tree density effects on resource use

Meadow butterflies foraged more often than did forest butterflies in all sites but meadow site M2 ($G = 14.09$, $df = 1$, $n = 315$, $p < 0.001$). The interaction between site and butterfly type was not significant; however, the difference in the proportions of each type foraging generally increased with tree density (Figure 4-5). No forest butterflies foraged in M1 or in the medium forest site F4. Incidences of *Colias* landing on its larval host plant *Astragalus* did not differ between sites ($G = 5.31$, $df = 5$, $n = 186$, $p > 0.05$).

Response to within-site heterogeneity

The terms retained in the generalized linear models differed among sites, as did their coefficients; therefore, the response to internal patchiness differed between sites (Table 4-3). Generally, in forest sites fewer butterflies moved through the denser sections. In sites F2 to F4, however, only forest butterflies showed this pattern of response. The number of butterflies moving through a section increased with the

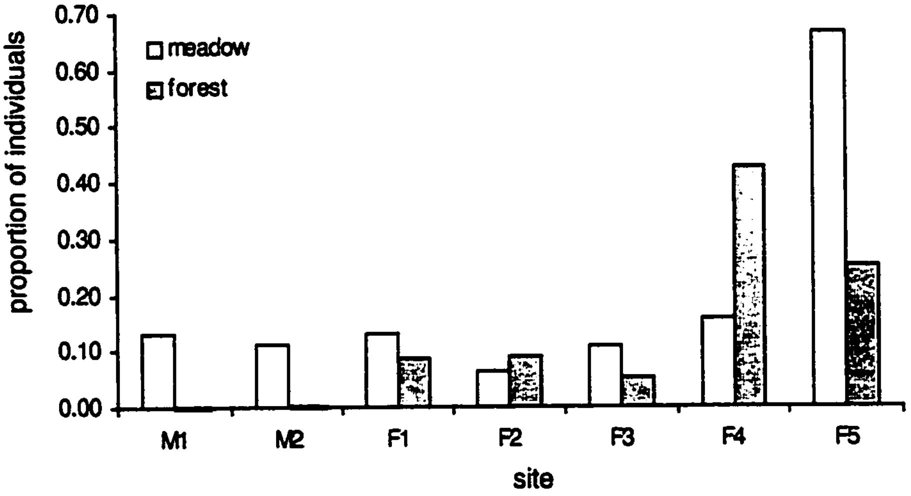

Figure 4-3. Proportion of meadow and forest butterflies showing an escape response in each site (n = 374).

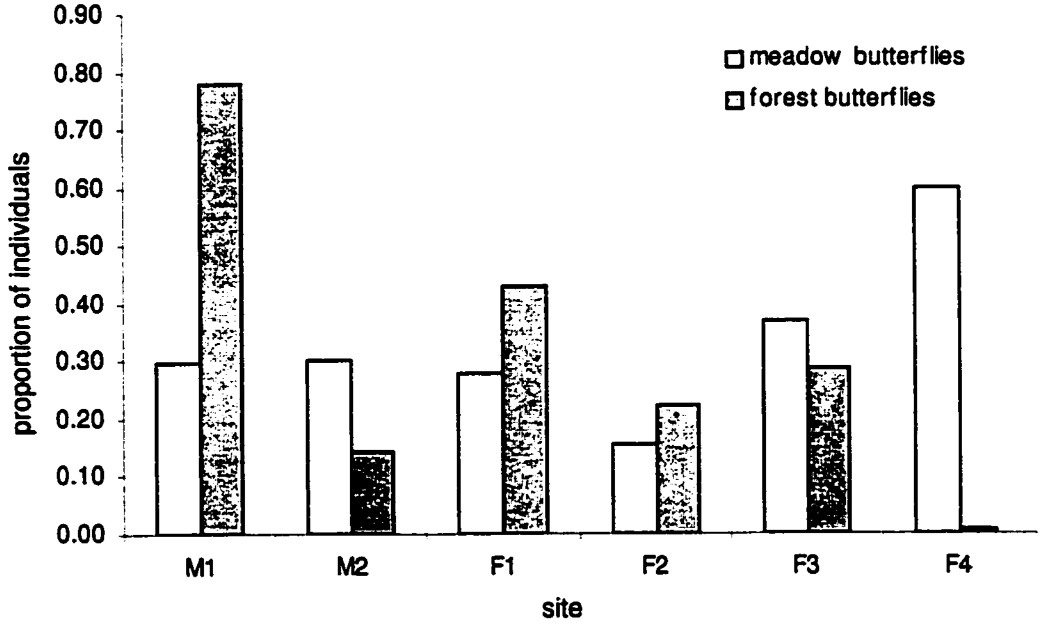

Figure 4-4. Proportion of meadow and forest butterflies flying straight (vs. erratic) in each site. The 3-way interaction between flight behaviour, site, and butterfly type was significant in a G test (G = 14.70, df = 5, n = 225, $p < 0.05$).

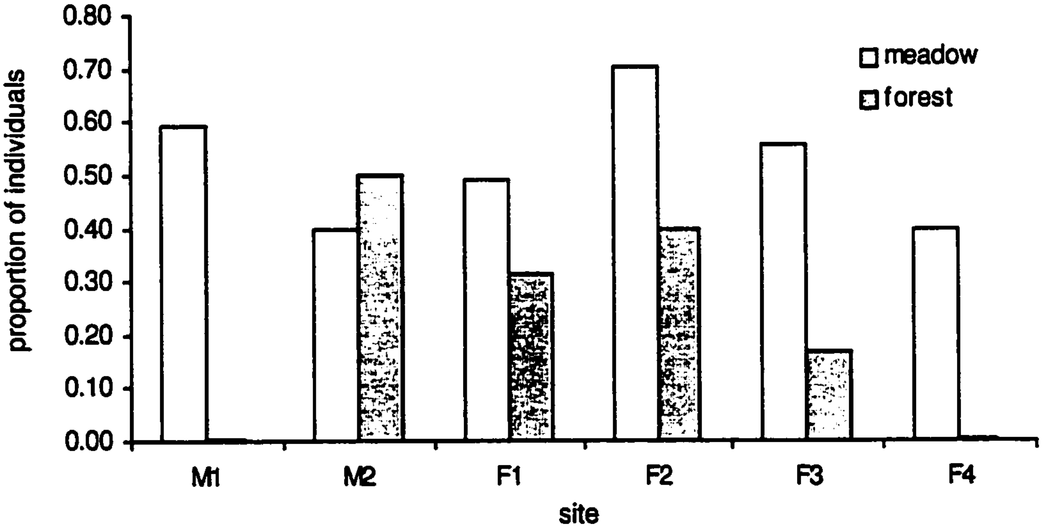

Figure 4-5. Proportion of meadow and forest butterflies foraging in each site. Meadow butterflies foraged significantly more often than forest butterflies (G = 14.09, df = 1, n = 315, $p < 0.001$)

amount of meadow visible from that section for the open forest site F1. In the two meadow sites, more butterflies flew through the sections that had the lowest meadow visibility; *i.e.* the sections that were closest to the surrounding forest.

Table 4-3. Significant terms retained in Poisson generalized linear models (MathSoft Inc. 1998) of numbers of butterflies moving through each section at different sites. *Type* = butterfly type, *meadow vis.* = meadow visible, *density* = section tree density (trees/m^2).

Site	Model r^2	Included terms	n	p	Coefficients
M1	0.35	type x meadow vis.	38	0.007	intercept = -1.03 forest x meadow vis. = 1.29 meadow x meadow vis. = 2.43
M2	0.19	meadow vis.	29	0.02	intercept = 3.85 meadow vis. = -3.56
F1	0.62	density meadow vis. type x meadow vis.	59	0.049 0.044 0.000	intercept = 1.78 density = -29.67 meadow vis. = 0.83 type x meadow vis. = 14.84
F2	0.41	type x density	41	0.000	intercept = 1.28 forest x density = -15.86 meadow x density = 2.19
F3	0.63	type x density	53	0.000	intercept = 1.57 forest x density = -10.98 meadow x density = 0.63
F4	0.57	type x density	34	0.000	intercept = 2.59 forest x density = -24.43 meadow x density = -9.81

Discussion

Viscosity of landscape elements is reflected in the speed with which organisms move through them, and is related to the hostility of the landscape elements. Viscosity may increase with increasing site hostility (scenario A, Introduction), or it may decrease with increasing site hostility (scenario B, Introduction). I expected to find that organisms would move quickly through hostile landscape elements; therefore, these elements should have low viscosity (scenario B). Of the sites used in this study, the dense forest site F5 was clearly hostile to butterflies, and had the lowest viscosity. This suggests a possible forest density threshold at which the forest becomes pure non-habitat. All butterflies released in this site moved very quickly, supporting the hypothesis that organisms should attempt to disperse from unsuitable habitat (Tischendorf and Wissel 1997, Zollner and Lima 1999). The relationships among movement rates, forest density, and butterfly type were more complex in the less dense sites.

The response of meadow specialist or "meadow" butterflies to tree density was different from that of habitat generalist or "forest" butterflies. The behavioural differences observed between these two groups of butterflies indicate that life-history characteristics like habitat preference and degree of habitat specialization affect the species-specific viscosity of a landscape element (Pither and Taylor 1998, Haddad 1999a, Jonsen and Taylor 2000). The species-specific viscosity of landscape elements increased with the degree of butterfly habitat specialization. All sites used in this study were more viscous to meadow butterflies than forest butterflies in terms of movement speed.

The non-linear relationships among butterfly type, tree density, and movement speed (Figure 4-2) indicate that viscosity is determined by the interaction between the hostility of an area and the ease with which butterflies can navigate through the area. I assumed that hostility increased with tree density, as resources become scarcer with increasing tree density (Chapter 2); therefore, I expected viscosity would decrease with increasing tree density (scenario B). With the assumption that stopping and foraging frequency reflect site hostility, I expected to see butterflies stopping and foraging less often and flying more quickly and straight as tree density increased. However, the medium density forest site F3 (tree density = 0.1135 trees/m^2) was the most viscous for both butterfly types. At densities less than this, meadow butterflies stopped as or more often as in F3, yet they moved more quickly through these sites. This suggests that the low viscosity of sites less dense than F3 was partially due to the ease with which meadow butterflies can navigate through these sites (scenario A). Conversely, these butterflies stopped less often in sites more dense than F3, and these sites were also less viscous than F3. In these cases it is more likely that low viscosity is a result of the hostility of the site: butterflies may be attempting to disperse from them as quickly as possible (scenario B).

Unlike meadow butterflies, the amount of time forest butterflies took to fly through each site directly reflected the number of stops they made (Figure 4-2 a and b) - forest butterflies flew faster through the sites in which they stopped less often. Forest butterflies are better adapted to navigating through forests, as they regularly do so to locate host plants (Bird *et al.* 1995). Additionally, the medium density sites are good habitat for forest butterflies (Chapter 2). For forest butterflies, the relationship between the viscosity of a landscape element and its hostility is described by scenario B: in sites that are not utilizable, forest butterflies move quickly in an attempt to disperse to more suitable habitat. For meadow butterflies, the patterns I observed appear to be a combination of scenarios A and B. At low tree densities, meadow butterflies can use landscape elements but can also fly through quickly (scenario A). At high tree densities, landscape elements are hostile, and meadow butterflies fly through them quickly.

Viscosity is clearly complex, influenced by both the movement paths taken by an organism and their stopping frequency. The tortuosity of an animal's movement path directly affects the rate at which they move through a landscape element (Merriam 1991, Wiens 1992). I expected butterflies to move more tortuously through suitable areas because they are successfully searching for resources (Stanton 1982, Odendaal *et al.* 1989, Schultz 1998) and to take direct paths in poor habitat (Tischendorf and Wissel 1997, Zollner and Lima 1999). Both butterfly types were more likely to show an escape response in the most dense forest site, and they therefore left this site quickly, indicating its low viscosity. Meadow butterflies flew straight more often in site F4 than the other sites, which decreased the amount of time that it took them to move through this site. Similarly, forest butterflies flew straight most often in site M1, through which they moved very quickly relative to the other sites. Therefore, these sites have low viscosity, and are likely to be poor habitat for each butterfly type. Both of these patterns reflect the findings of Chapter 2, where I found that F4 supported relatively few meadow butterflies and their resource plants, and M1 had few forest butterflies and their resource plants.

Although low butterfly abundance indicates that some sites are perceived by butterflies as poor habitat (Chapter 2), it appears that once individuals are within these sites they will opportunistically use those resources that are available. My expectation was that fewer butterflies would forage in sites with increasing forest density as a reflection of decreasing nectar plant availability (Chapter 2). I also expected this effect to be more pronounced for meadow butterflies, as a result of their higher degree of dependence upon open areas. Contrary to my expectations, I found that meadow butterflies foraged more than forest butterflies in almost all sites, and they foraged equally at all sites (Figure 4-6). Additionally, the number of *Colias* landing on *Astragalus* in each site did not differ. Meadow-specialist butterflies nectar-feed opportunistically in suboptimal habitat (Nève *et al.* 1996). Since nectar plants are often correlated with sunlight (Warren 1985, Haddad and Baum 1999) and butterflies tend to forage more in areas with low canopy cover (Grundel *et al.* 1998), it is likely that meadow butterflies are responding to fine-scale resource patches within forested landscape elements (With *et al.* 1997, Lord and Norton 1990, Mousson *et al.* 1999). The low abundance of meadow butterflies in forested areas is probably a result of their responses to meadow-forest boundaries (Chapter 3), rather than to the internal hostility of the site.

Although meadow butterflies appear to be able to locate small patches of nectar and host plants, this trend was not reflected in the direction they took when flying through the forest. Forest butterflies responded to and flew through open areas within each site while meadow butterflies generally did not. Species responses to landscape heterogeneity are often complicated by the differences in their vagility, as well as the scale at which they interact with the distribution of their resources (With *et al.* 1997). Forest openings and edges are preferred habitat for forest butterflies. Forests are generally novel habitat for meadow butterflies (Chapter 2) and it is likely that they cannot navigate through them as efficiently as forest butterflies. Meadow butterflies tend to fly erratically in patchy forests, and probably encounter resource patches haphazardly, rather than orienting towards them. *Pieris rapae*, a "meadow" butterfly and in the same family as *Colias* (Pieridae), is unable to orient towards patches of host plants at a distance greater than 1 m. (Fahrig and Paloheimo 1987). These results, along with my findings on foraging behaviour, emphasize the important role of open patches within forests for dispersing butterflies (Nève *et al.* 1996, Mousson *et al.* 1999). In the meadow sites, both types showed a weak tendency to orient towards forest which may be a response to variation of microclimatic suitability or resource microdistribution within these sites (Bourn and Thomas 1993).

Connectivity, or the amount of movement through landscapes, is partially determined by the flow of movement across boundaries (Chapter 3) as well as through the intervening areas between resource patches (Merriam 1984, 1991, Taylor *et al.* 1993). In this landscape, where forest canopy cover is shifting from open and patchy forest to 71 – 100% crown closure (Rhemtulla 1999) due to succession, the open patches within forest that both meadow and forest butterflies rely upon are disappearing. Forest butterflies will be less affected than meadow butterflies up to a certain point, as they are more likely to cross meadow-forest boundaries (Chapter 3), and are more efficient at navigating through patchy forests. Meadow butterflies are able to use forest up to a density of 0.1135 trees/m^2, although navigation seems to become more difficult with increasing forest density. Although both butterfly types move quickly through forests that are denser than 0.1135 trees/m^2, they are less likely to cross the meadow-forest boundary into these areas (Chapter 3). Therefore, the viscosity of a landscape element must be considered in conjunction with the boundary dynamics occurring at its edge (Chapter 5).

Conclusion

Most empirical studies treat the areas between habitat patches as black boxes, despite the fact that organisms must move through non-habitat areas to reach habitat patches (Diffendorfer *et al.* 1997, Bowne *et al.* 1999). This study is one of the first to empirically determine the internal viscosity of landscape elements and its relation to patch hostility, removing the effects of boundary permeability. It is clear that an increase in forest density through succession will affect butterfly movement behaviour, and therefore viscosity, in this system. At very high tree densities, the forest has low viscosity, but is also hostile to butterflies. In more open and patchy areas, viscosity within sites varies with tree density. Forest patches with moderate tree densities have high viscosity, due to the interaction between stopping frequency and the navigational ability of the butterflies moving through them. A multi-scale study examining the interactions between butterfly type, resource availability, flight speed, and forest patchiness would provide more insights into the relationship between forest density and viscosity. It would also be instructive to apply these methods to forest areas that have been burned, in order to determine if prescribed burning is an effective method of opening the canopy cover and creating new butterfly habitat. In conjunction with the results of the previous chapters, it is clear that patchy forests may provide habitat for both meadow and forest butterflies. After a threshold density, the forest is non-habitat, and reduces the connectivity of the landscape.

Literature Cited

Åberg, J., G. Jansson, J.E. Swenson, and P. Angelstam. 1995. The effect of matrix on the occurrence of hazel grouse (*Bonasa bonasai*) in isolated habitat fragments. Oecologia 103: 265 – 269.

Andrén, H., A. Delin, and A. Seiler. 1997. Population response to landscape changes depends on specialization to different landscape elements. Oikos 80: 193 – 196.

Bird, C.D., G.J. Hilchie, N.G. Kondla, E.M. Pike, and F.A.H. Sperling. 1995. Alberta Butterflies. The Provincial Museum of Alberta, Edmonton, Alberta.

Bourn, N.A.D. and J.A. Thomas. 1993. The ecology and conservation of the brown argus butterfly *Aricia agestis* in Britain. Biological Conservation 63: 67 – 74.

Bowne, D.R., J.D. Peles and G.W. Barrett. 1999. Effects of landscape spatial structure on movement patterns of the hispid cotton rat (*Sigmodon hispidus*). Landscape Ecology 14: 53 – 65.

Diffendorfer, J.E., M.S. Gaines, and R.D. Holt. 1995. Habitat fragmentation and movements of three small mammals (*Sigmodon*, *Microtus*, and *Peromyscus*). Ecology 76: 827 – 839.

Fahrig, L. and G. Merriam. 1994. Conservation of fragmented populations. Conservation Biology 8: 50 – 59.

Fahrig, L. and J.E. Paloheimo. 1987. Interpatch dispersal of the cabbage butterfly. Canadian Journal of Zoology 65: 616 – 622.

Grundel, R., N.B. Pavlovic, and C.L. Sulzman. 1998. Habitat use by the endangered Karner blue butterfly in oak woodlands: the influence of canopy cover. Biological Conservation 85: 47 – 53.

Gustafson, E.J. and R.H. Gardner. 1996. The effect of landscape heterogeneity on the probability of patch colonization. Ecology 77: 94 – 107.

Haddad, N.M. 1999a. Corridor use predicted from behaviours at habitat boundaries. The American Naturalist 153: 215 – 227.

Haddad, N.M. 1999b. Corridor and distance effects on interpatch movements: a landscape experiment with butterflies. Ecological Applications 9: 612 – 622.

Haddad, N.M. and K.A. Baum. 1999. An experimental test of corridor effects on butterfly densities. Ecological Applications 9: 623 – 633.

Ims, R.A. 1995. Movement patterns related to spatial structures. Pages 85 - 109 *in* Hansson, L., L. Fahrig, and G. Merriam, editors. Mosaic landscapes and ecological processes. Chapman and Hall, London, England.

Jonsen, I.D. and P.D. Taylor. 2000. Fine-scale movement behaviours of Calopterygid damselflies are influenced by landscape structure: An experimental manipulation. Oikos 88: 553 – 562.

Law, B.S. and C.R. Dickman. 1998. The use of habitat mosaics by terrestrial vertebrate fauna: implications for conservation and management. Biodiversity and Conservation 7: 323 – 333.

Lidicker, W.Z. Jr. 1999. Responses of mammals to habitat edges: an overview. Landscape Ecology 14: 333 – 343.

Lord, J.M. and D. A. Norton. 1990. Scale and the spatial concept of fragmentation. Conservation Biology 4: 197 – 202.

Merriam, G. 1984. Connectivity: a fundamental ecological characteristic of landscape pattern. Pages 5 – 15 *in* Brandt, J. and P. Agger, editors. Proceedings of the first international seminar on methodology in landscape ecological research and planning. International Association for Landscape Ecology, Roskilde University, Roskilde.

Merriam, G. 1991. Corridors and connectivity: animal populations in heterogeneous environments. Pages 133 – 142 *in* Saunders, D.A. and R.J. Hobbs, editors. Nature Conservation 2: the role of corridors. Surrey Beatty & Sons.

Moilanen, A. and I. Hanski. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. Ecology 79: 2503 – 2515.

Mousson, L., G. Nève, and M. Baguette. 1999. Metapopulation structure and conservation of the cranberry fritillary *Boloria aquilonaris* (Lepidoptera, Nymphalidae) in Belgium. Biological Conservation 87: 285 – 293.

Nève, G., B. Barascud, R. Hughes, J. Aubert, H. Descimon, P. Lebrun, and M. Baguette. 1996. Dispersal, colonization power and metapopulation structure in the vulnerable butterfly *Proclossiana eunomia* (Lepidoptera: Nymphalidae). Journal of Applied Ecology 33: 14 – 22.

Odendaal, F.J., P. Turchin, and F.R. Stermitz. 1989. Influence of host-plant density and male harassment on the distribution of female *Euphydryas anicia* (Nymphalidae). Oecologia 78: 283 – 288.

Pither, J. and P.D. Taylor. 1998. An experimental assessment of landscape connectivity. Oikos 83: 166 – 174.

Rhemtulla, J.M. 1999. Eighty years of change: the montane vegetation of Jasper National Park. M.Sc. Thesis. University of Alberta.

Roland, J., N. Keyghobadi, and S. Fownes. 2000. Alpine *Parnassius* butterfly dispersal: effects of landscape and population size. Ecology (in press)

Schultz, C. 1998. Dispersal behaviour and its implications for reserve design in a rare oregon butterfly. Conservation Biology 12: 284 – 292.

Scott, J.A. 1975. Flight patterns among eleven species of diurnal lepidoptera. Ecology 56: 1367 - 1377.

Shreeve, T.G. 1995. Butterfly mobility. *In* Pullin, A.S., editor. Ecology and Conservation of Butterflies. Chapman & Hall, New York.

S-Plus 4.0. 1998. Modern Statistics and Advanced Graphics. Data Analysis Products Division, MathSoft, Seattle, USA.

Stanton, M.L. 1982. Searching in a patchy environment: foodplant selection by *Colias p. eriphyle* butterflies. Ecology 63: 839 – 853.

Sutcliffe, O.L. and C.D. Thomas. 1996. Open corridors appear to facilitate dispersal by ringlet butterflies (*Aphantopus hyperantus*) between woodland clearings. Conservation Biology 10: 1359 – 1365.

Szacki, J. 1999. Spatially structure populations: how much do they match the classic metapopulation concept? Landscape Ecology 14: 369 – 379.

Taylor, P.D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. Oikos 68: 571 – 573.

Tischendorf, L. and C. Wissel. 1997. Corridors as conduits for small animals: attainable distances depending on movement pattern, boundary reaction and corridor width. Oikos 79: 603 – 611.

Turchin, P., F.J. Odendaal, and M.D. Rausher. 1991. Quantifying insect movements in the field. Environmental Entomology 20: 955 – 963.

Warren, M.S. 1985. The influence of shade on butterfly numbers in woodland rides, with special reference to the wood white *Leptidea sinapsis*. Biological Conservation 33: 147 – 164.

Watt, W.B., F.S. Chew, L.R.G. Snyder, A.G. Watt, and D.E. Rothschild. 1977. Population structure of pierid butterflies I. Numbers and movements of some montane *Colias* species. Oecologia 27: 1 – 22.

Wiens, J.A. 1992. Ecological flows across landscape boundaries: a conceptual overview. Pages 217 – 235 *in* Armand, A.O. *et. al.*, editors. Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows. Springer-Verlag, New York, USA.

Wiens, J.A., T.O. Crist and B.T. Milne. 1993a. On quantifying insect movements. Environmental Entomology 22: 709 – 715.

Wiens, J.A., R.L. Schooley, R.D. Weeks, Jr. 1997. Patchy landscapes and animal movements: do beetles percolate? Oikos 78: 257 – 264.

Wiens, J.A., N.C. Stenseth, B. Van Horne, and R.A. Ims. 1993b. Ecological mechanisms and landscape ecology. Oikos 66: 369 – 380.

With, K.A. 1997. The application of neutral landscape models in conservation biology. Conservation Biology 11: 1069 – 1080.

With, K.A. and T.O. Crist. 1995. Critical thresholds in species' responses to landscape structure. Ecology 76: 2446 – 2459.

With, K.A., R.H. Gardner, and M.G. Turner. 1997. Landscape connectivity and population distributions in heterogeneous environments. Oikos 78: 151 – 169.

Zollner, P.A. and S.L. Lima. 1999. Search strategies for landscape-level interpatch movements. Ecology 80: 1019 – 1030.

Chapter 5. General Discussion

"...management regimes that result in homogenization of habitats should be avoided" (Law and Dickman 1998)

The prevalent treatment of fragmented landscapes as discrete patches of habitat embedded in a neutral or hostile matrix ignores the complex movement capabilities and habitat preferences of animals (Ingham and Samways 1996), as well as the influence that the "matrix" may have on populations (Sisk *et al.* 1997, Szacki 1999). The nature of suboptimal landscape elements, or matrix, as well as the steepness of the boundaries between habitat and non-habitat affect the degree of fragmentation perceived by animals (Lord and Norton 1990). I examined how butterflies respond to the nature of landscape elements that represent suboptimal habitat. In Jasper National Park, the butterflies of the montane ecoregion are not restricted to open meadows or to resource patches. In this thesis I determined how butterfly abundance and movement behaviour are influenced by the gradient of tree densities produced by succession in the Athabasca River Valley. I used two groups of butterflies that differed in degree of habitat specialization: meadow specialists ("meadow" butterflies) and forest-tolerant generalists ("forest" butterflies). Vulnerability to habitat fragmentation is dependent upon degree of habitat specialization (Ims 1995).

Landscape fragmentation through succession produces mosaics of landscape elements differing in habitat suitability. Part of the response to fragmentation is patch occupancy and abundance within patches, which is an indication of habitat suitability (Dennis and Eales 1999). In Chapter 2 I surveyed landscape elements differing in tree density to determine butterfly abundance within them. Meadow butterfly abundance declined dramatically with increasing tree density, although they were always present in patchy forest sites. Forest butterfly abundance did not vary with tree density, except for a sharp decline at the highest forest density (0.1525 trees/m^2). This information on butterfly abundance provided baseline data for the following chapters. Patchy forests supported the most diverse butterfly communities. Prescribed burning is a possible method to increase the amount of open and patchy forest in this system, as butterfly diversity in one burned site was as high as that seen in the patchy forest sites.

Both meadow and forest butterflies were present in most forest sites, indicating that both types are capable of crossing meadow-forest boundaries. The flow of movement across landscapes is partially determined by the amount of movement occurring across boundaries (Taylor *et al.* 1993). Therefore, it is important to understand the role these boundaries play in butterfly responses to succession (Wiens *et al.* 1985). I quantified movement rates across boundaries for both butterfly types in Chapter 3. As tree density at the meadow-forest boundary increased, the amount of movement occurring across it decreased. Again, meadow butterflies responded more strongly to increasing tree density than did forest butterflies. Part of this response was the distance at which butterflies turned away from the boundary. Meadow butterflies tended to turn away at a distance of 4.5 m. or more, while forest butterflies often flew right up to the boundary before turning away. Both types moved across the boundary between low density forest and meadow readily, suggesting that open forest is not a barrier, but rather, is neutral or perhaps even utilizable as habitat.

The viscosity, or internal resistance to movement, of landscape elements also determines movement across landscapes (Wiens *et al.* 1997). In Chapter 4, I determined how increasing tree density affected movement within landscape elements by observing the behaviour of individual butterflies. I assessed both movement speeds and flight behaviour through each site – two of the most important factors determining patch viscosity (Wiens 1992). Patch viscosity is expected to be related to patch hostility (Wiens *et al.* 1997, Jonsen and Taylor 1999). Resource use within patches gives a direct indication of the degree of patch hostility: few butterflies will forage or oviposit in hostile patches. I therefore assessed the foraging probabilities of individuals moving through each site. Meadow butterflies moved more slowly than forest butterflies through all sites. This likely results from their tendency to forage and stop more in the six least dense sites. Both butterfly types dispersed very quickly from the densest forest site, indicating its hostility and resulting in low viscosity. These results, together with those of Chapter 3, show that in a landscape dominated by dense forest, butterflies would not be able to use or move through the areas between habitat patches.

The mechanism producing the patterns of meadow butterfly abundance that I observed appears to be the response to increasing tree density at the meadow-forest boundary, rather than the internal viscosity of forest patches. Other studies have found that forests are more resistant to butterfly movement than are meadows (Roland *et al.* 2000). I found that butterflies moved just as readily through patchy forests as through meadows, and that they used the resources available in these sites (Chapter 4), yet meadow butterflies are far less abundant in forests than in meadows (Chapter 2). The response of meadow butterflies to meadow-forest boundaries suggests that they are hesitant to enter forests (Chapter 3), which explains their low abundance in forests.

The area used in this study is a mosaic of species-specific filters, some of which are almost completely impermeable to most butterflies. Canopy cover in this area is shifting towards that seen in site F5: 0.1525 trees/m^2, or 71 – 100% canopy cover (Rhemtulla 1999). The continuation of this trend through succession would decrease movement across meadow-forest boundaries to less than half of what it currently is for open forests. This would effectively break this landscape into small isolated patches of meadow surrounded by an impassable matrix of forest.

The key to landscape connectivity for butterflies is landscape heterogeneity (Grundel *et al.* 1998). Open, patchy forests allow movement by butterflies (Chapter 3), and provide resources for butterflies whose larvae feed on forest plants (Chapter 2), complementing the nectar resources available in meadows (Merriam 1991, Dunning *et al.* 1992). Meadow butterflies are also able to use the resources present in open forests (Chapter 4), and may rely upon them to supplement those available in meadows (Dunning *et al.* 1992). Although resources like sunlight and nectar plants are scarcer in forests than in meadows, these small patches are utilizable as long as butterflies can reach them (Lord and Norton 1990, With *et al.* 1991). Small sunny patches may also act as stepping stones or temporary foraging sites for dispersing butterflies (Nève *et al.* 1996, Mousson *et al.* 1999). In dense forest areas, sunny patches are too small and isolated to be used by butterflies (With *et al.* 1997). In this landscape, it is likely that patchy forests may provide as much connectivity as would open corridors (Bowne *et al.* 1999).

Conclusion

In this study I demonstrated that butterflies move through and use patchy forested areas, dependent upon the tree density of the area. The forest may be utilizable to butterflies below a threshold tree density,. Beyond this threshold density, the forest is pure non-habitat, forming a barrier to movement and fragmenting the landscape. The system of patchy forests and meadows I studied acts as a species-specific filter (Ingham and Samways 1996, Szacki 1999). Butterflies whose host plants are found in forests are able to move through this successional landscape more than do butterflies that specialize in meadow habitats. Meadow butterflies, which are more sensitive to forests than forest butterflies, will likely be negatively affected by continued succession and are more vulnerable to habitat fragmentation (Ims 1995). In order to avoid the further loss of open patchy forests, managers should consider small prescribed burns in stands of forest with a tree density greater than 0.1325 trees/m^2.

Literature Cited

Bowne, D.R., J.D. Peles and G.W. Barrett. 1999. Effects of landscape spatial structure on movement patterns of the hispid cotton rat (*Sigmodon hispidus*). Landscape Ecology 14: 53 – 65.

Dennis, R.L.H. and H.T. Eales. 1999. Probability of site occupancy in the large heath butterfly *Coenonympha tullia* determined from geographic and ecological data. Biological Conservation 87: 295 – 301.

Dunning, J.B., B.J. Danielson, and H.R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65: 169 – 175.

Grundel, R., N.B. Pavlovic, and C.L. Sulzman. 1998. Habitat use by the endangered Karner blue butterfly in oak woodlands: the influence of canopy cover. Biological Conservation 85: 47 – 53.

Ims, R.A. 1995. Movement patterns related to spatial structures. Pages 85 - 109 *in* Hansson, L., L. Fahrig, and G. Merriam, editors. Mosaic landscapes and ecological processes. Chapman and Hall, London, England.

Ingham, D.S. and M.J. Samways. 1996. Application of fragmentation and variegation models to epigaeic invertebrates in South Africa. Conservation Biology 10: 1353 – 1358.

Jonsen, I.D. and P.D. Taylor. 2000. Fine-scale movement behaviours of Calopterygid damselflies are influenced by landscape structure: An experimental manipulation. Oikos 88: 553 – 562.

Lord, J.M. and D. A. Norton. 1990. Scale and the spatial concept of fragmentation. Conservation Biology 4: 197 – 202.

Merriam, G. 1991. Corridors and connectivity: animal populations in heterogeneous environments. Pages 133 – 142 *in* Saunders, D.A. and R.J. Hobbs, editors. Nature Conservation 2: the role of corridors. Surrey Beatty & Sons.

Rhemtulla, J.M. 1999. Eighty years of change: the montane vegetation of Jasper National Park. M.Sc. Thesis. University of Alberta.

Roland, J., N. Keyghobadi, and S. Fownes. 2000. Alpine *Parnassius* butterfly dispersal: effects of landscape and population size. Ecology (in press)

Sisk, T.D., N.M. Haddad and P.R. Erlich. 1997. Bird assemblages in patchy woodlands: modeling the effects of edge and matrix habitats. Ecological Applications 7: 1170 – 1180.

Szacki, J. 1999. Spatially structured populations: how much do they match the classic metapopulation concept? Landscape Ecology 14: 369 – 379.

Taylor, P.D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. Oikos 68: 571 – 573.

Wiens, J.A. 1992. Ecological flows across landscape boundaries: a conceptual overview. Pages 217 – 235 *in* Armand, A.O. *et al.*, editors. Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows. Springer-Verlag, New York, USA.

Wiens, J.A., C.S. Crawford, and J.R. Gosz. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. Oikos 45: 421 – 427.

Wiens, J.A., R.L. Schooley, R.D. Weeks, Jr. 1997. Patchy landscapes and animal movements: do beetle percolate? Oikos 78: 257 – 264.

With, K.A., R.H. Gardner, and M.G. Turner. 1997. Landscape connectivity and population distributions in heterogeneous environments. Oikos 78: 151 – 169.