University of Alberta

Effect of the habitat quality on metapopulations of three species of butterflies associated with Garry oak meadows in Southwestern British Columbia.

By

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Deep in the human unconscious is a pervasive need for
a logical universe that makes sense. But the real universe
is always one step beyond logic. – Frank Herbert

for my family,

thank you for your support
without which
this would not have been possible.

ABSTRACT

The effect of habitat quality on metapopulations of three butterfly species found in Garry oak meadows was examined. GLM regression results showed floral abundance and meadow connectivity explained the most variation in the data, and were consistently positively correlated to butterfly occurrence. Hostplant cover and meadow area were positively correlated with species occurrence, but less consistently so. Scotch broom was not found to affect butterfly occurrence except in one positive case (*Erynnis propertius*).

A nonlinear metapopulation model, tested for *Erynnis propertius*, fit the observed occurrence pattern much better than an unstructured linear model. Flower abundance was used to adjust the metapopulation model for 'effective habitat area', and make predictions to rank the viability of meadow populations given local habitat quality and spatial/metapopulation context. This type of method is also useful in the case of other taxa and areas of study, such as pest management, restoration, and reserve design.

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CHAPTER 1

General Introduction and Summary

Two approaches have been used to describe species distributions: one emphasizing the role of habitat quality (Dennis *et al*, 2003), and the other emphasizing the role of spatial configuration of the habitat and metapopulation effects (Hanski, 1994). This thesis combines both to compare their relative importance in determining species distributions. I do this by building habitat quality into a metapopulation model (Hanski, 1994; Moilanen and Hanski, 1998; Ovaskainen and Hanski, 2004), an approach that has rarely been done (Dennis and Eales, 1997; Thomas, 2001; Hanski and Ovaskainen, 2000; Walker *et al*, 2003; Ovaskainen and Hanski, 2003).

Many past analyses have ignored the role of spatial processes in ecology, focusing instead on local habitat effects on species distribution and population viability (Boggs and Ross, 1993; Hays *et al.*, 2000). This approach has been quite successful in predicting species occurrence in some cases such as butterfly habitat use (Schultz and Dlugosch, 1999; Matter and Roland, 2002) and may include aspects of biology such as behaviour (Young and Isbell, 1994), genetics (Fuerst and Maruyama. 1986), competition (Brown and Davidson, 1977), predation (Hassell, 1978), and disease (Bailey, 1975). The importance of resources in defining suitable habitat for a species is undeniable, but there are often situations where suitable habitats remain unoccupied. This may be due to habitat factors, but it has been shown that in some cases these empty patches remain empty for reasons that depend at least in part on the intervening environment between patches of a network (Levins, 1969 and 1970; Tilman and Kareiva, 1997; Moilanen and Hanski, 1998; Tischendorf and Fahrig, 2000). The effect of the intervening habitat may severely limit dispersal, and therefore colonization, through two mechanisms; increased distance between patches (Hokit *et al.*, 1999; Jonsen *et al*, 2001; but see Krauss *et al.*, 2004), and variable conditions encountered in the intervening habitat (Roland *et al.*, 2000; Ricketts, 2001; Walker *et al.*, 2003). Many of the models of species distributions have been substantially improved by including information about spatial context of both occupied and unoccupied habitat (Hanski *et al.*, 1995; Foley *et al.*, 1999; Antonovics, 2004). The role of space was initially ignored partially because it was not recognized as important and partially due to the difficulty of incorporating it into models (Clobert *et al*, 2001), but with the advent of quick and cheap mapping systems it has become easier to include connectivity measures in such analyses.

The invasion of weedy plants can affect habitat quality for animal species such as mammalian herbivores and herbivorous insects (Hays *et al*, 2000; Scheimann *et al*, 2003; Wallace *et al*, 2003), and thus may determine species ranges. There are a large and growing number of journal articles examining the problem of weeds affecting habitat for native species (Savage and Young, 1969; Bedunah, 1992; Wallace *et al.*, 1992; Olsen, 1995; Scheiman *et al*, 2003). This is another emerging modern problem that has been exacerbated by incidental movement of propagules by humans, over distances that are several orders of magnitude beyond their normal dispersal range (Parker *et al.* 1997; Parker 2000; Mack and Lonsdale, 2001). In most cases the impact of these exotic species has not been determined, but in cases where they have become established, their effect on other organisms through competition, predation and dispersal (Begon *et al.*, 1996) imply a coming crisis for both natural areas and anthropogenically-modified environments (Mooney and Hobbs, 2000).

OVERVIEW OF THESIS

My objectives in this thesis were to define suitable habitat for the butterfly species *Erynnis propertius*, *Incisalia mossii* ssp. *mossii*, and *Celastrina ladon*, in terms of patch area, patch connectivity, host plant density, flower abundance, and percent cover of the invasive weed Scotch Broom. The purpose was to determine what role habitat attributes have in the ecology of several species of butterflies, both locally and for interconnected metapopulations. Of particular interest was the role of Broom in defining habitat suitability given that Broom is spreading rapidly and has been implicated in habitat loss for butterfly species (*Speyeria zerene* ssp. *bremnerii, Polites mardon*, *Plebejus icarioides* ssp. *blackmorei*, *Euphydryas editha* ssp. *taylori*) in Garry oak habitat in Washington State (Hays *et al.*, 2000). Having identified the importance of each component of habitat quality at the local population level, a predictive model was developed to help define the best course of action for management. This was done using a form of metapopulation model, developed and tested for the butterfly species *E. propertius,* to assess the relative importance of individual patches within a metapopulation, and how the quality of those patches affects their relative importance at the regional (metapopulation) scale.

In Chapter 2 the distributions of three species of butterflies were identified and examined, in relation to their hostplants, flower abundance, habitat patch size, habitat patch connectivity, and the cover of the weed Scotch Broom. The results of these regression models were used to assess the relative role of each variable in determining the distribution of each butterfly species. Host plant density, flower abundance and density of Scotch broom all have significant effects on butterfly occurrence. Area did not have a consistent or strong effect, suggesting that accounting for habitat quality rather than habitat area may be worthwhile in more complex metapopulation models. Results of the analyses of patch occupancy in relation to connectivity of patches were also significant in most cases, implying that a more complex metapopulation approach may be justified. This was found to be the case for all species, although the magnitude of effects of each variable, including connectivity, varied between years.

Given that a metapopulation approach was potentially worthwhile, a simple Incidence Function Model (IFM; Hanski, 1994) that included habitat quality was built and tested for one butterfly species, *Erynnis propertius* (Scudder and Burgess, 1870), in Chapter 3. The IFM model with process-oriented assumptions relating to theorized metapopulation dynamics then was tested to determine if it provided a better fit to the butterfly occupancy data. This also was found to be the case, and prospective analyses using linear algebra (Caswell, 2001) were then developed to combine the metapopulation and habitat quality data into a predictive form that allows predictions about the effects of habitat quality, connectivity and patch area on patch occupancy into a spatial context. This new tool is likely to prove useful in many types of situations, including determining which specific patches to treat in weed or pest management (Shea and Possingham, 2000) and in restoration, and could aid in reserve design by considering which among several habitats are most worth preserving (Tuck and Possingham, 1994 and 2000; Hanski and Ovaskainen, 2000; Ovaskainen and Hanski, 2003; Cabeza *et al*, 2004). The results of this trial prospective model with the butterfly species (*E. propertius*) allows the identification of which habitat patches were most important to the metapopulation and how changes in resources (through management action) influences this importance. I then discuss potential uses of this model and possible improvements that may define the role of habitat quality in relation to spatial distribution more precisely.

LITERATURE

Antonovics, J. 2004. Long term study of a plant-pathogen metapopulation. In Hanski, I., and Gaggiotti, O. (eds.) *Ecology, Genetics, and Evolution of Metapopulations.* Pp.471-488. Academic Press.

Bailey, N. 1975. *The mathematical theory of infectious disease and its applications.* Griffin, London, UK

Bedunah, D. 1992. Complex ecology of weeds, grazing and wildlife. Western Wildlands 18:2.

Begon, M., M. Mortimer, and D.J. Thompson. 1996. *Population ecology: a unified study of animals and plants.* Blackwell Science Ltd. Cambridge.

Boggs, C.L., and C.L. Ross. 1993. The effect of adult food limitation on life history traits in *Speyeria mormonia* (Lepidoptera: Nymphalidae). Ecology 74:433-441.

Brown, J.H., and D.W. Davidson. 1977. Competition between seed-eating rodents and ants in desert ecosystems. Science 196: 880-882

Cabeza, M., Moilanen, A. and H.P. Possingham. 2004. Metapopulation dynamics and reserve network design. In: Hanski, I. and Gaggiotti, O. (eds.) *Metapopulation Ecology, Genetics, and Evolution,* pp. 541-564. Academic Press.

Caswell, H. Matrix population models: construction analysis and interpretation. Sinauer Assoc. Sunderland, MA.

Clobert J, E. Danchin, A. A. Dhondt and J. D. Nichols (eds). 2001. *Dispersal.* Oxford University Press, New York.

Dennis, R. L. H. and H. T. Eales. 1997. Patch occupancy in *Coenonympha tullia* (Lepidoptera: Satyridae): habitat quality matters as much as patch size and isolation. Journal of Insect Conservation 1: 167-176.

Dennis, R. L. H., Shreeve, T. G. and Van Dyck, H. 2003. Towards a functional resource-based concept for habitat: a butterfly biology viewpoint. Oikos 102: 417-426.

Foley, J.E., P. Foley, and N.C. Pedersen.1999. The persistence of a SIS disease in a metapopulation. Journal of Applied Ecology 36: 555-563.

Fuerst, P.A., and T. Maruyama. 1986. Considerations on the conservation of alleles and genetic heterozygosity in small, managed populations. Zoo Biology 5:171-179.

Hanski, I. 1994. A practical model of metapopulation dynamics. Journal of animal Ecology 63: 151-162.

Hanski, I., A. Moilanen, T. Pakkala, and M. Kuusaari. 1995. The quantitative incidence function model and persistence of an endangered butterfly metapopulation. Conservation Biology 10(2):578-590.

Hanski, I., and O. Ovaskainen. 2000. Metapopulation capacity of a fragmented landscape. Nature 404:755-758

Hassell, M.P. 1978. *The dynamics of arthropod predator-prey systems.* Princeton University Press, Princeton.

Hays, D.W., A.E. Potter, C.W. Thompson, and P.V. Dunn. 2000. Critical habitat components for four rare south Puget Sound butterflies. Report prepared for Washington Department of Fish and Wildlife, and The Nature Conservancy of Washington, Seattle.

Hokit, D.G., B.M. Stith, and L.C. Branch. 1999. Effects of landscape structure in Florida scrub: a population perspective. Ecological Applications 9(1):124-134.

Jonsen, I.D., R.S. Bourchier, and J. Roland. 2001. The influence of matrix habitat on *Apthona* flea beetle immigration to leafy spurge patches. Oecologia 127:287-294.

Krauss, J., I. Steffan-Dewenter, and T. Tscharntke. 2004. Landscape occupancy and local population size depends on host plant distribution in the butterfly *Cupido minimus*. Biological Conservation IN PRESS.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the entomological society of America 15:237-40.

Levins, R. 1970. Extinction. IN *Some mathematical problems in biology*. (Gerstenhaber M. Ed.), pp77-107. American mathematical society, Providence, R.I.

Mack, R.N., and W. M. Lonsdale (2001). Humans as Global Plant Dispersers: Getting More Than We Bargained For. Bioscience, 51(2): 95-102

Matter. S., and J. Roland. 2002. An experimental examination of the effect of habitat quality on the dispersal and local abundance of the butterfly *Parnassius smintheus*. Ecological entomology 27:308-316.

Moilanen, A., and I. Hanski. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. Ecology 79(7):2503-2515

Mooney, H.A., and R.J. Hobbs. 2000. *Invasive species in a changing world*. Island Press. Washington, DC.

Olsen, R. 1995 Impact of noxious weeds on wildlife. IN *Proceedings of symposium on non-native invasive plants: a biological disaster*. Denver, Colorado. Sept. 19, 1995.

Ovaskainen, O., and I. Hanski. 2003. How much does an individual habitat fragment contribute to metapopulation dynamics and persistence? Theoretical Population Biology 64:481-495

Ovaskainen, O. and I. Hanski. 2004. Metapopulation dynamics in highly fragmented landscapes. "*Ecology, Genetics, and Evolution in Metapopulations*" (Hanski, I. and Gaggiotti, O., eds), Academic Press.

Parker, I.M.,W.S. Harpole, and D. Dionne.1997. Plant community diversity and invasion of the exotic shrub *Cytisus scoparius*: Testing hypotheses of invasibility and impact. IN *Ecology and conservation of the South Puget Sound prairie landscape* (P.V. Dunn, and K. Ewing, eds.), pp.149-162, Seattle: The Nature Conservancy Press.

Parker, I. 2000. Invasion dynamics of *Cytisus scoparius*: a matrix model approach. Ecological applications 10(3):726-743.

Pimentel, D. 2000. *Environmental and economic costs of non-indigenous species in the United States*. USA BLM, Ithaca, New York.

Ricketts, T.H. 2001. The matrix matters: effective isolation in fragmented landscapes American Naturalist 158: 87-99.

Roland, J., N. Keyghobadi, and S. Fownes. 2000. Alpine *Parnassius* butterfly dispersal: effects of landscape and population size Ecology 81:1642-1653.

Savage, D., J. Young, and R. Evans. 1969. Usage of medusahead and downy brome caryopses by Chukar partridge. Journal of range management 33(4):975-978

Scheiman, D., E. Bollinger, and D. Johnson. 2003. Effects of leafy spurge on grassland birds. Journal of Wildlife Management 67(1):115-121.

Schultz, C.B., and K.M. Dlugosch. 1999. Nectar and hostplant scarcity limit populations of an endangered Oregon butterfly. Oecologia 119:231-238.

Shea, K. and Possingham, H. P. 2000. Optimal release strategies for biological control agents: an application of stochastic dynamic programming to population management. Journal of Applied Ecology 37:77-86.

Thomas, J.A., N.A.D. Bourn, R.T. Clarke, K.E. Stewart, D.J. Simcox, G.S. Pearman, R. Curtis, and B. Goodger. 2001. The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. Proceedings of the Royal Society of London SERIES B 268:1791-1796.

Tilman, D., and Kareiva, P. *(Editors*). 1997. *Spatial ecology: the role of space in population dynamics and interspecific interactions.* Princeton University Press, Princeton.

Tischendorf, L. and L. Fahrig. 2000. How should we measure landscape connectivity? Landscape Ecology 15: 633-641.

Tuck, G.N. and H. P. Possingham. 2000. Marine protected areas for spatially structured stock. Marine Ecology Progress Series 192:89-101.

Tuck, G. and H. P. Possingham. 1994. Optimal harvesting strategies for a metapopulation. Bulletin of Mathematical Biology 56:107-127

Wallace, N., J. Leitch, and F. Leistritz. 1992. Economic impact of leafy spurge on North Dakota wildlands. North Dakota Farm research 49(5):9-13.

Walker, R.S., A.J. Novarro, and L.C. Branch. 2003. Effects of patch attributes, barriers, and distance between patches on the distribution of a rock-dwelling rodent (*Lagidium viscacia*). Landscape Ecology 18: 187-194.

Young, T.P., and L.A. Isbell. 1994. Minimum group size and other conservation lessons exemplified by a declining primate population. Biological Conservation. 68: 129-134.

CHAPTER 2

Effect of patch area, connectivity and habitat quality on occupancy by three butterfly species.

INTRODUCTION

One of the primary goals of ecology is to predict the distribution and abundance of species (Andrwartha and Birch, 1954). Two approaches used recently to describe these characteristics emphasize either metapopulation structures or local habitat quality (Hanski, 1994; Thomas 2001; Dennis *et al.*, 2003). The two approaches are often not integrated with each other however, due to specialization of researchers in each topic. For example, scientists interested in the role of habitat quality measures in determining species occurrences often do not use a theoretical and mathematical framework such as metapopulation theory to describe the role of spatial arrangement of the resources in their models of habitat choice (Kinvig and Samways, 2000). As pointed out previously, (Levins, 1966; Hilborn and Mangel, 1997; Smith *et al.*, 1997), mathematically-oriented theorists are often not familiar with the difficulties of obtaining empirical data demonstrating the same points as simulations.

Current metapopulation theory grew out of a realization that dispersal of organisms is of primary importance in establishment of populations and colonization of new habitats (Andrewartha and Birch 1954; Levins, 1969) in a real world of constantly changing environments. Combined with a recognition of the importance of dispersal was the idea that, at some sites, species will go extinct when factors such as high predation rates (Maunder *et al.*, 2002; Thibault, 2002; Hooson and Jamieson, 2003), poor food availability (van Apeldoorn, 1992; Hochberg *et al.*, 1998; Briers and Warren. 2000; Fleishmann *et al.*, 2002; Johst and Schoeps, 2003), small population size/demographic stochasticity (Kendall and Fox, 2002) and/or genetic inbreeding (Gaggiotti, 2003; Lesbarreres *et al.*, 2003; Palo *et al.*, 2003) the population there fails to reproduce well enough to sustain itself.

Levins' (1969) original description of metapopulation theory did not explicitly include effects of varying population size or population isolation; these were instead implicit in the model as constant values across all patches. Current formulations of metapopulation theory have modified Levins' idea to include some estimate of variation in population isolation and variation in local population size, usually represented by inter-patch distances and habitat area respectively (Hanski, 1994, Ackakaya, 2000). Although Levins's original theory of metapopulations did not account for variable habitat qualities, in all real-world examples of metapopulations, habitats can be highly heterogeneous, and so two sites of the same area are unlikely to be of a similar carrying capacity. Species do prefer, and survive better, in certain habitats (Gilbert and Singer, 1975; Thomas, 1983; Goodman, 1987) such as butterflies exhibiting a higher occupancy rate and population persistence in sites with higher host plant densities (Fred and Brommer, 2003). Often species exhibit habitat preferences and may move substantial distances to find suitable sites (Brommer and Fred, 1999; Matter and Roland, 2002, Matter *et al.*, 2005), implying that both habitat quality and patch isolation are important determinants of species persistence.

Rather than assuming that all habitat patches of the same or similar area are equal, habitat quality has been increasingly incorporated into metapopulation studies (Hanski, 1994, Sjogren-Gulve and Ray, 1996). A recent trend is to attempt to extend the approach of emphasizing habitat quality by including simple metrics representing the spatial context of the patch as a variable affecting its quality (Gutierrez *et al.*, 1999; Jonsen *et al.*, 2001; Thomas *et al.*, 2001; Fleishmann, 2002; Walker *et al.*, 2003). Studies such as these demonstrate that using only simple metrics to represent patch spatial context does indeed produce as good or better fit of the model to the data than more complex models (Hokit *et al.*, 2001).

One way in which habitat quality varies between habitat patches for an herbivorous species is in the composition of plant species, for example including host plant abundance and nectar plant composition affecting food availability for butterflies. The most important component of plant composition for butterflies, are the larval host plants and nectar food plants for adults (Ehrlich, 1961; Thomas, 1983; Luoto *et al.*, 2001; Dennis *et al.*, 2003). Food plant species may in turn be affected by introduced plant species that may have a profound impact on the vegetative composition of the area they colonize (Colton and Alpert, 1998; Simberloff, 1999; IUCN, 2000; Mooney and Hobbs, 2000). Analysis of the impact of plant weeds until recently has been focused on how weeds affect native plants (Vila *et al.*, 2004), however, very little effort has been put into examination of the effect that introduced weeds have on native animals (Price *et al.*, 1994; Scheiman *et al.*, 2003).

The purpose of this chapter is to examine the impact of an invasive weed, Scotch broom (*Cytisus scoparius*, (L.), Link; sometimes referred to as *Saromanthus scoparius*), on the availability of habitat for three native species of butterfly. *C. scoparius* is the most ubiquitous and serious woody invasive species currently in the Garry oak (Oregon white oak; *Quercus garryanna*, Douglas ex. Hook.) communities in BC, having invaded most of Vancouver Island and the Gulf Islands (Zielke *et al.*, 1992; Erickson, 1996, Ussery, 1997). In other locations, removal experiments have demonstrated that increase in cover of this plant has reduced population size of many native plant species and perhaps facilitated the invasion of other invasive non-native weeds, resulting in a decline in overall plant diversity (Parker *et al.*, 1997; Ussery, 1997). As well, the abundance of several other species of butterflies found in Garry oak meadows in Washington State has been found to drop in sites with high cover of broom, likely through an indirect negative effect of the broom on the butterflies through its' negative effect on the flowering plants (Hays *et al.*, 2000). In the case of these butterfly species, there was generally preference exhibited for sites with lower % cover of broom (below 20% cover) and for sites with smaller broom plants that were less dense (plants <1m in height and also younger and less filled out). Scotch broom is also a threat in other parts of the Pacific coast, from California (found in Redwood Park) to Washington State, and has begun to invade interior BC (Ussery, 1997). Broom forms dense aggregations in areas that had previously been grassland and low forbs, displacing smaller plants by shading and possibly competing for water, and preventing regeneration of native conifer trees (Williams, 1981; Waterhouse, 1988; Ussery, 1997).

In Canada, Garry oak (*Q. garryanna*) meadows and their associated insects and plants are found only in southwestern British Columbia. Only five percent of the original distribution of Garry Oak ecosystems in Canada remains in an undeveloped state (Fuchs, 2001; Appendix A, Mitter and Lea, 2004) and a similar situation of habitat loss and fragmentation exists for many other temperate and chaparral ecosystems elsewhere in the world (Lu and Samways, 2002). Much of the Canadian Garry oak habitat has been lost to urban expansion and invasion by the weed Scotch broom (Erickson, 1996; Ussery, 1997). Within Garry oak meadows in British Columbia, several species of butterfly already have been extirpated or seriously reduced in number due to habitat loss and invasion by weeds (Guppy and Shepard, 2001; Eastman, pers. comm.). The Garry oak system was chosen for this project because it is ideal for the study of impact of a weed on metapopulations of a butterfly, due to its natural patchiness and many sites that have been exposed to various levels of weed invasion over the past 100 years. This ecosystem exists as a series of meadow 'patches', surrounded by conifer forest. If an organism living within these patches has limited dispersal, this structural arrangement of habitats into patches may function as a metapopulation. My study differs from that of Hays *et al.*, (2000) in that it 1) examines three previously unexamined butterfly species, 2) includes the effect of patch size and patch isolation on the occupancy of Garry oak meadows by butterflies, and 3) tests for effects of Scotch broom, host plant density, and flower availability. The three butterfly species in this study are *Erynnis propertius*, Scudder & Burgess, 1870 (Propertius duskywing), *Incisalia mossii* ssp. *mossii*, Edwards (Moss's elfin; sometimes placed in genus *Callophrys*), and *Celastrina ladon*, Cramer (Spring azure). Inclusion of the above explanatory variables allows statistical evaluation of each of these variables as contributing to patch occupancy by each butterfly species, and analysis of multiple species permits search for generalities of effects and for differences among species.

I hypothesized that Scotch broom would reduce the occurrence of butterflies by lowering habitat quality. Meadows with higher availability of flowers and/or larval host plants and lower density of Scotch broom were the hypothesized preferences for all butterfly species. In terms of the metapopulation variables, I predicted that more highly connected meadows and larger meadows would be more likely to have a butterfly population for all three species. Overall, rather than only simple area and connectivity measures, I hypothesized that an 'effective area' measure which is represented by both the physical area and the habitat quality would produce a better model fit to the data.

I also predicted that each butterfly species would be distributed differently within the same habitat network given that they would each key in to different habitat qualities of the sites; a pattern seen for butterfly species in Britain (Thomas, 2001), and dung beetle species in ephemeral habitat patches in Finland (Roslin, 2000). Specifically, I hypothesized that each butterfly species would be distributed in the network in response to the distribution of its respective host plant, the floral resources, the distribution of Scotch broom, and the potential two-way interactions between variables. For all species, I hypothesized that there would be a positive effect of increased flower availability on patch occupancy by the butterfly species, and that this would decrease at higher levels of broom. This was because butterflies were not observed to nectar at this plant (though bees use the flowers regularly, Parker and Engel, 2002; Hallstrom, unpublished data), and increased cover of it could decrease the ability of the butterflies to forage efficiently by the addition of the shrubby broom plant creating structural interference with their movement.

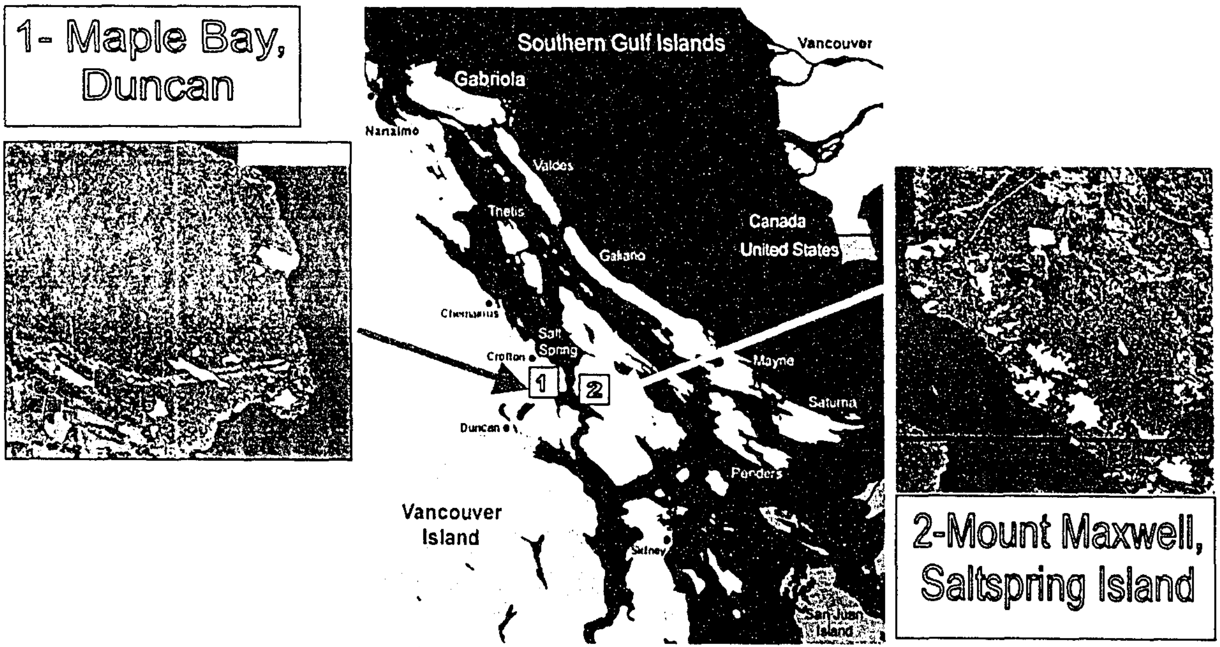
METHODS

Study Area

The study was conducted in two Garry oak meadow networks (Fig 2-1) on two islands, separated by 1.5km of ocean. The two networks were chosen because, despite invasion by broom, they were largely undisturbed by anthropogenic developments, large in size and relatively isolated from other Garry oak meadows. This area has a Mediterranean-type climate due to both the mitigating influence of the ocean keeping temperatures relatively warm for such northerly latitudes, and the influence of two mountain ranges that cause a double rainshadow effect. This region of biogeoclimatic oddity is defined as the Coastal Douglas Fir biogeoclimatic zone (Fuchs, 2001) and it covers southeast Vancouver Island from Courtenay to Victoria and includes the Southern Gulf Islands. In Canada, Garry oak ecosystems are the driest and most rare subsection of this rare biogeoclimatic zone. Average precipitation of 68.5cm is low for this region, and average summer temperatures are mild (16.1°C). For comparison, these ranges are substantially warmer and drier relative to more typical coastal British Columbia rainforest that receives average precipitation of 243cm with average summer temperatures of 14°C. Garry oak meadows are typically found on southerly aspects, and most of the remaining sites are located on shallow, well-drained soils. Combined with the low rainfall this produces a summer moisture deficit and prevents conifers from becoming established. The scrub oak community on these sites therefore represents an edaphic climax (Roemer, 1972).

Since the arrival of European settlers in the 1800's, the *Q. garryanna* vegetation community has been altered by fire suppression, grazing by livestock, invasions of exotic species, and clearing for agriculture and urbanization (Roemer, 1972; Erickson, 1996). Remnant patches of *Q. garryanna* vegetation communities are currently ranked as "critically endangered" or "endangered" and have received the highest S1 ranking (following the Nature Conservancy criteria for listing endangerment) on the red list of endangered species and ecotypes by the BC Conservation Data Center (British Columbia Conservation Data Center, 2004).

The two networks are two of the largest remaining contiguous, intact, and relatively undisturbed mosaics of Garry oak meadows in Canada. They were chosen by preliminary surveys of potential sites during summer 2001, based on government Sensitive Ecosystem Inventory maps (Ward *et al.*, 1998; Caskey and Henigman, 2004). The two meadow networks were approximately 16 km^2 and 25 km^2 in area, and are located at Maple Mountain, adjacent to the town of Duncan, and at Mount Maxwell, on Saltspring Island (Figure 2-1). They are designated as protected areas and have remained largely, or entirely, undisturbed by anthropogenic actions such as building houses and roads. Although the networks are relatively pristine in terms of human development pressures, they were chosen because the Maple Mountain site is heavily invaded by broom and the Mount Maxwell site remains relatively broom free. This contrast in the amount of broom makes the two networks well suited to a study of the effect of the invasion of Scotch broom, given that both sites are classed biogeographically as a combination of Coastal Douglas Fir type and the subtype Garry oak ecosystems and so are otherwise similar.



(after Orca Hosting Inc., 2004)

Figure 2-1: Map of general location of study site within Canada and British Columbia, including locations of the two meadow networks within this smaller coastal region of British Columbia.

Predictive models developed from this work will have application over other areas of remaining Garry oak meadows affected by invasion of Scotch broom, as well as spanning a range of flower abundance and host plant densities.

Butterfly species

Five species of butterfly were initially included in this study, but two were dropped from this analysis based on a lack of data, leaving three. Three species were examined to assess and compare metapopulation and habitat effects on both abundant and rare butterfly species, species with different host plant dispersion or abundance, and species with differing dispersal abilities. It was hypothesized that dispersal differed among the three butterfly species, given their differences in morphology, behaviour, and size, and thus there should be different effects of connectivity on each.

Incisalia mossii ssp. *mossii* (Moss' elfin) and the *Erynnis propertius* (Propertius duskywing) were included because they are considered 'rare' in general in the Garry oak meadows. The more common species, the *Celastrina ladon* (Spring azure), was included to permit comparison to a more abundant and widespread species, as species distribution and abundance may be related to the habitat variables and spatial arrangement of habitat. General surveys for Lepidoptera conducted during summer of 2001 determined that these three species differed in abundance, but that all were sufficiently abundant to provide statistically useful quantitative data. Extremely rare species in this region such as *Euphydryas editha* ssp. *taylorii* (Edith's checkerspot) and *Speyeria zerene* ssp. *bremnerii* (Zerene fritillary) may only appear at a very few sites (Guppy and Shepard, 2001; Hallstrom, unpublished data), and were thus not appropriate for this analysis. *Incisalia mossii* ssp. *mossii* and the *Erynnis propertius* are listed as threatened (British Columbia Conservation Data Center, 2004).

In addition, each of these species exhibits different emergence dates and uses a different larval host plant, each differing in growth form, leaf flush date, and dispersion. Results from previous studies (Guppy and Sheppard, 2001) were used to evaluate the degree of monophagy for each butterfly species. All three species have a narrow range of obligate host plants, and are almost completely restricted to the Garry oak savanna ecosystems, because their hostplants are found either primarily or entirely in this ecosystem (Pojar and MacKinnon, 1994; Guppy and Shepard, 2001). Species also differed in the relative size of their host plants, which may affect the impact of broom. *E. propertius* larvae feed exclusively on the Garry oak tree (*Q. garryanna*), which is not affected by broom (Erickson, 1996; Ussery, 1997). *I. mossii mossii* larvae feed monophagously on the small herb *Sedum* spp. (Guppy and Shepard, 2001; though only *Sedum spathulifolium* is found in this region) growing on sunny, steeper sites and rock faces often in conjunction with Garry oak. This small host plant may be negatively affected by broom since it is susceptible to shading by the larger shrub. Caged rearing experiments have demonstrated that larval *C. ladon* feed on the shrubs *H. discolor*, *Prunus* spp, and *Spirea* (Guppy and Shepard, 2001), although only *H. discolor* and *Prunus* spp are found in this part of British Columbia. Individual *Prunus* spp trees were found at only 5 out of 214 sites and *Spirea* shrubs were not observed at all. I thus excluded both from the analysis, leaving only *H. discolor* as the primary larval food source for *C. ladon*. *H. discolor* plants often grow in conjunction with Garry oak as well, though they have been found not to be strongly affected by competing broom plants (Parker *et al.*, 1997).

Patch Size and Connectivity

Defining habitat patches

Habitat patches in each network were defined using 1:10,000 orthorectified digital airphotos of the study networks as a base layer, and tracing them using the program ARCVEIW 3.2/8.1 (ESRI, 1996). Based on observations of butterfly behaviour of turning at patch edges and a lack of observations of butterflies in matrix conifer forest, any meadow separated by at least 10m of non-habitat (conifer forest) from another Garry oak meadow was considered to be an individual patch. The boundaries of these meadows were then ground-truthed with a Garmin GPS12 the following summer (average positional error +/- ~8m) and the boundaries redefined on the map created from the digital image. The area of each meadow was calculated using the built in calculate area script for the ArcView 8.1 program.

Metapopulation context/qualities

Patch-specific connectivity measures for each meadow were calculated as

$$S_i = \Sigma\, p_j \exp(-d_{ij} \cdot \alpha_f) A_j\,, \qquad \underline{\text{Eqn. 1}}$$

where S_i is a composite measure accounting for all possible immigration to the patch i from all other adjacent meadows j that are occupied (p_j=1 if the patch is occupied, p_j=0 if it is not). Dispersal ability of each species f is estimated by the parameter α_f, and weighted negatively for increasing distance ($-d_{ij}$) between pairs of patches, and weighted positively for increasing area of the contributing patch (A_j). Although this measure is more complex than the nearest neighbour distance, it has been found that composite measures such as this are more accurate in defining spatial connectivity and produce better results than simple nearest neighbour measures in both field studies and modelling exercises (Moilanen and Hanski, 2001; Moilanen and Nieminen, 2002).

The species-specific dispersal coefficient, α_f, was estimated indirectly based on the conservative assumption that patches were colonized from the nearest occupied neighbour. The α_f coefficient was calculated by classifying each previously empty patch i as colonized or not based on the observed turnover between 2002 and 2003 and then measuring distance d_{ij} between each patch i and the nearest occupied neighbour j. All these previously empty sites were then categorized/binned based on concentric circles of radius r = 100m distance from the previously empty patch i, and calculating the ratio of occupied to unoccupied patches for each 100m distance interval. The 100m distance class was used since it was the shortest distance at which the ratio of occupied to unoccupied patches did not become highly variable in a histogram. A nonlinear regression model was fit using the formula:

$$P = \exp\,(-d_{ij}\, \alpha_f) \qquad \underline{\text{Eqn. 2}}$$

where P, the proportion of occupied patches in each 100meter distance class is a function of d_{ij}, the distance to the nearest occupied patch, and α_f, the species dispersal ability coefficient (Hokit *et al.*, 1999). The species specific dispersal parameter, α_f for each species, was then used in Eqn.1 to define species specific connectivity functions for determination of the effect of connectivity on species occurrence.

Habitat Quality

As discussed in the Introduction, habitat quality can change the effective area available to a species in a habitat patch. A given meadow may be large, but if it is of poor quality it will not support as large a population as a smaller meadow of higher quality. In this study, habitat quality was defined by three variables 1) flowering plant abundance, 2) host plant density/abundance, 3) cover of Scotch broom.

Flower Abundance

For each meadow in the butterfly surveys, a subjective, categorical abundance estimate was made of all flowering plant species observed, based on the scale in Table 2-1. The sum of the median % cover levels of flower abundance for all flower species observed was calculated for each survey period for each meadow. These sums were then averaged, producing an average index of flower abundance in the meadow at the time of that survey. Common flower species observed are listed in Appendix B.

TABLE 2-1: Categorical abundance classes for vegetation cover data.

Categorical abundance class	% cover levels for Flower abundance, *C. scoparius*, and *H. discolor*	% cover levels for *S. spathulifolium*	Median % cover levels as assigned for regressions
0	0	0	0 – none
1	1% or less (trace)	1% or less (trace)	0.5 – trace
2	1-5%	1-2.5%	3 – sparse
3	6-33%	2.5-5%	20 – moderate
4	34-66%	5-10%	50 – abundant
5	67-100%	>10% (higher is rare)	80 – ubiquitous

Larval Host Plants

Vegetation was sampled in both 2002 and 2003. On the rainy days from spring (March) through July and August, 1m^2 quadrats were randomly located along transects run through each meadow. At each point, categorical estimates of cover of these plants were recorded (see Table 2-1). This protocol was used for assessing the density of the butterfly host plants *S. spathulifolia* (stonecrops), and *H. discolor* (oceanspray), and for *C. scoparius* (Scotch broom). Due to scale and dispersion differences between trees and shrubs or herbs, Garry oak density was estimated by plotless sampling using the point-quarter method at these same randomly located points (Pollard, 1971; Beasom and Haucke, 1975; Krebs, 1999). Laser rangefinders were used to measure distances to trees to the nearest meter. A total of 2415 of these plots were completed in the two meadow networks. Data from the first summer (2002) were found to be highly variable due to the clumped distribution of the Garry oak trees (Erickson, 1996; Fuchs, 2001; Hallstrom, pers. obs.). Based on a power analysis (using data variability from the 2002 data), I determined that I would need to collect more samples in some of the meadows so that I would have more precise data to be able to detect a difference of 50 Garry oak trees per hectare between meadows. Approximately half of the sites had data that allowed me to determine this difference after the 2002 sampling season, and so did not need to be resampled. Based on time available, remaining meadows which did not yet have high enough quality of data were sampled until either the 50 tree difference criteria was met, or until the SE of the estimate was within 20%, of the mean. The maximum number of plots required to reach this level of precision for a given meadow was 122. A similar analysis of data quality was done for the other larval host plants.

Butterfly Surveys

Butterfly species were surveyed on sunny days during March-August 2002 and 2003, along haphazardly located 'belt' transects of 20m width (~1000 transects in each year; Sparrow *et al.*, 1994; Spalding, 1997). Transects were run for timed intervals, with longer times in larger meadows, in order to put more effort into surveying larger areas (Table 2-2). Moving transect locations for each survey examined a wider range of available habitat in each meadow and thus minimized the possibility of missed observations of a species due to inadvertently not searching a small but suitable microhabitat region within a given meadow. Binoculars were occasionally used to help determine butterfly species presence/absence and sex without disturbing them. Each meadow was visited up to five times during the flight season of each butterfly species to reduce the possibility of attributing false absences.

Table 2-2: Search time allocated for meadows of each given area class.

Area Class by m^2 [HA]	Search time per visit (min.)
0-2500, [0.25]	5
2501-10000, [1]	10
10000-40000, [4]	20
40000+, [over 4]	30

Statistical Analysis

Presence or absence of butterfly species in a meadow (patch occupancy) was related to the explanatory variables of site area, site isolation, host plant density, average flower abundance, and cover of Scotch broom by using a combination of generalized additive models (GAM; Hastie, and Tibshirani, 1990) and generalized linear models (GLM - logistic regression; McCullagh, and Nelder, 1989). First, to account for potential non-linearities, a GAM cubic spline model was fit to the data, with all possible explanatory variables included. This GAM model was used as a basis against which to compare all subsequent parametric models (Insightful, 1999; Roland *et al.*, 2000).

Second, a GLM was run which included individual linear responses for those variables showing linear fit and individual nonlinear responses for those variables with significant non-linearity based on the GAM analysis. Categorical variables were fit with ordinal data treated in a quantitative manner (Agresti, 1996). This has the advantage that it is simpler, easier to interpret and easier to present compared to the strictly categorical style of analysis. Also, it is generally more powerful than the strictly categorical style analysis that requires the calculation of several parameters (one for each different class of the categorical explanatory variable), since only a single parameter is calculated for each variable (Agresti, 1996). Various types of non-linear responses were assessed for those variables showing non-linear effects, until a best fit was attained for that variable. This best fit was assessed based on both the Cp statistic (equivalent to AIC; Insightful, 1999) and ANOVA tables comparing the competing models. This approach accounts for both effect size of each explanatory variable and for model parsimony by penalizing models with more explanatory terms (Burnham and Anderson, 1998). This method also allows comparison of 'non-hierarchical' alternative models in order to identify a more parsimonious model.

Interaction terms were then added, using the combined linear and non-linear approaches as judged appropriate in the previous analysis. A manual backward-stepwise method was used, to reduce the number of variables in the model and again assessing the resultant Cp statistic. The final model was compared to a GAM and a GLM containing equivalent variables. Statistical analysis was performed using SPLUS 2000 Professional, Release 2 (Insightful, 1999; Crawley, 2002).

Comparison among models was done using AIC and Akaike weights because some of these model comparisons were non-hierarchical. Several plausible alternative models were compared by means of AIC (Appendix C), and coefficients for each explanatory variable were then assessed by the model averaging procedure (Burnham and Anderson, 1998; Johnson and Olmand, 2004). The relative importance of a given explanatory variable was assessed by means of its model-averaged coefficient and the model-averaged SE of this coefficient, and the percent of total model deviance that the term explained in the best-fit model. If the coefficient was significantly different from zero then it was concluded to have an effect on that species' patch occupancy.

RESULTS

Species Dispersal and Dispersion

Each species was found to have a different distribution in the Mt. Maxwell network

(Figure 2-2.a-c) and dispersal ability varied (Table 2-3), as measured implicitly by the fit of Eqn.2 to the observed distribution and colonization events data for each species. Higher values of alpha represent lower dispersal ability, so it was found that *C. ladon* could disperse farthest, while *E. propertius* had intermediate dispersal ability and *I. mossii mossii* dispersed the shortest distance. Dispersal ability estimates for these species were similar to the values obtained by other researchers on similar species (Bidwell, 1995; Fuchs 2001).

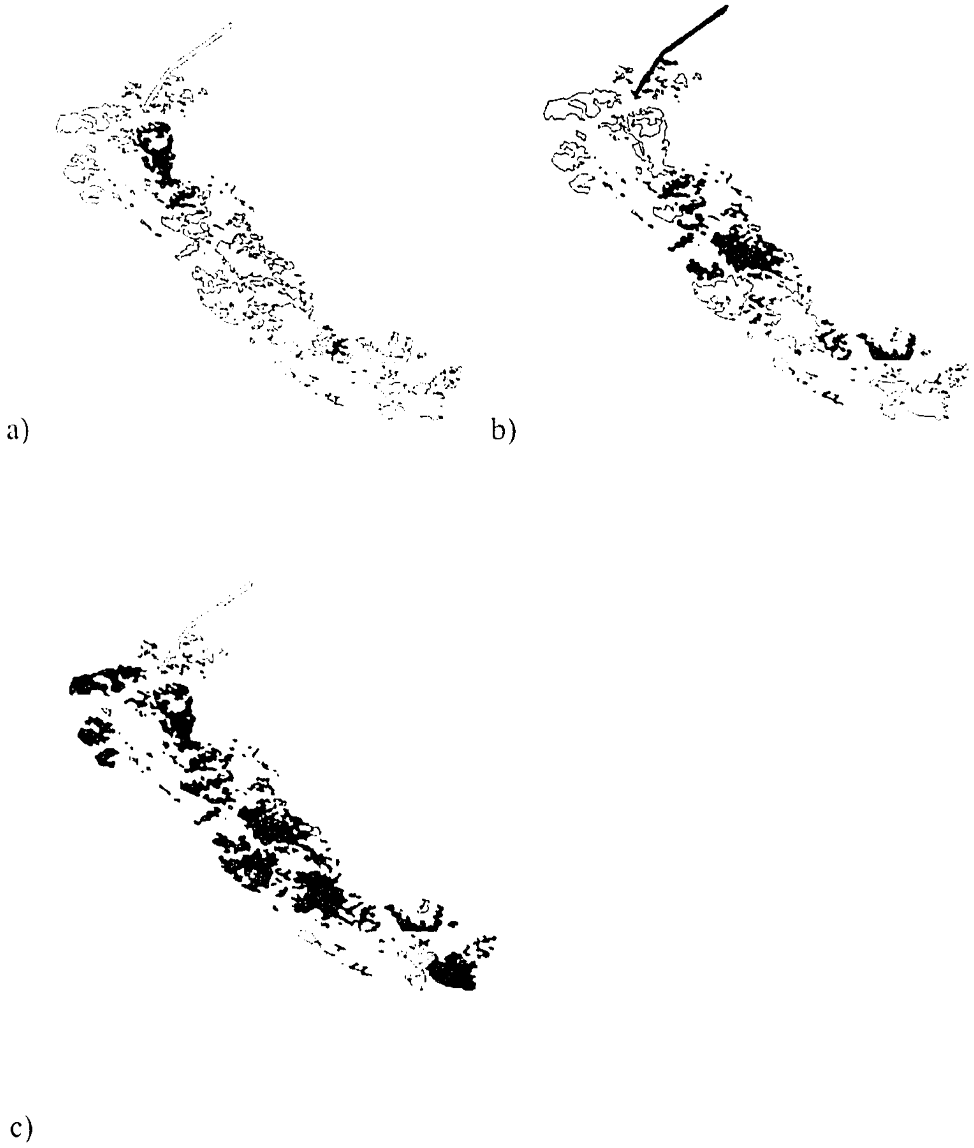


Figure 2-2. Distribution of the three study species in the Maxwell meadow network, in 2002, Black is occupied, white is not. a) *Incisalia mossii* ssp *mossii*, b) *Celastrina ladon*, c) *Erynnis propertius*.

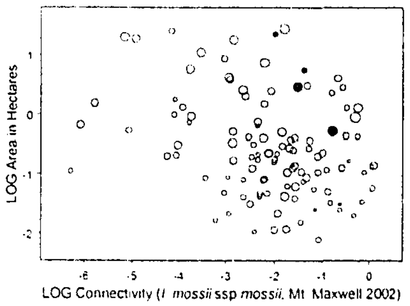
Table 2-3: Species alpha dispersal parameters (+/- SE) from nonlinear regression (Eqn.2). Higher values of alpha represent lower dispersal ability.

Species	2002-2003 turnover event	2002-2003 turnover event
	Maxwell	Maple
E. propertius	4.02 (1.19)	8.55 (8.13)
I. mossii mossii	16.9 (24.3)	Not enough data
C. ladon	3.72 (0.87)	5.31 (1.96)

Effect of Patch Area

Patch area was a significant predictor of patch occupancy by *Incisalia mossii* ssp. *mossii* for one year (2002) in the Mt. Maxwell network (1/2 models; Table 2-4.1; Figures 2-3.a and 2-3.b; no observations were made of this species at the Maple site). In the year for which area was a significant predictor of occupancy, it alone explained a relatively large proportion of the total model deviance (~25%; Table 2-5.1)

For *C. ladon*, area was a significant predictor of patch occupancy in one of two years in each of the two networks sites (2/4 models; Table and 2-4.2; Figure 2-3.c-f). At Maple Mtn. in 2002 the model averaged coefficients show a negative correlation of area with patch occupancy, while at Mt. Maxwell in 2003 there was a positive correlation of occupancy with area (Table 2-4.2)., The model with negative correlation however may not be a biologically significant result, as this model only explain 0.25% (Maple 2002) of the total model deviance (Table 2-5.2). Given the scatter of the plots of the Maple 2002 data for the effect of area (Figure 2-3.e) makes the biological relevance even more suspect. At the most area only explains 3% of the model deviance (Maxwell 2003), and relative to other variables area is not particularly important for explaining patch occupancy by *C. ladon*. The shift from positive to negative correlation is odd, but could be due to correlation of area with another term that was unmeasured in that year.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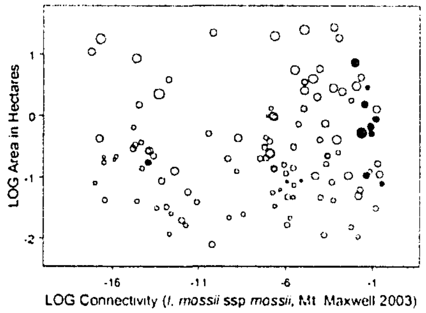
LOG Connectivity (*I. mossii* ssp *mossii*, Mt Maxwell 2002)

a)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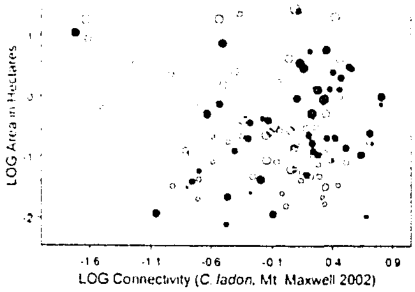
LOG Connectivity (*I. mossii* ssp *mossii*, Mt Maxwell 2003)

b)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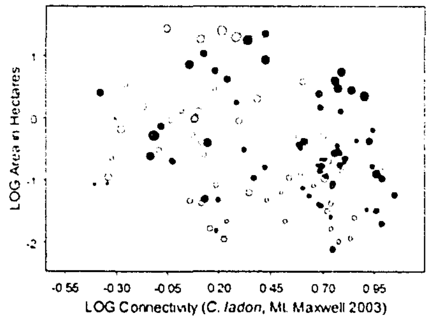
c)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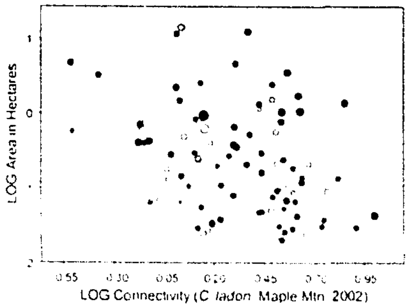
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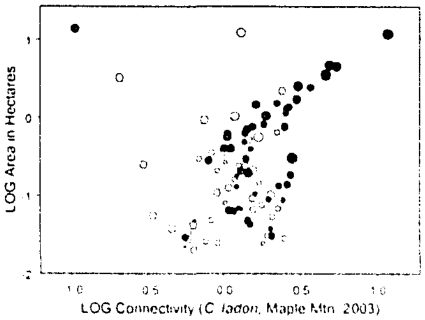
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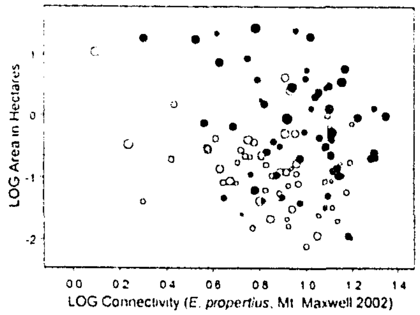
LOG Connectivity (*C. ladon*, Maple Mtn 2003)

f)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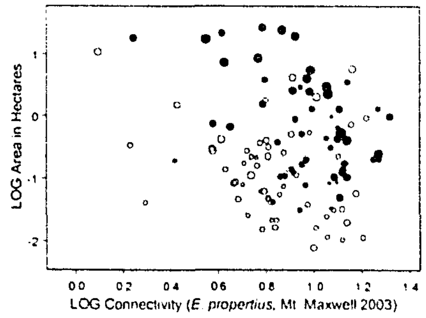
LOG Connectivity (*E. propertius*, Mt Maxwell 2002)

g)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LOG Connectivity (*E. propertius*, Mt Maxwell 2003)

h)

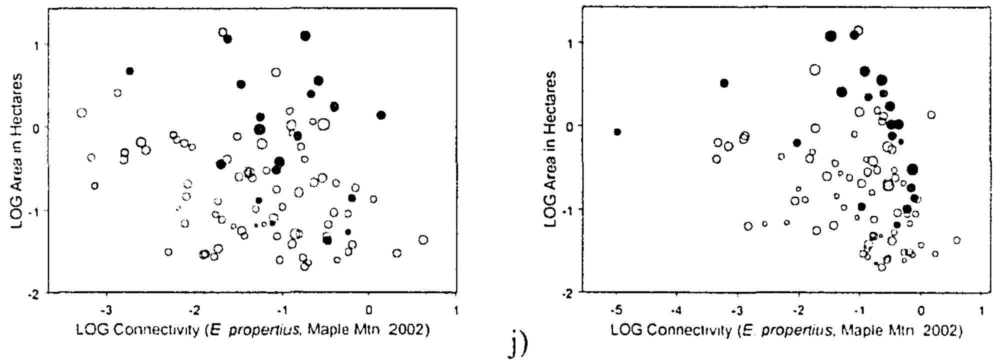

Figure 2-3: Patch occupancy as a function of area and isolation. Larger points represent sites with greater Flower abundance, and filled circles represent sites occupied by the respective butterfly species: a) *I. mossii mossii* in 2002 Mt. Maxwell, b) *I. mossii mossii* 2003 Mt. Maxwell, c) *C. ladon* 2002 Mt. Maxwell, d) *C. ladon* 2003 Mt. Maxwell, e) *C. ladon* 2002 Maple Mtn., f) *C. ladon* 2003 Maple Mtn., g) *E. propertius* 2002 Mt. Maxwell, h) *E. propertius* 2003 Mt. Maxwell, i) *E. propertius* 2002 Maple Mtn., j) *E. propertius* 2003 Maple Mtn.

Table 2-4.1: Model averaging results for coefficients of explanatory variables. Average taken across the top models for each site-year of data for the butterfly species *I. mossii mossii*. Only models comprising the top 90% of the ω_i were used in the model averaging calculations. Coefficients shown in bold type are significantly different from zero, as judged by use of their associated model-averaged SE values.

Model structure	β_{NULL} (SE)	β_{BROOM} (SE)	$\beta_{S.Spathulifolium}$ (SE)	$\beta_{CONNECT}$ (SE)	β_{AREA} (SE)	β_{FLOWER} (SE)	$\beta_{S.Spathulifolium\ BROOM}$ (SE)	$\beta_{BROOM\ FLOWER}$ (SE)
Year / site								
Maxwell 2002	**-7.01 (2.77)**	-0.34 (0.36)	0.0282 (0.2)	0.4734 (2.8)	**1.28 (0.583)**	**0.0261 (0.0152)**	-0.0176 (0.0338)	-
Maxwell 2003	**-3.148 (0.58)**	0.00185 (0.0048)	**0.0703 (0.0323)**	**14.28 (5.76)**	-0.0027 (0.00652)	0.00228 (0.0317)	-	-
Maple 2002	**Not enough data**	-	-	-	-	-	-	-
Maple 2003	**Not enough data**	-	-	-	-	-	-	-

NOTE: Model averaging calculations were done according to formulas: mean coefficient values = $\theta = \sum\omega_i\,\theta_i$; and average SE of the coefficient = $\sigma = \sum\omega_i\,[\sigma_i + (\theta_i - \theta)^2]$, where *i* represents the *i*th model of the set (Johnson and Olmand, 2004).

Table 2-5.1: Deviance explained by best-fit model, showing total model r^2 and percent of the total deviance explained attributable to each explanatory variable in the model, for each site-year of data for the butterfly species *I. mossii* ssp. *mossii*.

Year / site	Null Deviance [deviance explained] (best model R^2)	Broom Deviance (% of total)	*Sedum* Deviance (% of total)	Connectivity Deviance (% of total)	Area Deviance (% of total)	Flower Deviance (% of total)	*Sedum*:Broom Deviance (% of total)	Broom:Flower Deviance (% of total)
Maxwell 2002	34.73 [15.67] (.45)	0.46 (1.3%)	2.85 (8.2%)	-	8.78 (25.28%)	3,58 (10.3%)	-	-
Maxwell 2003	68.13 [15.22] (0.22)	-	5.27 (7.7%)	9.95 (14.6%)	-	-	-	-
Maple 2002	No Data	-	-	-	-	-	-	-
Maple 2003	No Data	-	-	-	-	-	-	-

In the case of *E. propertius*, patch area was found to be a good predictor of patch occupancy in only a single year at one of the two sites (1/4 models; Table 2-4.3; Figure 2-3.g-j). Although this variable explained a relatively large proportion of the total model deviance in the best-fit model of the set of AIC test models (5.6-15.5%; Table 2-5.3), the estimate of effect size fluctuated widely in the top models (Table C.3 of Appendix C). Thus, after model averaging was taken into account, patch area predicted patch occupancy by *E. propertius* in only one of the two sites in one year (Table 2-4.3).

Effect of Patch Connectivity

Connectivity of meadows was a significant predictor of patch occupancy by *Incisalia mossii* ssp. *mossii* for one year (2003) in the Mt. Maxwell network (1/2 models; Table 2-4.1; Figures 2-3.a and 2-3.b; there were no observations of this species at the Maple site). In 2003, connectivity explained ~15% of the total model deviance (Table 2-5.1). The strong effect of connectivity in 2003 is associated with the observed increase in patch occupancy from 4 sites to 11 between 2002 and 2003.

In the case of *C. ladon*, connectivity was positively correlated with patch occupancy in both years at the Mt. Maxwell site, and in one of two years at the Maple Mtn. site (3/4 models; Table 2-4.2; Figure 2-3.c-f). The connectivity measure explained 6.7-20% of the total model deviance, and was the best or one of the top two predictor variables in all three models in which it was a significant factor (Table 2-5.2).

Occupancy by the species *E. propertius* was positively related to meadow connectivity in both years at the Maxwell site but in neither at the Maple site (2/4 models; Table 2-4.3; Figure 2-3.g-j). Although this variable was only significant at the $\alpha=0.10$ level in the individual models of the test set for Maxwell 2003 (Table C.3 of Appendix C), these results were consistent among the candidate model set and resulted in a significant effect after AIC analysis and model averaging. Connectivity explained a relatively large proportion of the total model deviance in one of the models where it was a significant factor (8.8% Maxwell 2002), but not the second (2%, Maxwell 2003; Table 2-5.3).

Table 2-4.2: Model averaging results for coefficients of explanatory variables. Average taken across the top models for each site-year of data for the butterfly species *C. ladon*. Only models comprising the top 90% of the ω_i were used in the model averaging calculations. Coefficients values shown in bold type are significantly different from zero, as judged by use of their associated model-averaged SE values.

Model structure	β_{NULL} (SE)	β_{BROOM} (SE)	$\beta_{HDISCOLOR}$ (SE)	$\beta_{CONNECT}$ (SE)	β_{AREA} (SE)	β_{FLOWER} (SE)	β_{HB} (SE)	β_{HA} (SE)	β_{BF} (SE)	β_{HF} (SE)
Year / site										
Maxwell 2002	**-1.94 (0.55)**	-0.0586 (0.0433)	0.0108 (0.0176)	**0.507 (0.172)**	0.00034 (0.0049)	**0.01 (0.00748)**	**0.012 (0.005)**	-	0.001 (0.0008)	0.00025 (0.0002)
Maxwell 2003	**-1.38 (0.572)**	**0.0425 (0.0252)**	0.015 (0.0485)	**0.388 (0.11)**	**0.34 (0.15)**	0.0027 (0.009)	-0.0024 (0.002)	0.0018 (0.007)	**-0.00107 (0.00053)**	**0.0093 (0.0046)**
Maple 2002	-0.5147 (-0.557)	-0.00238 (0.003515)	-0.02277 (0.01658)	0.08996 (0.09971)	**-1.283 (0.354)**	**0.0834 (0.02247)**	-0.00001 (0.00001)	**0.0726 (0.0238)**	0.000017 (0.000056)	-0.000006 (0.000011)
Maple 2003	**-6.026 (1.506)**	**-0.3535 (0.1213)**	**0.3046 (0.1593)**	**1.668 (0.497)**	0.05 (0.04)	**0.975 (0.358)**	0.0005 (0.0015)	-0.0027 (0.0039)	0.005667 (0.0042)	0.00564 (0.00677)

NOTE: Model averaging calculations were done according to formulas: mean coefficient values = $\theta = \sum\omega_i\,\theta_i$;
and average SE of the coefficient = $\sigma = \sum\omega_i\,[\sigma_i + (\theta_i - \theta)^2]$, where *i* represents the *i*th model of the set (Johnson and Olmand, 2004).

Table 2-5.2: Deviance explained by best-fit model, showing total model r^2 and percent of the total deviance explained attributable to each explanatory variable in the model, for each site-year of data for the butterfly species *C. ladon*.

Year / site	Null Deviance [deviance explained] (best model R^2)	Broom Deviance (% total)	*H.discolor* Deviance (% total)	Connectivity Deviance (% total)	Area Deviance (% total)	Flower Deviance (% total)	*H.discolor*:Flower Deviance (% total)	Broom:Flower Deviance (% total)	*H.discolor*:Broom Deviance (% total)	*H.discolor*:Area Deviance (% total)
Maxwell 2002	156.3 [29.76] (.19)	0.05 (0.03%)	3.51 (2.2%)	10.3 (6.7%)	-	4.92 (3.1%)	10.98 (7%)	-	10.98 (7%)	-
Maxwell 2003	159.6 [35] (.22)	0.82 (0.5%)	-	14.31 (9%)	4.49 (3%)	1.81 (1.1%)	8.5 (5.3%)	5.07 (3.2%)	-	-
Maple 2002	111.6 [36.1] (.32)	-	1.37 (1.2%)	-	0.28 (0.25%)	15.05 (13.5%)	-	-	-	19.4 (17.4%)
Maple 2003	124.4 [42.55] (.34)	3.16 (2.5%)	4.89 (3.9%)	24.73 (20%)	-	9.77 (8%)	-	-	-	-

Table 2-4.3: Model averaging results for coefficients of explanatory variables. Average taken across the top models for each site-year of data for the butterfly species *E. propertius*. Only models comprising the top 90% of the ω_i were used in the model averaging calculations. Coefficients values shown in bold type are significantly different from zero, as judged by use of their associated model-averaged SE values.

Model structure	β_{NULL} (SE)	β_{BROOM} (SE)	$\beta_{Q\ Garryanna}$ (SE)	$\beta_{CONNECT}$ (SE)	β_{AREA} (SE)	β_{FLOWER} (SE)	$\beta_{B\ F}$ (SE)	$\beta_{B\ O}$ (SE)	$\beta_{A\ O}$ (SE)	$\beta_{F\ O}$ (SE)
Year/Site										
Maxwell 2002	**-2.72 (0.75)**	0.009595 (0.00844)	**-0.00319 (0.002525)**	**0.184 (0.0615)**	0.069 (0.133)	**0.0203 (0.00796)**	-	-	**0.0058 (0.0031)**	-
Maxwell 2003	**-4.478 (0.7952)**	-0.003255 (0.005715)	**0.00583 (0.00418)**	**0.19878 (0.0609)**	-0.7421 (0.4804)	**0.02758 (0.00668)**	-0.00016 (1.76e-8)	0.000146 (1.51e-8)	**0.0763 (0.0182)**	**-0.00015 (0.00006)**
Maple 2002	**-5.71 (1.382)**	-0.00101 (0.03906)	**0.5987 (0.2201)**	-0.2327 (0.317)	-1.051 (2.023)	**0.787 (0.364)**	-	-	0.2426 (0.266)	-
Maple 2003	**-2.16 (0.91)**	**0.19 (0.11)**	-0.0004 (0.00054)	0.013 (0.02)	**0.465 (0.22)**	0.159 (0.22)	-	-	-	-

<u>*NOTE:*</u> Model averaging calculations were done according to formulas: mean coefficient values = $\theta = \sum \omega_i\ \theta_i$; and average SE of the coefficient = $\sigma = \sum \omega_i\ [\sigma_i + (\theta_i - \theta)^2]$, where *i* represents the *i*th model of the set (Johnson and Olmand, 2004).

Table 2-5.3: Deviance explained by best-fit model, showing total model r^2 and percent of the total deviance explained attributable to each explanatory variable in the model, for each site-year of data for the butterfly species *E. propertius*.

Year / site	Null Deviance [deviance explained] (best model R^2)	Broom Deviance (% of total)	*Q.Garryanna* (Oak) Deviance (% of total)	Connectivity Deviance (% of total)	Area Deviance (% of total)	Flower Deviance (% of total)	*Q.Garryanna*:Area Deviance (% of total)	*Q.Garryanna*:flower Deviance (% of total)
Maxwell 2002	159.42 [48.52] (.30)	-	7.04 (4.4%)	14.03 (8.8%)	12.51 (7.8%)	6.98 (4.4%)	7.96 (5%)	-
Maxwell 2003	159.57 [71.25] (.45)	-	47.89 (30%)	2.93 (2%)	8.99 (5.6%)	11.44 (7.2%)	18.62 (11.7%)	2.47 (1.5%)
Maple 2002	93.71 [29.8] (.32)	-	16 (17%)	-	-	13.8 (14.7%)	-	-
Maple 2003	99.35 [51.83] (.52)	16.28 (16.4%)	-	9.5 (9.6%)	15.25 (15.5%)	10.8 (11%)	-	-

Effect of Habitat Quality

In all cases models including habitat quality factors fit significantly better than did models with only area and connectivity. Model selection and model averaging (Johnson and Omland, 2004) resulted in none of the final models being based on only the area and/or connectivity measures as is usually assumed to be adequate in metapopulation models (Tables 2-4.1, 2-4.2, 2-4.3, and tables C.1, C.2 and C.3 of Appendix C). Specific quality measures replaced the vague measurement provided by area with a more precise definition of habitat, and obviously played a more important role than did area because the area term was often not included in either the best-fit or the final 'averaged' models, whereas the habitat quality factors were (Table 2-4.1, 2-4.2, 2-4.3) and the deviance explained by these alternative variables was often higher (Table 2-5.1, 2-5.2, 2-5.3). For a given species, habitat quality effects were not consistent between years however, indicating an inconsistent relationship of the patch occupancy of each butterfly species to the specific habitat quality factors between years.

Hostplants

Incisalia mossii ssp. *mossii* is monophagous on *S. spathulifolium*, but this plant was a significant predictor of patch occupancy in only one year (2003) in the Mt. Maxwell network (1/2 models; Table 2-5.1; Figure 2-4.a; there were no observations of this species at the Maple site). There was also a general trend towards hostplant density being an important determinant of patch occupancy in 2002 (see Maxwell 2002 model set in Table C.1 of Appendix C), but this was not borne out as a significant result after model averaging (Table 2-4.1). In the year when the effect was significant, 2003, Hostplant density explained 7.7% of the total model deviance (Table 2-5.1).

In the case of *C. ladon*, increasing hostplant density was not a good predictor of patch occupancy, and was positively correlated with patch occupancy for only Maple Mtn. in 2003 (1/4 models; Table 2-4.2; Figure 2-4.b). As well, the explanatory power of this variable as measured by the deviance explained was relatively low at 3.9% of the total model deviance (Table 2-5.2).

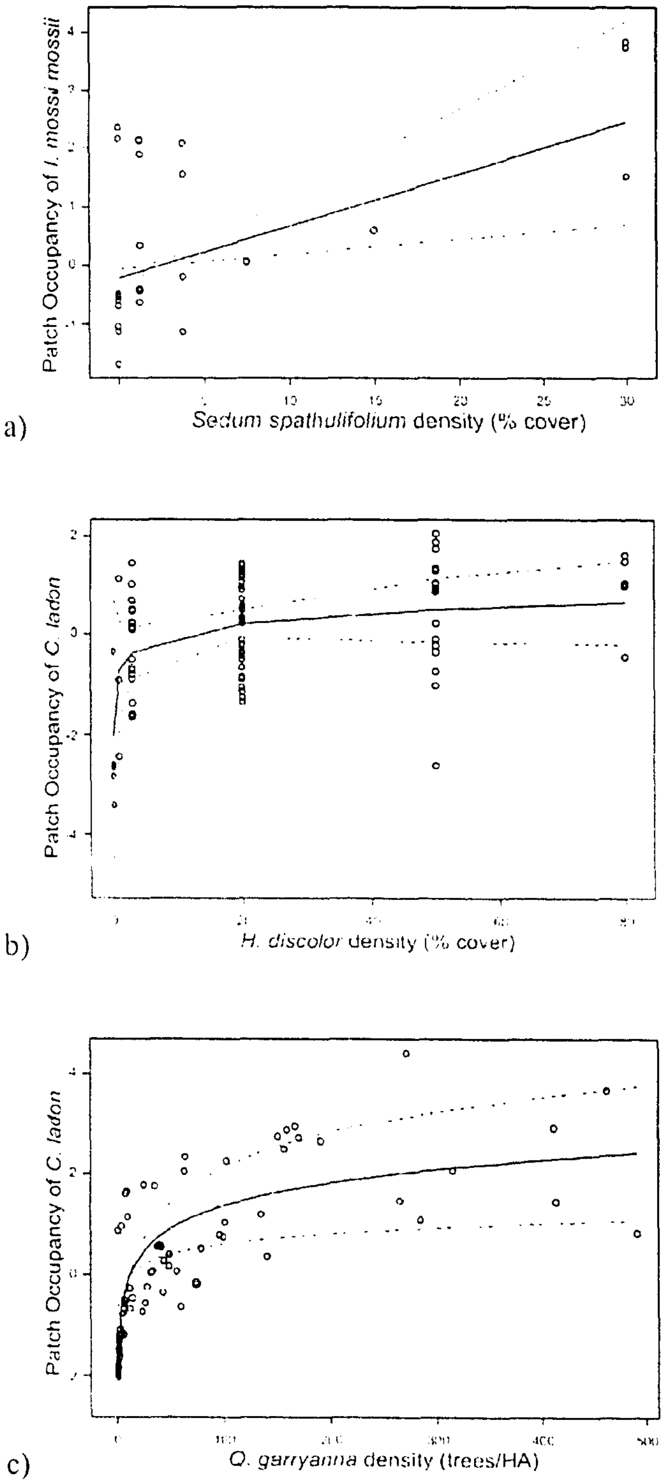

Fig 2-4: Effect of hostplant on butterfly patch occupancy: a) *I. mossii mossii* on *S. spathulifolium* (data from Mt Maxwell in 2003), b) *H. discolor* on *C. ladon* (data from Maple Mtn. in 2003), c) *Q. garryanna* on *E. propertius* (Maple Mtn. 2003). Lines are the best fir GLM models, dotted lines are pointwise confidence intervals.

E. propertius also is monophagous, feeding exclusively on, *Q. garryanna*. Occupancy of this butterfly was significantly related to hostplant density in half the cases (2/4 models; Table 2-4.3; Figure 2-4.c). There was a positive relationship between occupancy and hostplant density in both Maxwell in 2003 and Maple in 2002. *Q. garryanna* density explained a relatively large proportion of the total deviance in the two models where it was significant (17% and 30%, Maple 2002 and Maxwell 2003 respectively; Table 2-5.3), meaning that for this species hostplant density is one of the most important predictors of occupancy.

Flower availability

Flower availability was a strong predictive variable for all species. In the case of *Incisalia mossii* ssp. *mossii*, flowers predicted occupancy in Maxwell 2002 (1/2 models; Table 2-4.1; Figure 2-5.a). Although this variable was only significant at the α=0.10 level in the individual models of the AIC test set (Table C.1 of Appendix C), these results were consistent and resulted in a significant effect after AIC analysis and model averaging (Table 2-4.1). In 2002 flower abundance explained 10.3% of the total model deviance (Table 2-5.1).

Occupancy of *C. ladon* increased with increasing flower abundance in all but the Mt. Maxwell network during 2003 (3/4 models; Table 2-4.2; Figure 2-5.b). The explanatory power of this variable as measured by the deviance explained was variable, ranging from a relatively low 3.1% (Maxwell 2002), to substantially higher values of 13.5% and 8% ((Maple 2002 and 2003 respectively; Table 2-5.2).

E. propertius occupancy also increased with increasing flower abundance (3/4 models; Table 2-4.3; Figure 2-5.c). Flower abundance explained a relatively large proportion of the total model deviance in two of the models where it was a significant factor (14.7% and 7.2%, Maple 2002 and Maxwell 2003 respectively), but not the third (4.4%, Maxwell 2002; Table 2-5.3).

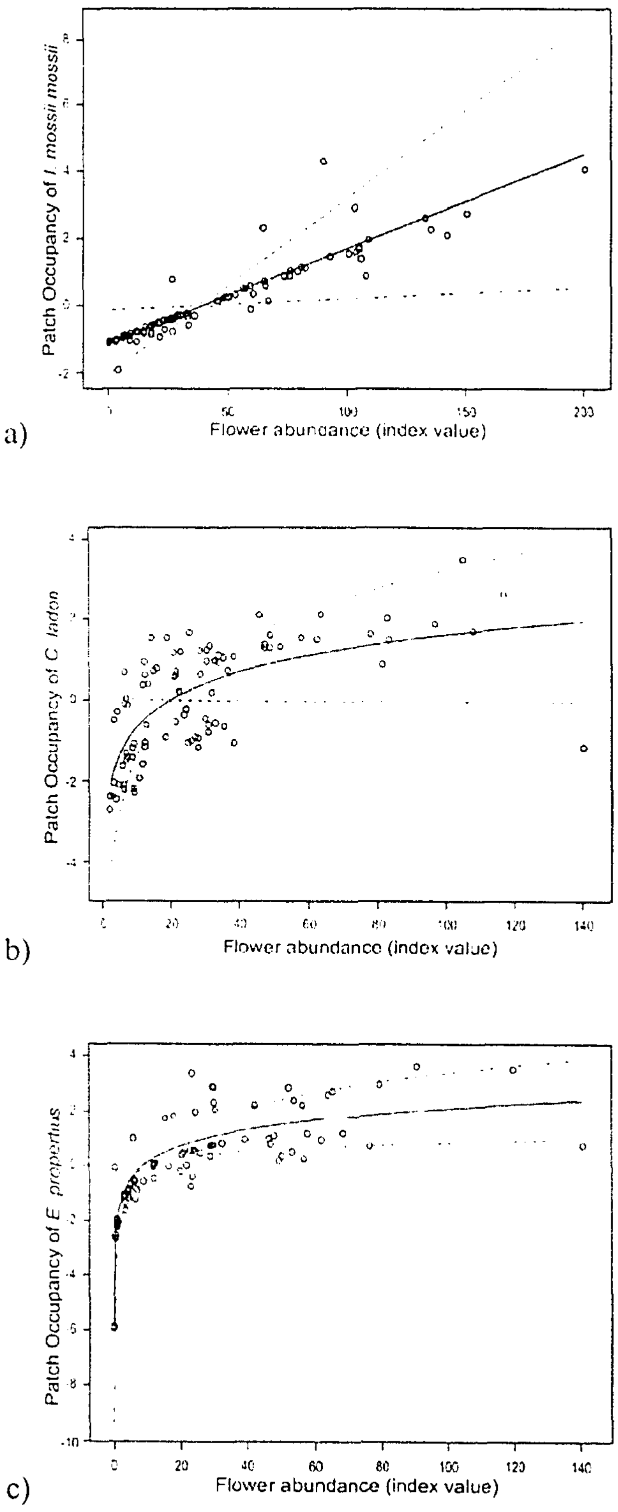

Fig 2-5: Effect of flower availability on a) *I. mossii mossii* (data from Mt Maxwell in 2002), b) *C. ladon*, (data from Maple Mtn. in 2003), and c) *E. propertius* patch occupancy (Maple Mtn. 2002). Line as for Fi.2-4.

Scotch Broom

The cover of the weedy broom shrub was not a significant predictor of patch occupancy in the case of *Incisalia mossii* ssp. *mossii*. Models in the candidate set always showed a general negative trend of patch occupancy with broom, and were sometimes found to be marginally significant (Table C.1 of Appendix C). These results were variable, however, and thus did not produce a significant relationship in the model averaging results (Table 2-4.1). The best fit model of the set of AIC candidate models for Maxwell 2002 showed broom explaining only 1.3% of the total model deviance (Table 2-5.1).

Broom was significantly related to occupancy of *C. ladon*, however the results were somewhat inconsistent. There was a general trend toward lower patch occupancy with increasing broom in the full set of candidate models for all years and sites (Appendix C, Table C.2), but of the two significant model averaged results, one was negative and one was positive (2/4 models; Table 2-4.2; Figure 2-6.a-b). Although this variable was only significant at the α=0.10 level in the individual candidate models of the AIC test set for Maple in 2003 (Table C.2 of Appendix C), results of the candidate models were consistent among the set and resulted in a significant effect after AIC analysis and model averaging (Table 2-4.1). The explanatory power of this variable as measured by the deviance explained was variable, with the positive association seen at the Maxwell network during 2003 explaining a low percent of the deviance (0.5%), and the negative association case in Maple during 2003 explaining 2.5% of the total deviance (Table 2-5.2). Neither of these can be considered strong relationships of patch occupancy with Broom, and may not be biologically significant. In particular, the observed positive association found at Mt. Maxwell in 2003 is driven by only three data points, making the conclusion of a statistically significant positive association of broom with occupancy highly suspect (Figure 2-6.b) and not likely to be truly biologically significant.

E. propertius occupancy also showed a significant increase with increasing broom in one instance (1/4 models; Table 2-4.3; Figure 2-6.c), where it explained a relatively large proportion of the deviance (16.4%, Maple 2003; Table 2-5.3). There was a negative trend

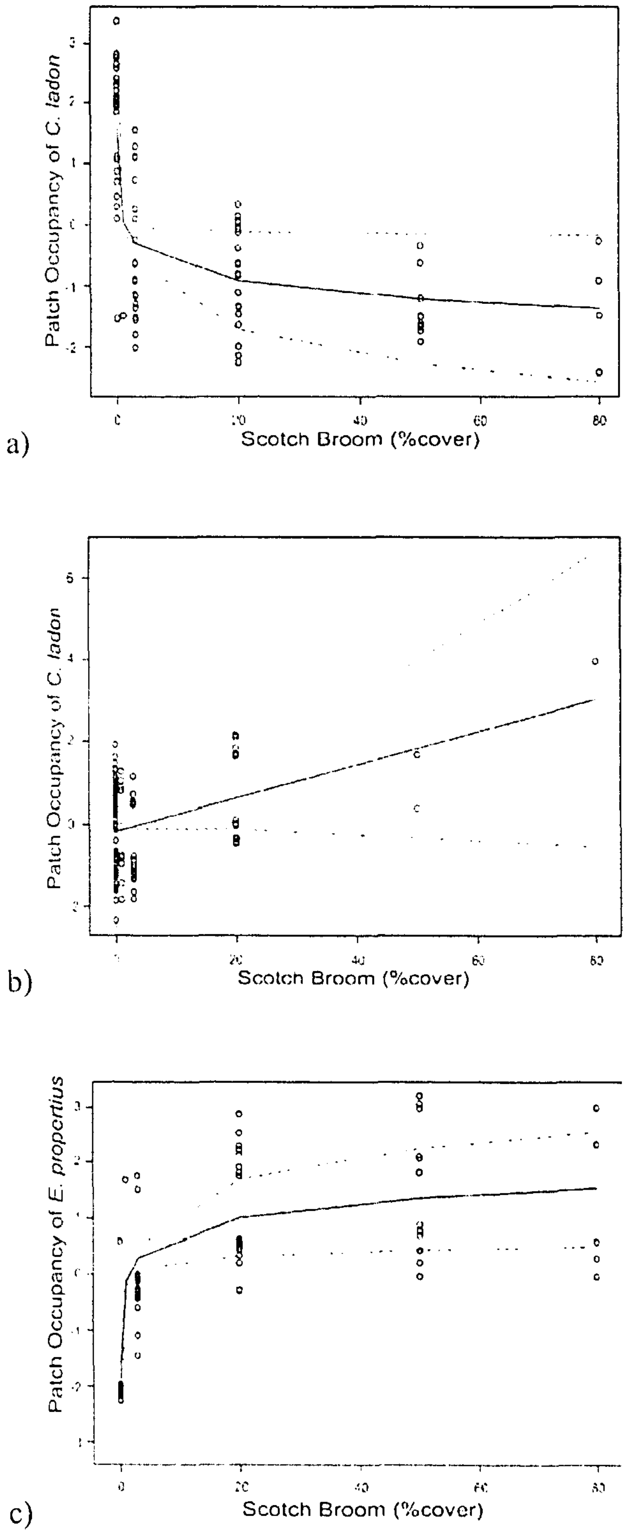

Figure 2-6: Effect of increasing cover of Scotch Broom (*Cytisus scoparius*) on patch occupancy of: a) *C. ladon* (Maxwell 2002), b) *C. ladon* (Maxwell 2003), c) *E. propertius* (Maple 2003). There were no significant effects of Scotch broom observed on *I. mossii* ssp. *Mossii*. Lines as in Fig 2-4.

in occupancy with increasing broom in 2/4 models (Maxwell 2003 and Maple 2002), but these cases were not significant after model averaging (Appendix C, Table C.1).

Interaction Effects

There were no significant interaction effects in the case of the species *Incisalia mossii* ssp. *mossii*, although these had been tested for. For *C. ladon*, there were four cases of significant interactions observed (Table 2-4.2). First, there was one case of an interaction between larval host plant (*H.discolor*) and broom, which explained 7% of the model deviance (Maxwell 2002, Table 2-5.2, Figure 2-7.a-d). This occurred when the normally strongly positive association of *C. ladon* with *H. discolor* changed to be only slightly positive and at only the highest densities broom (Figure 2-7.a). Second, there was once instance of an interaction between *H.discolor* x area on occupancy, this occurring when the normally positive association of *C. ladon* with area changed to be negative in those patches with little cover of *H.discolor* (Figure 2-7.b). This explained 17.4% of the model deviance. Third, the interaction between broom x flowers on occupancy showed a significant interaction for the Maxwell network in 2003, explaining 3.2% of the model deviance (Table 2-5.2). This was for an increasingly positive association of *C. ladon* with flowers as cover of broom increased (Figure 2-7.c). Finally, the fourth significant interaction was also found for the Maxwell network in 2003, and was an increasingly positive association of *C. ladon* with flowers as cover of *H. discolor* increased (Figure 2-7.d). This interaction explained 5.3% of the total model deviance (Table 2-5.2)

Interactions were also observed for occupancy by *E. propertius*. A significant oak (*Q. garryanna*) by area interaction was found in 2 of 4 year/network combinations for *E. propertius* (Table 2-4.3), explaining 4.4% and 7.2% of the model deviance (Table2-5.3). In these interactions there was a positive effect of increasing meadow area on patch occupancy, but only at the intermediate oak densities (Figure 2-8.a and b). At the highest level of oak density the sites were always occupied regardless of area and at the lowest oak density the sites were consistently unoccupied regardless of meadow area. As well, the interaction between oak density and flowers (Table 2-4.3), explained 11.7% of the

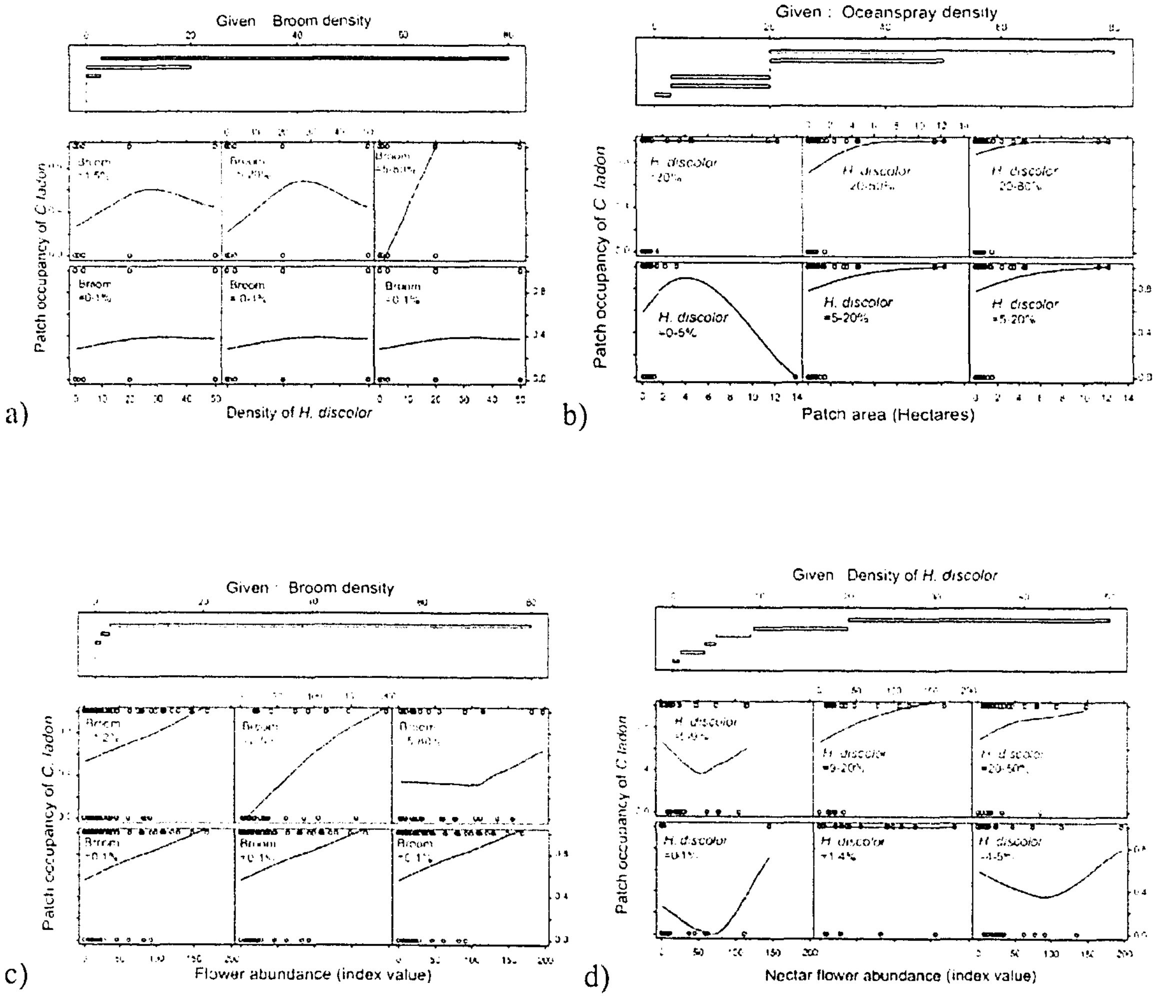

Figure 2-7: Significant interaction effects for occupancy by the butterfly *C. ladon*: a) *H. discolor* x broom interaction (Mt. Maxwell 2002), b) *H. discolor* x area interaction (Maple Mtn. 2002), c) flower x broom interaction (Mt. Maxwell 2003), and d) *H. discolor* x flower interaction (Mt. Maxwell 2003).

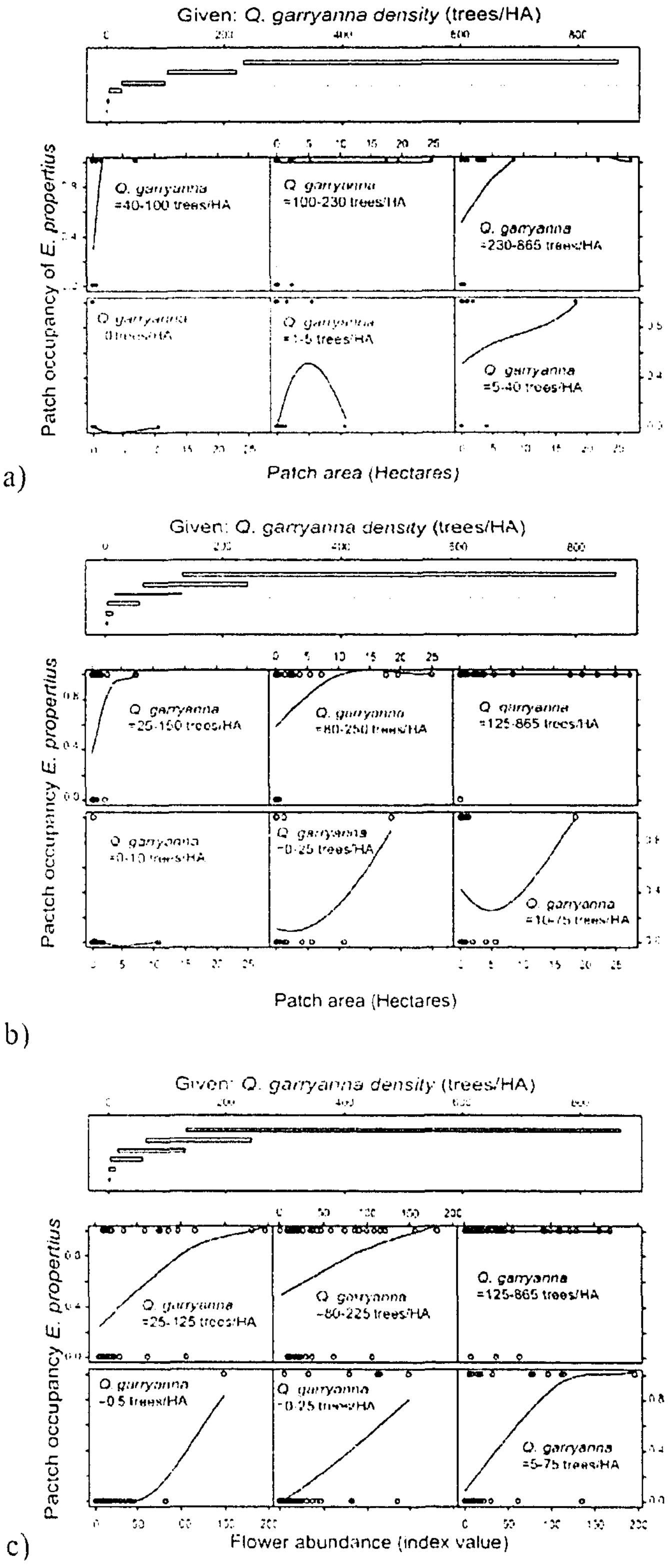

Figure 2-8: Significant interaction effects for occupancy by the butterfly *E. propertius*: a) *Q. garryanna* x area interaction (Mt. Maxwell 2002), b) *Q. garryanna* x area interaction (Mt. Maxwell 2003), c) *Q. garryanna* x flower interaction (Mt. Maxwell 2003).

model deviance (Table 2-5.3). Although this variable was only significant at the $\alpha=0.10$ level in the individual models of the AIC test set, these results were consistent and resulted in a significant effect after AIC analysis and model averaging (Table 2-5.3). This interaction was for higher occupancy at higher flower abundance, but was a pattern less pronounced at the highest levels of oak density, where the sites are always occupied (Figure 2-8.c).

Overall

The relative importance of the terms in the models may be examined by looking at the deviance explained by each term (Tables 2-5.1, 2-5.2, and 2-5.3). Models with only area or area and connectivity in them were found to have consistently lower deviance explained than did models including broom, flower availability, and/or hostplant density. Although the predictive power of more detailed models that included habitat quality variables was not always a large improvement (Tables C.1 C.2 and C.3 of Appendix C), they consistently explained a much larger proportion of the original null deviance than did models that included only area and connectivity terms. Although these models include more variables, they were still better in terms of parsimony. Patch area alone was always less important than was the best individual or total combined effect of habitat quality variables in almost all models (Tables 2-5.1, 2-5.2, 2-5.3 – deviance explained).

Patch connectivity was consistently one of the most important variables predicting patch occupancy. In some cases connectivity was a strong predictor of patch occupancy, similar in terms of deviance explained to the combined effect of the habitat quality variables. The significant correlation between butterfly occupancy and connectivity implies that limited dispersal between patches is important in determining patch occupancy, and in turn metapopulation effects may be occurring at the scale of this study. Hostplants and flower availability were also important predictors, with flowers explaining a bit more of the deviance in some models (Tables 2-5.1, 2-5.2, 2-5.3). As an example of the interactions in the model, the relationship of flower availability, area and connectivity is shown in Figures 2-3.a-j. These plots demonstrate that generally butterflies occupy patches that are both large and well connected, and usually also that have more flowers available.

DISCUSSION

The main purpose of this study was to examine the occurrence of three butterfly species in relation to the habitat qualities of hostplant density, flower availability, density of Scotch broom, and to patch area and connectivity. Secondary goals were to determine if broom was an important predictor of habitat use by these butterfly species, and to determine whether patch connectivity was related to observed patch occupancy and colonization events, which would justify trying a metapopulation-type analysis.

The area term is one commonly used in metapopulation studies (Hanski, 1994, Hokit *et al.*, 1999), but I found that area was not often in the final best-fit models, demonstrating that there may be one or more relatively easily measured habitat quality factors that better predict occupancy of a patch. For example, as indicated by the relative deviance explained in the models (Tables 2-6.1, 2-6.2, 2-6.3), broom, hostplants, and flowers overall, had greater explanatory power than did habitat area in all models but one. The effect size of each of these terms differed between years, and this variability means that a cautious approach is warranted to substituting these terms as an alternative to area in a metapopulation model.

For two butterfly species, *E. propertius* and *Incisalia mossii* ssp. *mossii*, hostplant was found to be a significant factor, supporting the initial hypothesis that each butterfly species would occur more frequently in sites with greater abundance of its hostplant. This is hardly surprising given that adult butterflies will be found where they metamorphosed as pupae, and where they lay their eggs as adults near or on hostplants. The importance of hostplant density has been demonstrated for other butterflies such as *Euphydryas editha* (Ehrlich, 2003), *Melitiea cinxia* (Hanski *et al.*, 1995), *Parnassius apollo* (Fred, 2004), *Speyeria nokomis apacheana* (Fleishmann *et al.*, 2002), and *Parnassius smintheus* (Roland *et al.*, 2000; Matter and Roland, 2002). In the case of *C. ladon* however, the effect of hostplant was significant in only one of four models, and the weak explanatory power seems to contradict the initial hypothesis. Likely this is due to the scope of measurement where data were collected regarding density of the hostplant (*H. discolor*) for this species. *H. discolor* mainly grows in the open meadows, where measurements were made, but it can also grow in tiny forest gaps which were not included in this study. As the species may therefore also be persisting on hostplants at meadow edges and in the conifer forest, this could be contributing to the poor results of the data regarding *H. discolor* abundance in the meadows for predicting the distribution of *C. ladon*. In this case it may be better to use a continuous model structure to represent hostplant availability across the landscape for this species, rather than assuming discrete patches when collecting the data, as was done here.

Flower abundance was also significant in almost all models, for all three butterfly species, supporting the initial hypothesis that butterflies would be found in sites with greater availability of floral nectar food resources. Which specific floral species are required by each butterfly species remains unknown, but additional behavioural observations data could identify these species. Nectar food availability has been observed to be an important predictor of distribution and abundance for other butterfly species (Bidwell, 1995; Schultz and Dlugosch, 1999; Matter and Roland, 2002; Fred, 2004). In fact, flower abundance was found to be the most consistent and reliable of the variables in this analysis for predicting butterfly occurrence. The high predictive power of floral abundance implies that conservation measures for all of these butterfly species should focus on flower availability as well as suitable breeding sites with abundant hostplants.

Contrary to the initial hypothesis there was little or no effect of the weed broom on the three butterfly species. Rather than degrading the butterfly habitat, two of the three cases with a significant effect of broom were positive. The low amount of deviance explained by this variable in these models (both for *C. ladon*) was likely not strong enough to be biologically significant, and was suspect in one case due to overly strong influence of a few data points. Only the positive relationship between broom and *E. propertius* at Maple Mtn in 2003 was strong enough and consistent enough to be of biological significance. This result is interesting in that broom was not a significant predictor of occupancy in the Maple network in 2002, but it was in 2003. Given that broom abundance did not change between years, this shift in relationship of occupancy to broom may be explained by the mechanism of colonization of new patches and extinction of others redistributing the butterfly population. In the Maple network in 2003, *E. propertius* exhibited a balanced ratio of 12 colonization events and 9 extinction events ($\chi^2_{0.05,1}$=0.42, p=0.86). Obviously some of these colonizations occurred in meadows with substantial broom cover. Unfortunately, without further years of turnover data or running simulation models, it is impossible to evaluate whether sites with broom differ from sites lacking broom in terms of how this habitat attribute may affect population persistence and whether these new populations are in suitable locations or in 'sink' habitat (Pulliam, 1988).

Area was found to be a significant predictor of patch occupancy in less than half the cases in this study (4/10 models). Area may be a simple measure to obtain, but not all habitat is equal in quality and the results of this study imply that there may be better measures to use as a surrogate for population size. AIC-based model averaging for all three species (Johnson and Omland, 2004) resulted in 'final models' that often did not include the area term (Tables 2-4.1, 2-4.2, 2-4.3), although connectivity and habitat quality attributes of hostplants and flower abundance remained important terms in predicting occupancy in most cases.

I. mossii ssp. *mossii*

Sedum spathulifolium, the obligate hostplant of *I. mossii mossii,* is highly restricted to rock outcrops where there is usually little broom. *I. mossii mossii* is therefore restricted to breeding where flowers of the hostplant and other nectar plant species grow abundantly. Table 2-5.1 demonstrates that the primary determinants of persistence of a population into the first survey season of 2002 were *Sedum spathulifolium* cover, meadow area, and flower abundance. This makes sense intuitively, as larger meadows with more food resources are most likely to provide a stable resource base for a population. Large meadows generally contain more internal heterogeneity as well, and would thus be more likely to provide for the broad needs of a species in the event of variable conditions, enhancing its persistence (Kindvall, 1996). *Incisalia mossii* ssp. *mossii* was initially found to persist in larger, well-connected meadows in the first survey year, 2002 (Figures 2-3a and b). There are few populations of this rare species in these networks, and all the well-connected and larger meadows in which it was found in 2002 were either sites with high hostplant availability or were near ones that were.

A greater number of colonizations (7) than extinctions (1) occurred between 2002 and 2003, more than doubling the number of occupied sites from 4 to 11. Most of these colonizations occurred in sites that were close to source populations, and thus highly connected, regardless of patch size. This may result from limited dispersal of this species, which was observed in the small dispersal kernel (large observed α parameter, Table2-3), small size of the species (Guppy and Shepard, 2001), and behavioural observations that it flies rarely and weakly, and often returns quickly and directly to the same place from which they originated (Hallstrom, personal observation).

The combination of persistence in large sites and colonization of well-connected sites fits well with metapopulation theory (Hanski, 1994), and implies that metapopulation dynamics may be occurring for this species. Most patches of the hostplant are small, and so extinctions may be relatively common for these small populations. The persistence of the populations in the larger sites, combined with lack of satellite populations in more distant locations (Figure 2-2.a) suggests that large meadows are of key importance for conservation of this species. As well, some of the well-connected surrounding sites would be worth monitoring or preserving as they may play an important role as ephemeral population reservoirs or as stepping stones in the colonization of other sites.

With regard to floral availability, *I. mossii mossii* often nectars at its' own hostplant (Hallstrom, pers. obs.) and so in years of low flower abundance this species would be better positioned to forage for food at the hostplant patch, without need for the high energetic demands of long flights to reach these resources. The lack of flower resources in a poor year however, may also decrease the connectivity of the landscape by making individuals less able to find food to fuel travel between patches, resulting in fewer colonizations of new patches/locations. Given that in a good year more food energy resources are available, greater numbers of individuals of the species should survive, and so more individuals will be available to disperse. At Mt. Maxwell, 2003 was a 'good year' with suitable weather in the spring flight season, the warmest in 30 years, and a greater flower availability in the meadows than there had been in 2002 (flower abundance index value of 32 in 2002 versus 40.7 in 2003, paired t-test, $T_{0.05,114}=2.13$, $p=0.0354$). This warm year followed an extremely poor flight season for this species in the previous spring, the coldest in the past 20 years (Ian Stewart Complex weather station data). In good conditions the greater flower abundance available may also have resulted in individuals having additional energy to travel farther, and surviving in patches that are normally marginal, thus colonizing more new patches than in a poor year. The large number of colonization events, the high average flower availability, and the highly significant connectivity variable in the 2003 analysis (vs 2002) imply that this may be what was occurring. Future years may not be as good however, and there may be a subsequent transient state of unstable shifting occupancy occurring due to the unbalanced colonization and extinction rates observed.

C. ladon

Patch occupancy by *C. ladon* was also only weakly correlated to the abundance of its' hostplant *H. discolor*, and with patch area. *C. ladon* distribution was most strongly influenced by connectivity and by flower abundance, with the effect of connectivity the stronger of the two as judged by deviance explained. These two factors far outweigh the influence (again measured by deviance explained) of the other variables (Table 2-5.2). The significant effect of connectivity and flower abundance, but not area or hostplant, implies that this species uses meadows as a source of nectar foods and that it is limited in its ability to reach these resources by poor dispersal/colonization ability. Occupancy in these landscapes may then depend more on connectivity of the flower resources than connectivity of the hostplant.

The lack of a correlation between *C. ladon* occurrence and hostplant abundance was likely due to the fact that its larval hostplant *H. discolor* can grow as an understory shrub within thin conifer forest and in tiny forest gaps. Therefore there may have been intervening forest gaps containing *H. discolor* that were not included in the analysis, and which increase persistence. Given that distribution of *H. discolor* is not as restricted as are the hostplants of the other two butterfly species, the use of a habitat model based more on continuous resource distributions rather than discrete clumps may be more appropriate (Caswell, 2001).

Broom had a varied effect on *C. ladon* patch occupancy, being negative in one network but time positive in the other, even in the same year (Figure 2-6.a+b). This inconsistency may result from a lack of data in the case of the positive result (Figure 2.6.b), which is overly influenced by a single data point at the broom = 80 level and two points at the broom = 50 level. Considering that in this case broom is also accounting for only 0.5% of the deviance of the model, it seems to be a result of these individual points.

There was a significant broom x flower interaction on occupancy (Figure 2-7.c), with no effect of flowers at higher levels of broom. This supports the suggestion that broom interferes with the ability of the butterflies to find nectar by creating structural complexity where there previously was none before. There was also an interaction between broom x *H. discolor* (Table 2-5.2; Figure 2-7.a) on *C. ladon* occupancy, only showing a positive trend in occupancy with increased *H. discolor* at low levels of broom, but a more strongly positive effect at high levels of broom. This refutes the hypothesis that broom would interfere with the ability of *C.ladon* to find hostplants, since broom had a positive effect. The implication of this is that an area with more shrubs of any type (not only host plant shrubs) may simply be more attractive to *C.ladon* due to various factors associated with their habitat preferences.

Two other interactions also were noted for this species. There was a positive effect of flowers at low levels of *H. discolor*, which was less pronounced at high levels of *H. discolor*, as the combined effect of both flowers and hostplant resulted in high occupancy (Figure 2-7.d). This result parallels that for *E. propertius*, where an interaction of a similar nature between flowers and hostplant on occupancy was observed. The final interaction effect was that of a positive effect of patch area being least pronounced at high levels of *H. discolor*; most sites were occupied when both were high (Figure 2-7.b) This also parallels the result of a similar host x area interaction observed for *E.*

propertius. In general then, the increase of two positive attributes resulted in a synergistic effect and compounded probability of occupancy and a higher quality site.

E. propertius

In contrast to *I. mossii mossii*, *E. propertius* feeds exclusively on the oak tree *Q. garryanna*, the distribution of which is not as restricted as *S. spathulifolium*. *E. propertius* was strongly affected by connectivity in the Maxwell network, implying that there was a significant effect of dispersing individuals from adjacent patches on patch occupancy in this network; a pattern not observed in the Maple network (Table 2-5.3). This contrast may be due to the distances being generally greater between patches at Maple Mtn, thereby reducing colonization from adjacent patches and emphasizing patch quality. In this case, local persistence, rather than colonization of small semi-ephemeral habitat patches for one or a few years, would become the primary determinant of patch occupancy. The finding that both of the models for Mt Maxwell had a significant effect of connectivity while there was none for the Maple network suggests that there may be a threshold effect of landscape connectivity (With, 1997; With *et al.*, 2002) on distribution of this species, for which Mt Maxwell lies above and Maple lies below, a topic for future investigation.

The hostplant, *Q. garryanna* (Garry oak), grows in a clumped distribution, due to local rock and soil qualities, water availability, and clonal growth patterns (Roemer, 1972; Erickson, 1996; Ussery, 1997; Fuchs, 2001). Like *S. spathulifolium*, the density of oaks was highly variable among and within meadows (from 0 to over 1000 trees per hectare), and had a strong influence on patch occupancy of *E. propertius*. The significant area x oak interaction on patch occupancy (Table 2-5.1, Fig 4.b) is also understandable, as patch area had an effect only at the mid-level oak densities; occupancy was driven by the strong effect of oak density when at the extremes of high and low.

Higher occupancy in the largest meadows, (Fig. 2-8.a and b), also implies that the increased habitat heterogeneity (such as increased flower diversity and variation in microclimates) associated with the larger meadows, likely begins to play a substantial role in making a site of consistently high enough quality through time to ensure high patch occupancy. Kindvall (1996) found a similar result of increased habitat heterogeneity associated with greater population size and persistence for a metapopulation of crickets.

E. propertius is a very active species but it does not nectar at its larval host plant, and so must move to obtain nectar resources. The high energetic requirements of this behaviour may be reflected in the strong main effect of flower abundance on occupancy. The overriding importance of the hostplant to this species was also evident in the significant interaction between flowers and oak on occupancy (Figure 2-8.c). This pattern of interaction was inconsistent, with only one instance of a significant effect at the Mt Maxwell site. This variability implies that another factor is likely interacting with these terms as well, perhaps weather influences on plant growth, or variation in connectivity between years.

Counter to the initial hypothesis, broom did not reduce occupancy by *E. propertius.* Strangely, there was in fact a positive effect of broom on occupancy. Broom cover generally changes plant composition by reducing diversity and abundance of other species (Hays *et al.*, 2000; Parker, 1997; Roemer, pers. comm.), and thus the effect of broom on butterfly habitat should be negative for this species. Perhaps the absence of a negative effect could be due to temporary transient shifts in occupancy (unrelated to habitat) induced by metapopulation dynamics.

Conclusions about Connectivity

Overall, connectivity was a significant predictor in most cases (6/10 models). The hypothesis that metapopulation theory may be applicable to these butterfly species is thus supported. The two networks were not compared with respect to their connectivity, however, the fact that 5/6 of the models for Mt Maxwell had a significant connectivity effect while only 1/4 did for the Maple network, suggests that there may be thresholds for the effect of landscape connectivity on species distributions occurring in this system. The greater inter-patch distances and overall lower connectivity of the Maple Mt. site relative to the Mt. Maxwell site supports this argument, and seems worthwhile to explore further in a future analysis.

Conclusions regarding use of Area and Quality measures

For these three butterfly species, the lack of a strong effect of area and patch occupancy seems to be most closely related to the uneven distribution of required resources; in this case the between meadow unevenness in the distribution of hostplants and flower abundance. This unevenness may occur both within and between patches. This study, however, examines the effect of only the among patch differences in habitat factors. A mixed model approach to incorporate both within and among patch effects might yield better results than this analysis. To expand the extent of applicability of the current results, ground surveys and digital remote sensing data or aerial photos could be used to match known densities of plant cover with the digital images. The use of these images to define the spatial extent and the density of plant species such as Garry oak and the spread of the broom infestation (Odom *et al.*, 2003), combined with the results of the GLM models, could be tested and used in a predictive sense to define other important habitat patches without the need for detailed 'on the ground' surveys (Nicholls, 1989; Cowley *et al.*, 2000). With a relatively small amount of extra surveying it could extend the power of this analysis to provide a regional model of habitat for these butterflies (similar to an RSF – Boyce and McDonald, 1999) that could save substantial money, effort, and time.

Conclusions about the effect of Broom

One of the main goals of this study was to examine the impact of an invasive weed on one component of the fauna of a region that has been invaded. Invasive weeds can, and do, change the composition of the native flora in many habitats worldwide (Colton and Alpert, 1998; IUCN, 2000). They are an increasing problem for farming, range management, and conservation of natural areas. The impact of weed invasion on animal populations has rarely been evaluated quantitatively (but see Schieman *et al.*, 2003) and is likely to occur through indirect effects on plants that animals such as butterflies require to survive (such as larval hostplants or nectar flowers), and may have a direct effect by changing habitat structure.

Scotch broom was found to not have a significant main effect in most models of occupancy for three butterfly species. For *I. mossi mossii*, there were no significant effects. The one case of a statistically significant negative association involves a low deviance explained (0.5% of deviance, *C. ladon*, Maple 2003), and thus may not be biologically significant. In fact, the only case where the significant association explained a substantial portion of the model deviance was for *E. propertius* (16.4% of deviance, Maple 2003), where patch occupancy showed a positive association with Broom cover. Why would there be a positive association of occurrence with growth of a weed that causes loss of adult nectar food plants? One possibility is that deterministic turnover of sites through metapopulation dynamics, unrelated to habitat attributes, may shift *E. propertius* distribution, and the resultant colonization of patches, so new populations may establish in patches with some percent cover of broom. This is supported by the observation that the sites occupied by *E. propertius* were all well connected in 2003, and it could be that this shift in occupancy from 2002 to higher connectivity sites in 2003 (Figures 2-3i and j) may have resulted in the species occupying some sites with broom cover. This is particularly likely in the Maple network, where this positive association of occupancy with broom was observed, since many more sites at this location have broom in them. The true cause of this positive effect of broom cover however, is unknown at this time, and again a mixed model approach and more years of data are the likely the best solution.

Contrary to the initial hypothesis, broom does not have a negative impact on the butterflies at the scale of measurement of this study. Hays *et al.*, (2000), however, found that at the local scale, increasing broom cover did reduce use of that sub-area of a meadow by butterflies. They found, the presence of this weed may be causing direct physical/structural changes to the environment by reducing plant diversity and abundance, negatively influencing local site use/occupancy by the butterflies (if over 20% broom cover of larger plants >1m tall). In the current study, the scale of measure was the entire meadow, and at this scale there did not prove to be an effect of broom on the butterflies, even when up to 80% of a meadow was covered by broom. This is likely due to the fact that there are still interstices of usable habitat, even if broom density is relatively high, which the butterflies continue to occupy. Judging from the findings of Hays *et al.*, (2000) of negative effects of broom on butterflies at local sub-areas of meadows, and Parker *et al.*, (1997) regarding the negative effect of broom on plant populations, it seems likely that at some point a critical threshold will be crossed when the effect of habitat loss to local broom degradation will begin to take measurable effect at the landscape scale. Simulation studies of general habitat loss (Hanski and Ovaskainen, 2000) support this conclusion, but the physical evidence found during this study shows no effect, and so the level of meadow degradation by broom observed in these two systems appears to be below that threshold, resulting in little effect at the between meadow scale. One way to tease apart these two effects would be to run a more involved, redesigned experiment, using a mixed model approach that can account for both within and between meadow differences in broom cover on butterfly occupancy. Without such a multi-scale experimental test, the only way to convincingly demonstrate between meadow level effects would, unfortunately and ironically, be to allow spread of broom to cause substantial and irreversible loss of our natural areas to physically demonstrate this process.

Caskey and Henigman (2004) found that during a 10 year interval between sampling periods in Garry oak meadows, up to 10% of the meadow areas had been lost to disturbances such as housing developments and roads, and ingrowth of conifer trees due to fire suppression. These additional factors may also be reducing the effective area of the meadows and thus causing a decline in butterfly metapopulations across this region.

General conclusions about use of habitat quality measures versus area

Resources are better estimates for defining habitat quality for a species (Dennis *et al.*, 2003) rather than relying on vague measures of habitat quality such as patch area that subsume many habitat attributes. I found that the best models included habitat quality terms, implying that area is a poor measure of habitat quality and perhaps inappropriate for use as a surrogate for population size in metapopulation models (*i.e.* Hanski, 1994), resources probably being a better surrogate. Hokit *et al.*, (1999) and Crone *et al.*, (1998) also included habitat quality in their studies, but did not explicitly test whether inclusion improved their models. Moilanen and Hanski (1998) tried a similar approach incorporating simple habitat measures into their analysis of metapopulation dynamics of the Glanville fritillary (*Melitea cinxia*) and found that such data did not improve the fit of their metapopulation model substantially. They suggested that this occurred because the simple delineation of the habitat patches to calculate area included many of the most important habitat variables implicitly. This may be so, but will only be true if the quality of the patches is relatively homogeneous among patches. Analysis in the current study followed a similar approach of defining discrete habitat and yet still found significant improvements when habitat quality was included. The finding by Moilanen and Hanski (1998) of little improvement with additional habitat variables may have been an artifact of the low resolution of habitat quality measures used (satellite data and general forest cover maps).

The lack of an effect of habitat quality in determining patch occupancy may not occur in cases of species that exist in more heterogeneous habitats, or if measures of habitat variability are more appropriately scaled to a finer resolution, as was done from more detailed surveys in this study. For example, Walker *et al.*, (2003) collected detailed on-the-ground measurements of habitat quality, and found a weak relationship between patch occupancy of mountain vizcachas (ecologically analogous to pika) and patch area, but a stronger one with habitat quality measured as rock crevice depth within the patches, where the vizcachas may hide from predators. They also noted that metapopulation effects were likely to be taking place since intervening matrix characteristics (distance, and matrix quality of rivers/no rivers) were significant predictors of occupancy in their model.

Metapopulation structure is likely to occur if there is a significant influence of matrix habitat on inter-patch movements and thus on colonization rates and 'rescue effects' (Brown and Kodrick-Brown, 1977). Thomas *et al.*, (2001) demonstrated that, for three species of British butterflies, connectivity was important in addition to habitat quality, implying that metapopulation effects were occurring in their study as well. They found no relationships between habitat area and patch occupancy, and as such, they determined that patch quality should be used instead. On the other hand, Krauss *et al.*, (2004) found that connectedness of the patch was not an important factor in determining patch occupancy by the butterfly *Cupido minimus*. They proposed that this was because the butterfly is a particularly good disperser. In the absence of an isolation effect, they determined that management activity should focus on the maintenance of good quality habitat, rather than the purchase or protection of a specially-designed network of patches to protect the species.

The consensus among these studies is that the use of habitat quality is consistently a better measure of occupancy than is area and should be used instead (but see Steffan-Dewenter and Tscharntke, 2000, and Krauss, 2003a, 2003b, and 2004 for strong area effect). Metapopulation-level effects are also thought to be important in determining patch occupancy, since inclusion of connectivity terms describing the intervening matrix between the habitat patches in the model was often significantly correlated with patch occupancy in most studies. Inclusion of these terms can only be realistically related to patch occupancy if this matrix habitat is in some way restricting the dispersal ability of the species and slowing colonization of patches that are more difficult to reach, either through simple distance isolation (Hanski, 1994), or differential qualities of 'viscosity' of the intervening habitat (Roland *et al.*, 2000; Rickets, 2001).

Though there was a great improvement in the models with habitat quality, a note of caution should be considered. Although most habitat variables were consistently important in the models, there were differences in the importance of individual habitat quality factors between years. These factors still could be considered to be of primary importance, but are obscured by interactions with other events/conditions, such as weather. These could alter availability of resources in a given year or season (Ovaskainen, 2002), as was demonstrated to occur with the flower availability in this study. During the two years of surveying for the current study, 2002 was the coldest spring/summer in the past 30 years, and 2003 was the hottest and driest on record for the region. Such variations in weather have been shown to have a strong influence on butterflies, insects and other in the past (Pollard, 1988; Swanson, 1998; Wellington *et al.*, 1998; Roy *et al.*, 2001).

With only one year of data, parameter estimates for the impact of habitat quality may prove unreliable if assumed to remain constant in the long term (Hellmann *et al.*, 2003). Two or more years of data reduce such bias, by accounting for variability and providing a better estimate of the model parameters for habitat quality measures. Use of two or more years of data does not, however, preclude transient effects (Hastings, 2001) induced in one year by one-time events (such as weather anomalies) that could have a substantial long-term lagged effect on the population and metapopulation trajectories of the species in question. Although powerful overriding effects like these may be important and may have high predictive power in a given year, they may be difficult to measure and assess in typical short term ecological studies and so their importance cannot be assessed with short term datasets. If required (and properly quantified), these types of influences could be included in a model as a periodic event that may be spatially correlated (for example spatial correlation functions are possible with the SPOMSIM/IFM program by A. Moilanen).

Finding the average effect for a particular habitat quality factor may still provide a description better than one such as area, but may not account for these transient effects due to nonlinearites. Of course this problem also applies to the use of the regular area term, rather than 'effective area' based on habitat quality. Habitat factors that are important every year, or almost every year, are factors that should always be included in the models as basic and primarily important variables. In this study hostplant density and flower availability were consistently found in the final model, regardless of the particular network or year.

The r^2 for most of the statistical models in this study were relatively low (range from 0.223-0.578) compared to those for similar studies (*e.g.* Hokit, 1999). This is likely due to the large number of sites included in the analysis introducing variability, and to the observed extreme weather events that may have compounded this variability due to spatial variation of interactions of weather and attributes of individual site conditions. In addition to weather events, this study may have been affected by other population pressures such as competing herbivores and predation/parasitism/disease mortality (Clinchy *et al.*, 2002), which were not measured and almost undoubtedly account for some of the unexplained model deviance.

In conclusion, the results of this study imply that management decisions would be better made based on habitat quality and connectivity, rather than on patch area and connectivity. Broom was not a good predictor of butterfly occupancy at the patch scale, although it does negatively affect both native plant diversity and abundance (Parker *et al.*, 1997). Since flower abundance is the most important predictor of occupancy by the butterflies, there are likely to be indirect impacts of broom on the butterflies through lost flower availability when broom is at high levels of cover. Hays *et al.*, (2000), demonstrated this when they found that broom had a negative impact on both the flowers and butterfly habitat use at the sub-site within meadow scale. Hostplants were in some cases good predictors of occupancy, but the scale and extent of measurement of these resources needs to be addressed and may not fit the discrete patch model. There was a consistent and convincing significant associations of increasing flower abundance and increasing connectivity with an increase in probability of butterfly occurrence, and this effect was noted in both meadow networks, and for all three butterfly species. These effects are strong enough that they should be considered to be of primary importance in any management actions, and could be used to rank locations where treatments would likely be most effective in improving butterfly habitat (Chapter 3).

Broom removal and native plant revegetation are management tools currently used in the region to preserve and restore Garry oak meadows. Any management intervention in natural systems is a perturbation experiment with uncertain outcome, no matter how well planned (Walters and Holling, 1990). It would be best to take advantage of the opportunity presented, and treat it as a controlled experiment in order to better evaluate the relative role of native plants and that of broom in defining habitat quality for the butterflies, and to also examine in greater detail the effect of weed removal on other plant species. Broom can have a negative effect on the butterflies at a local scale (Hays *et al.*, 2000), and it is likely that this occurs through an indirect effect of broom on native flowers and hostplants that in turn affects the butterflies. Therefore, management actions could be adapted to include experimental revegetation treatments, nested within broom removal trials. The findings of these new studies could be incorporated as they become available, into an adaptive management plan (Holling, 1978, Walters, 1986, Walters and Holling, 1990).

Of the other quality factors, both hostplant and flower abundance were important in the habitat models. Both these factors were often the most important determinants of the occurrence of the respective butterfly species and so it is recommended that habitat management plans aimed at butterfly habitat should be designed primarily to focus on preserving and enhancing these two habitat attributes. Given that these effects were consistently strong, and often outweighed the effect of habitat area in the final models, this implies that perhaps the area term which is typically used in metapopulation models should be replaced by a different term which represents the real required habitat features the species is keying in on. This possibility was assessed for a simple metapopulation model (Hanski, 1994) and resulted in a better fit of the model to the data (Chapter 3). Caution must be taken due to the potential for finding relationships that are not consistently strong between years and then using these when such use is neither warranted nor wise. I recommend that a minimum of two years of data be used to define the species/area/habitat relationships when attempting this type of modeling for management application. In the case of rare or endangered species this should preferably be increased to include as many more years of data as possible.

LITERATURE CITED

Agresti, A. 1996. *An Introduction to Categorical Data Analysis*. John Wiley and Sons, Toronto.

van Apeldoorn, R.C., W.T., Oostenbrink, A. van Winden, and F.F. van Der Zee. 1992. Effects of habitat fragmentation on the bank vole, *Clethrionomys glareolus*, in an agricultural landscape. Oikos 65(2):265-274.

Andrewartha H.G., and L.C. Birch. 1954. *The distribution and abundance of animals. University of Chicago Press*, Chicago.

BC CDC. 2004. Tracking lists for vertebrate animals, vascular plants, invertebrates, and plant communities. July 2004. Available online at: http://srmwww.gov.bc.ca/atrisk/

Beasom S., and H. Haucke. 1975. A comparison of four distance sampling techniques in South Texas live oak mottes. Journal of Range Management 28:142-144.

Bidwell A.D. 1995. Karner Blue butterfly (*Lycaeides melissa samuelis*) dispersal and habitat disturbance at Fort McCoy military reservation, Wisconsin. MS thesis, University of Wisconsin, Stevens Point.

Boyce, M.S. and L.L. McDonald. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution 14: 268-272.

Briers, R.A., and P.H. Warren. 2000. Population turnover and habitat dynamics in Notonecta (Hemiptera: Notonectidae) metapopulations. Oecologia 123:216-222.

Brown, J, and A. Kodrick-Brown. 1977. Turnover rates in insular biogeography: effects of immigration on extinction. Ecology 58: 445-449.

Brommer, J., and M. Fred. 1999. Movement of the Appollo butterfly *Parnassius apollo* related to hostplant and nectar plant patches. Ecological Entomology 24:125-131.

Burnham, K.P., and D.R. Anderson. 1998. *Model selection and inference: a practical information-theoretic approach*. Springer, NY.

Caskey M., and M. Henigman. 2004. Audit of selected polygons of the sensitive ecosystems inventory of east Vancouver island and the gulf islands, 1999-2001: summary report. British Columbia Ministry of Water, Land and Air Protection.

Caswell, H. 2001. *Matrix population models: construction analysis and interpretation*. Sinauer Assosc. Sunderland, MA.

Clinchy, M., D.T. Haydon, and A.T. Smith. 2002. Pattern does not equal process: what does patch occupancy really tell us about metapopulation dynamics? American Naturalist 159(4): 351-362.

Colton, T.F., and P. Alpert. 1998. Lack of public awareness of biological invasions by plants. Natural Areas Journal 18(3):262-266.

Coweley, M.J.R., R.J. Wilson, J.L. Leon-Cortes, D. Gutierrez, C.R. Bulman, and C.D. Thomas. 2000. Habitat-based statistical models for predicting the spatial distribution of butterflies and day-flying moths in a fragmented landscape. Journal of Applied Ecology 37(Suppl. 1): 60-72.

Crawley M. 2002. *Statistical Computing: an introduction to data analysis using Splus*. John Wiley and Sons Ltd. New York.

Crone, E., D. Doak, and J. Pokki. 2001. Ecological influences on the dynamics of a field vole metapopulation. Ecology 82: 831–843.

Dennis R.L.H., T.G. Shreeve, and H. Van Dyck. 2003. Towards a functional resource-based concept for habitat: a butterfly biology viewpoint. Oikos 102 (2): 417-426.

Eastman, D. 2001. Personal comment. University of Victoria Professor in restoration biology.

Ehrlich, P.R. 1961. Intrinsic barriers to dispersal in the checkerspot butterfly *Euphydryas editha*. Science 134:108-109.

Ehrlich, P. 2003. Butterflies, tests systems, and biodiversity. IN *Butterflies: ecology and evolution taking flight* (Boggs CL, WB Watt, and PR Ehrlich eds.) University of Chicago Press, Chicago.

Ellis, B. J. Mills, J. Childs, M. Muzzini, K. Mckee Jr., D. Enria, and G. Glass. 1997 Structure and floristics of habitats associated with five rodent species in an agroecosystem in central Argentina. Journal of Zoology-London 243:437-460.

Ennis, T. 2002. Personal comment. Nature Conservancy of Canada representative for Vancouver Island.

Erickson, W. 1996. Classification and interpretation of Garry oak (Quercus garyanna) plant communities and ecosystems in southwestern British Columbia. MSc thesis, University of Victoria.

ESRI. 1996. *ARCview 3.2 User's Guide*. ESRI, Redlands, CA, USA.

Fleishmann, E., C. Ray, P. Sjogren-Gulve, C. Boggs, and D. Murphy. Assessing the roles of patch quality, area, and isolation in predicting metapopulation dynamics. Conservation Biology 16(3): 706-716.

Fred, M., and J. Brommer. 2003. Influence of habitat quality and patch size on occupancy and persistence in two populations of the Apollo butterfly (*Parnasius apollo*). Journal of Insect Conservation 7:85-98.

Fuchs, M. 2001. *Towards a recovery strategy for Garry Oak and associated ecosystems in Canada*. Environment Canada, Canadian Wildlife Service, Franzen Print Communications Ltd.

Gaggiotti, O.E. 2003. Genetic threats to population persistence. Annales Zoologica Fennica 40(2):155-168.

Gilbert L.E., and M.C. Singer. 1975. Butterfly Ecology. Annual Review of Ecology and Systematics 6:365-397.

Gillespe, T. 2002. Personal comment. Garry oak meadow preservation society representative.

Goodman, 1987. How do any species persist? Conservation Biology 1:59-62.

Guppy C. and J. Sheppard. 2001. *Butterflies of British Columbia*. Royal British Columbia Museum Press, Victoria, BC.

Gutierrez, D., C.D. Thomas, and J.L. Leon-Cortes. 1999. Dispersal, distribution, patch network and metapopulation dynamics of the dingy skipper butterfly (*Erynnis tages*). Oecologia 121(4):506-517.

Hastings, A.1991. Structured models of metapopulation dynamics. Biological Journal of the Linnean Society 42:57-71.

Hastings, A. 2001. Transient dynamics and persistence of ecological systems. Ecology Letters 4:215-220.

Hanski, I., 1994. A practical model of metapopulation dynamics. Journal of Animal Ecology 63:151-162.

Hanski I., A. Moilanen, T. Pakkala, and M. Kuusaari. 1995. The quantitative incidence function model and persistence of an endangered butterfly metapopulation. Conservation Biology 10(2):578-590.

Hastie, T.J., and R.J. Tibshirani. 1990. *Generalized Additive Models*. Chapman and Hall, NY.

Hays D.W., A.E. Potter, C.W. Thompson, and P.V. Dunn. 2000. Critical habitat components for four rare south Puget sound butterflies. Report prepared for Washington Department of Fish and Wildlife, and The Nature Conservancy of Washington, Seattle.

Hellmann, J.J., S.B. Weiss, J.F. Mclaughlin, C.L. Boggs, P.R. Ehrlich, A.E. Launer, and D.D. Murphy. 2003. Do hypotheses from short term studies hold in the long term? An empirical test. Ecological Entomology 28:74-84.

Hilborn, R., and M. Mangel. 1997. *The Ecological Detective: Confronting models with data*. Princeton University Press, Monographs in Population Biology. Princeton New Jersey.

Hochberg, M.E., G.W. Elmes, J.A. Thomas, and R.T. Clarke. 1998. Effects of habitat reduction on the persistence of *Ichneumon eumerus* (Hymenoptera: Ichneumonidae), the specialist parasitoid of *Maculinea rebeli* (Lepidoptera: Lycaenidae). Journal of Insect Conservation 2(1): 59-66.

Hokit, D.G., B.M. Stith, and L.C. Branch. 1999. Effects of landscape structure in Florida scrub: A population perspective. Ecological Applications. 9(1): 124-134.

Hokit, D.G., B.M. Stith, and L.C. Branch. 2001. Comparison of two types of metapopulation models in real and artificial landscapes. Conservation Biology 15(4): 1102-1113.

Holling, C.S. (ed.). 1978. *Adaptive environmental assessment and management*. Toronto, John Wiley and Sons.

Hooson, S., and I.G. Jamieson. 2003. The distribution and current status of New Zealand Saddleback *Philesturnus carunculatus*. Bird Conservation International. 13 (2): 79-95.

Insightful. 1999. *S-Plus 2000 Professional Release 2, S-PLUS 2000 User Manual, Vol.1+Vol.2*. Insightful Corp, Seattle, WA, USA.

IUCN SSC Invasive species specialist group. 2000. IUCN guidelines for the prevention of biodiversity loss caused by alien invasive species. Lift out from the bi-annual newsletter Aliens 11. http://www.issg.org, issg@auckland.ac.nz.

Johst, K. and K. Schoeps. 2003. Persistence and conservation of a consumer-resource metapopulation with local overexploitation of resources. Biological Conservation 109(1): 57-65.

Johnson, J., and K.Olmand. 2004. Model selection in ecology and evolution. TREE 19(2): 101-108.

Jonsen, I.D, R.S. Bourchier, and J. Roland. 2001. The influence of matrix habitat on *Apthona* flea beetle immigration to leafy spurge patches. Oecologia 127: 287-294.

Kendall, B.E., and G.A. Fox. 2002. Variation among individuals and reduced demographic stochasticity. Conservation Biology 16(1): 109-116.

Kindvall, O. 1996. Habitat heterogeneity and survival in a bush cricket metapopulation. Ecology 77: 207–214.

Kinvig, R.G., and M.J. Samways. 2000. Conserving dragonflies (Odonata) along streams running through commercial forestry. Odonatologica 29(3): 195-208.

Krauss J., I. Steffan-Dewenter, and T. Tscharntke. 2003a. How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? Journal of Biogeography 30: 889-900.

Krauss J., I.Steffan-Dewenter, and T. Tscharntke. 2003b. Local species immigration, extinction, and turnover of butterflies in relation to habitat area and habitat isolation. Oecologia 137: 591-602.

Krauss J., I. Steffan-Dewenter, and T. Tscharntke. 2004. Landscape occupancy and local population size depends on host plant distribution in the butterfly *Cupido minimus*. Biological Conservation XXXX-IN PRESS.

Krebs, Charles J. 1999. Ecological Methodology, 2nd ed., Addison-Welsey Educational Publishers, Inc., Menlo Park, CA. 620 pp.

Lesbarreres, D., A. Pagano, and T. Lode. 2003. Inbreeding and road effect zone in a Ranidae: The case of the Agile frog, *Rana dalmatina* Bonaparte, 1840. Comp. Rend. Biol. 326(Suppl. 1): S68-S72.

Levins, R. 1966. The strategy of model building in population biology. American Scientist 54: 421-431.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15: 237-240.

Lindenmayer, D.B., M.A. Burgman, H.R. Ackakaya, R.C. Lacy and H.P. Possingham. 1995. A review of the generic computer programs ALEX, RAMAS/space and VORTEX for modeling the viability of wildlife metapopulations. Ecological Modelling 82: 161-174.

Lu S.S., and M.J. Samways. 2002. Behavioural ecology of the Karloof blue butterfly *Orachrysops ariadne* (Lepidoptera: Lycaenidae) relevant to its conservation. African Entomology 10(1): 137-147.

Luoto, M. M. Kuussaari, H. Rita, J. Salminen, and T. von-Bonsdorff. 2001. Determinants of distribution and abundance in the clouded apollo butterfly: A landscape ecological approach. Ecography 24(5): 601-617.

Macdougall, A. Personal comment. UBC PhD student working on invasive species in Garry oak meadows.

Mack R. N. and W. M. Lonsdale (2001). Humans as Global Plant Dispersers: Getting More Than We Bargained For. Bioscience 51(2): 95-102.

Matter, S.F., and J. Roland. 2002. An experimental examination of the effect of habitat quality on the dispersal and local abundance of the butterfly *Parnassius smintheus*. Ecological Entomology 27: 308-316.

Matter, S.F., and J. Roland, A. Moilanen, and I. Hanski. 2005. The migration and survival of *Parnassius smintheus*: Effects of the habitat matrix for individual butterflies. Ecological Applications. IN PREP.

Maunder, M., W. Page, J. Mauremootoo, R. Payendee, Y. Mungroo, A. Maljkovic, C. Vericel, and B. Lyte. 2002. The decline and conservation management of the threatened endemic palms of the Mascarene Islands. Oryx 36(1): 56-65.

McCullagh P., and J.A. Nelder. 1989. Generalized Linear Models. Chapman and Hall, NY.

Mitter K., and T. Lea. 2004. Historical Garry oak ecosystems of the Cowichan Valley and Saltspring Island. 1:50,000 map. Biodiversity Branch, BC Ministry of Water Land and Air Protection. Victoria, BC.

Moilanen, A., and I. Hanksi. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. Ecology 79(7): 2503-2515.

Moilanen, A. and Hanski, I. 2001. On the use of connectivity measures in spatial ecology. Oikos 95: 147-151.

Moilanen, A. and M. Nieminen. 2002. Simple connectivity measures in spatial ecology. Ecology 84: 1131-1145.

Mooney, H.A., and R.J. Hobbs. 2000. *Invasive species in a changing world.* Island Press. Washington, DC.

Nicholls A.O. 1989. How to make biological surveys go further with generalized linear models. Biological Conservation 50:51-75.

Odom D., G.R. Griffith, M. Schroder, and J.A. Sinden. 2003. Using aerial mapping to analyse factors affecting the spread of Scotch Broom. Plant Protection Quarterly 18(1): 6-10.

Ovaskainen, O. 2002. The effective size of a metapopulation living in a heterogeneous patch network. American Naturalist 160: 612-628.

Palo, J.U., H. Hyvarinen, E. Helle, H.S. Makinen, and R. Vainola. Postglacial loss of microsatellite variation in the landlocked Lake Saimaa ringed seal. Conservation Genetics 4(2): 117-128.

Parker, I.M.,W.S. Harpole,and D.Dionne.1997. Plant community diversity and invasion of the exotic shrub Cytisus scoparius: Testing hypotheses of invasibility and impact. IN *Ecology and conservation of the South Puget Sound prairie landscape* (P.V.Dunn,and K.Ewing,eds.), pp.149-162, Seattle: The Nature Conservancy Press.

Parker, I., and A. Engel. 2002. Pollination of *Cytisus scoparius* (Fabaceae) and *Genista monspessulana* (Fabacea), two invasive shrubs in California. Madrono 49(1): 25-32.

Pimm, S.L. 1987. Determining the effects of introduced species. Trends in Ecology and Evolution 2: 106-108.

Pojar, J. and A. MacKinnon (eds.). 1994. *Plants of Coastal British Columbia.* B.C. Ministry of Forests and Lone Pine Publishing. Canada.

Pollard, E. (1988) Temperature, rainfall and butterfly numbers. Journal of Applied Ecology 25: 819–828.

Pollard, E. and T.J. Yates. 1993. *Monitoring Butterflies for Ecology and Conservation.* Chapman and Hall, London.

Pollard, J.H. 1971. On distance estimators of density in randomly distributed forests. Biometrics 27: 991-1002.

Price, M. R. Goldingay, L. Szychowski, and N. Waser. 1994. Managing habitat for the endangered Stephens' kangaroo rat (*Dipodomys stephensi*): Effects of shrub removal. American Midland Naturalist 131: 9-16.

Pulliam, R. H. 1988. Sources, sinks and population regulation. The American Naturalist 132:652

Randall, J.M. 1993. Exotic weeds in North American and Hawaiian natural areas: the Nature Conservancy pan of attack. Pp159-172 IN McKnight WN (ed.) *Biological* *pollution: the control and impact of invasive exotic species*. Proceedings of a Symposium held at Indiana University-Purdue University, Indianapolis, IL.

Roemer, H. 1972. Forest vegetation and environments of the Saanich peninsula, Vancouver Island. PhD thesis, University of Victoria.

Roemer, H. 2001, 2002. Personal comment. BC Parks Ecological Reserves section head.

Roland J., N. Keyghobadi, and S. Fownes. 2000. Alpine *Parnassius* butterfly dispersal: effects of landscape and population size Ecology 81:1642-1653.

Roslin, T. 2000. Dung beatle movements at two spatial scales. Oikos 91: 323-335.

Roy, D.B., P. Rothery, D. Moss, E. Pollard and J. A. Thomas. 2001. Butterfly numbers and weather: predicting historical trends in abundance and the future effects of climate change. Journal of Animal Ecology 70: 201–217.

Scheiman, D., E. Bollinger, and D. Johnson. 2003. Effects of leafy spurge on grassland birds. Journal of Wildlife Management 67(1): 115-121.

Schultz, C. and K. Dlugosch. 1999. Nectar and host plant scarcity limit populations of an endangered Oregon butterfly. Oecologia 119: 231-238.

Simberloff, D., W.M. Lonsdale, K. Goodell, M. Wonham, P.M. Kareiva, M.H. Williamson, B.von Holle, P.B. Moyle, J.E. Byers, and L. Goldwasser. 1999. Impact: Towards a framework for understanding the ecological effects of invaders. Biological Invasions. 1: 3-19.

Sjogren-Gulve, P., and C. Ray. 1996. Extinction and isolation gradients in metapopulations: the case of the pool frog (*Rana lessonae*). in *Metapopulations and Wildlife Conservation*. Ed. D.R.McCullough. Island, Washington D.C.

Smith, E. S. Haarer, and J. Confrey. 1997. Seeking Diversity in Mathematics Education: Mathematical Modeling in the Practice of Biologists and Mathematicians. Science and Education 6(5): 441-472.

Soule, M.E. 1990. The onslaught of alien species and other challenges in the coming decades. Conservation Biology 4: 233-239.

Spalding, A. 1997. The use of the butterfly transect method for the study of the nocturnal moth *Luperina nickerlii leechi* Goater (Lepidoptera: Noctuidae) and its possible application to other species. Biological Conservation 80: 147-152.

Sparrow, H.R., T.D. Sisk, P.R. Ehrlich, and D.D. Murphy. 1994. Techniques and guidelines for monitoring neotropical butterflies. Conservation Biology 8: 800-809.

Steffan-Dewenter, I., and T. Tscharntke. 2000. Butterfly community structure in fragmented habitats. Ecology Letters 3: 449-456.

Swanson, B.J. 1998. Autocorrelated Rates of Change in Animal Populations and their Relationship to Precipitation. Conservation Biology 12(4): 801-808.

Thibault, J., J. Martin, A. Penloup, and J. Meyer. 2002. Understanding the decline and extinction of monarchs (Aves) in Polynesian Islands. Biological Conservation 108(2): 161-174.

Thomas, J.A. 1983. The ecology and conservation of *Lysandra bellargus* (Lepidoptera: Lycaenidae) in Britain. Journal of Applied Ecology 20: 59-83.

Thomas, J.A., N.A.D. Bourn, R.T. Clarke, K.E. Stewart, D.J. Simcox, G.S. Pearman, R. Curtis, and B. Goodger. 2001. The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. Proceedings of the Royal Society of London SERIES B 268: 1791-1796.

Ussery, J.1997. Managing invasive plant species in Garry Oak meadow vegetation communities: a case study of Scotch Broom. Report No. 203, School of Resource and Environmental Management, Simon Fraser University, Burnaby, BC.

Vila, M., M. Williamson, and M. Lonsdale. 2004. Competition Experiments on Alien Weeds with Crops: Lessons for Measuring Plant Invasion Impact? Biological Invasions 6(1): 59-69.

Walker, R.S., A.J. Novarro, and L.C. Branch. 2003. Effects of patch attributes, barriers, and distance between patches on the distribution of a rock-dwelling rodent (*Lagidium viscacia*). Landscape Ecology 18: 187-194.

Walters, C.J. 1986 *Adaptive management of renewable resources*. McGraw-Hill, New York.

Walters, C.J., and C.S. Holling. 1990. Large-scale management experiments and learning by doing. Ecology 71: 2060-2068.

Ward, P., G. Radcliffe, J. Kirkby, J. Illingworth and C. Cadrin. 1998. Sensitive Ecosystems Inventory: East Vancouver island and the gulf islands 1993-1997. Volume 1: Methodology, ecological descriptions and results. Technical Report series No. 320. Canadian Wildlife Service, Pacific and Yukon region, BC.

Waterhouse, B.M. 1988. Broom (*Cytisus scoparius*) at Barrington Tops, New South Wales. Australian Geographical Studies 26:239-248.

Wellington, W.G., D.L. Johnson, and D.J. Lactin. 1998, Weather and insects. Chapter 13, pp. 313-353, in Gutierrez A (ed.), *Ecological Entomology*, John Wiley & Sons, New York, 850 pp.

Williams, P.A. 1981. Aspects of the ecology of broom (*Cytisus scoparius*) in Canterbury, New Zealand. New Zealand Journal of Botany 19: 31-34.

With, K. A., and A. W. King. 1997. The use and misuse of neutral landscape models in ecology. Oikos 79: 219-229.

With, K. A., D. M. Pavuk, J. L. Worchuck, R. K. Oates, and J. L. Fisher. 2002. Threshold effects of landscape structure on biological control in agroecosystems. Ecological Applications 12: 52-65.

Zielke, K., J.O. Boateng, N. Caldicott, and H. Williams. Broom and Gorse in British Columbia: a forestry perspective problem analysis. Silviculture Branch, Ministry of Forests, Victoria, BC.

CHAPTER 3

Metapopulation level effects of flower abundance on the distribution of the rare butterfly *E. propertius* in a network of Garry Oak meadows

INTRODUCTION

Many studies have examined how habitat quality affects the occurrence of patchily distributed species (Price *et al.*, 1994; Ellis *et al.*, 1997; Thomas *et al.*, 2001; Scheiman *et al.*, 2003; Krauss *et al.*, in press). One of the resources commonly found to influence this patch distribution is food availability, which, for lepidopterous insects, is supplied by larval hostplants and adult nectar plants. Food resources such as larval hostplant and adult nectar resources have been found to limit population size (Begon *et al.*, 1996; Dennis and Eales, 1997), and so a lack of nectar and hostplant resources can result in a smaller population. As such, it is an important consideration when managing to maintain viable populations of rare butterfly species (Schultz and Dlugosch, 1999). An individual butterfly may have to move relatively large distances to obtain both larval and adult food resources (Brommer and Fred, 1999). As a result, the spatial arrangement of these resources among patches becomes important in maintaining viable populations (Thomas, 1994; Brommer and Fred, 1999; Matter and Roland, 2002). Many studies have included measures of patch geometry (area and connectivity) with those of patch quality in an attempt to model patterns of movement (Roland *et al.*, 2000) and distribution (Hanski, 1994; Walker *et al.*, 2003) often resulting in a better model fit to the data, and greater success in predicting species occurrences (Fred, 2004; but see Krauss *et al.*, 2004).

Habitat quality may affect species distributions, but a simple regression approach to describing their presence/absence has limitations. Simple regression cannot make detailed predictions of the effect of habitat quality variables if the spatial arrangement of the habitat patches is not taken into account. Similarly, the strict patch-geometry approach, without consideration of patch quality, has limitations that may not account for an overriding importance of habitat patch quality (Thomas *et al.*, 2001). Combining the two approaches allows for the examination of how population dynamics may depend on the spatial configuration of the resources (Wiens, 1997), by placing the broader ecology of a species within a metapopulation context.

Few studies build on a model of hypothesized metapopulation processes (Tuck and Possingham, 1994; Moilanen and Hanski, 1998; Hanski and Ovaskainen, 2000; Crone *et al.*, 2001; Hokit *et al.*, 2001), although there is substantial support for this approach (Hanski, 1999; Ackakaya, 2000). Despite improvement in fit and predictive power of doing so (Moilanen and Hanski 1998; Roland *et al.*, 2000; Hokit *et al.*, 2001; Matter *et al.*, in prep), there are few examples combining the two approaches of using habitat quality and metapopulation theory. The original metapopulation theory of Levins (1969) was a single species description of population occurrences that evolved from a closely related precursor, the Dynamic Theory of Island Biogeography (DTIB, Macarthur and Wilson, 1967). In this chapter I develop a statistical model based on the Incidence Function model (IFM), originally developed by Hanski (1994) as a more flexible extension of the Levins (1969) metapopulation concept.

The Incidence Function Model (IFM - Hanski, 1994) differs from Levins' metapopulation model in that it examines the effect of variable patch areas and patch isolation on occupancy by an organism, whereas in Levins' model these terms are always uniform. The IFM uses nonlinear regression to fit presence-absence data for the species in a patch network, by combining formulae for colonization (C_i) and extinction (E_i) into a nonlinear formula that predicts of incidence of occupancy, J_i. The J_i values are then fit to the presence/absence data, which assesses whether the J_i values, that represent connectivity to other occupied patches and theoretical ideas about metapopulation dynamics, fit the data. Hanski's IFM model assumes a sigmoid relationship between the number of immigrants M_i, and the colonization probability C_i (Fig. 3-1), given by:

$$C_i = M_i^2 / (M_i^2 + y^2) \qquad \text{Eq 1}$$

The parameter y defines how quickly the colonization probability increases with increasing immigrants M_i.

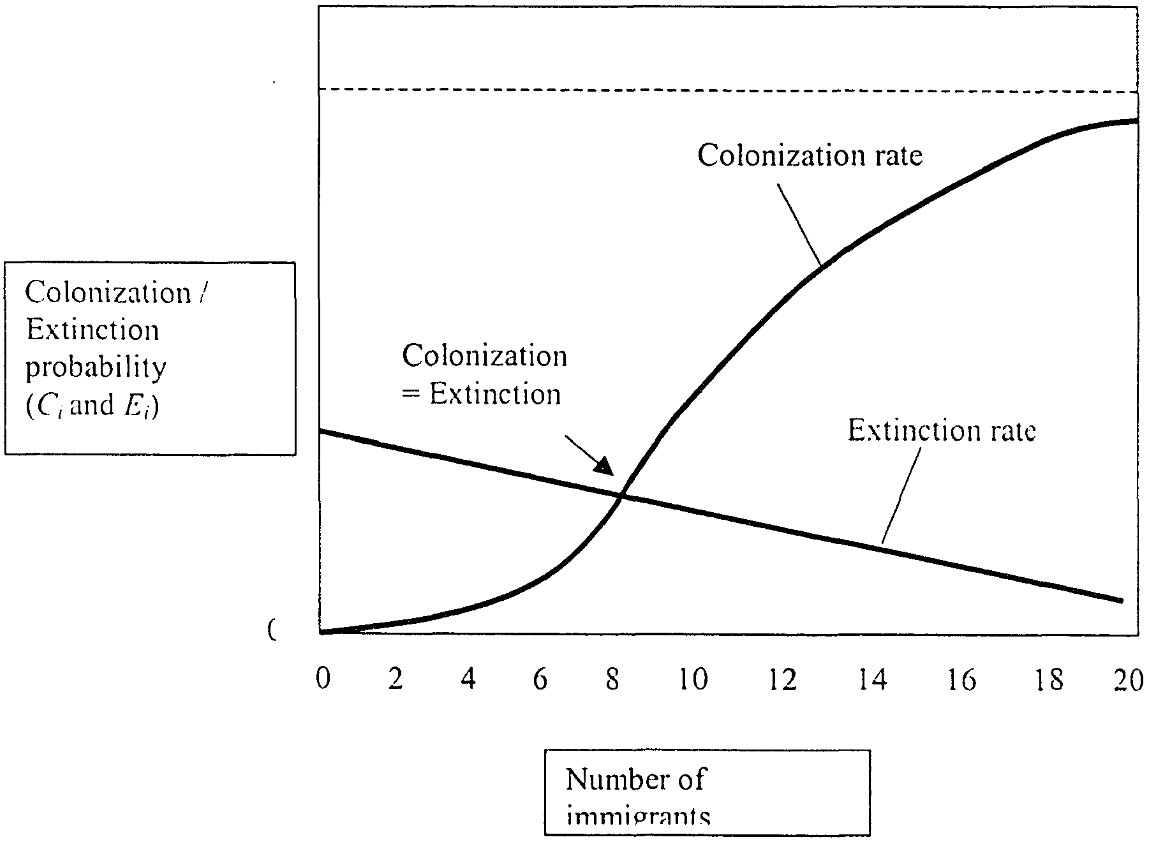

Figure3-1: Decreased probability of colonization with low numbers of immigrants due to a hypothetical 'Allee effect'.

The number of immigrants M_i is a difficult parameter to measure directly, and so in this model a phenomenological approach is taken to define it using basic key elements that must be involved in migration. In this description, M_i is broken down into component parts, given by:

$M_i = \beta S_i$, Eq 2

Where β is a constant that is a product of several factors, including emigration rate from a patch, and density of individuals in the patches. S_i represents the connectedness of the patch i, and is defined as:

$S_i = \Sigma\, p_j \exp(-d_{ij}\alpha)A_j$ Eq 3

Where d_{ij} is a measure of the interpatch distances, α is the species-specific dispersal parameter, A_j is the area of the contributing patch j, and p_j is the occupancy of the contributing patch. Using these assumed phenomenological functions, equation 1 becomes:

$C_i = 1 / (1 + [y'/S_i]^2)$ Eq 4

Where $y' = y/\beta$, by combining these two parameters related to colonization during the algebraic reduction process. Thus colonization C_i is dependent on y', a constant which describes the colonization ability of the species, and S_i, a parameter representing the connectedness of a given patch.

To produce the incidence of occupancy J_i, this colonization probability C_i is balanced against the extinction probability E_i as described by the formula:

$E_i = e/A_i^x$ Eq 5

Where e defines the minimum occupied patch size and x the role of environmental variability/stochasticity, and where A_i is the area of the patch i. The formulas from equations 4 and 5 are then combined in the formula defining the J_i incidences:

$J_i = C_i / (C_i + E_i)$ Eq 6

Once this is algebraically reduced it becomes:

$J_i = 1 / \{1 + (1 + [y' / S_i]^2) * e / A_i^x\}$ Eq 7

In this model, e is a parameter defining the critical patch size below which the probability of extinction in a given interval is 1 (all $E_i > 1$ and $C_i > 1$ are set to 1, because the upper limit of a probability is 1), and x is a constant relating patch area to extinction rate. S_i is a composite measure of the patch connectivity, accounting for all possible immigration to the patch of interest from other occupied patches, y' is a constant which describes the colonization ability of the species. By ignoring local population dynamics the model makes the somewhat unrealistic assumption that all occupied sites are at their carrying capacity and that this capacity is related directly to the area of the patch. In addition to using distance-weighted dispersal, this model assumes theorized connections between extinction and colonization to reach a prediction of how these two processes will interact to produce the incidences J_i (Hanski, 1994). One of these assumptions is the presence of an "Allee effect" (Allee, 1938; Lewis and Kareiva, 1993; Amarasekare, 1998), which can be obtained by using a sigmoid curve of decreased colonization probability at low numbers of immigrants (Figure 3-1).

This formula may be further modified to incorporate a second structural assumption, that of a "rescue effect" (Brown and Kodrick-Brown, 1977). This represents the possibility of simultaneous extinction and colonization events, which together leave the patch occupied. In the IFM model, Hanski accounts for this possibility by using a different form of equation 4, where the value for extinction probability, E_i is replaced by $(1 - C_i)\ E_i$, the realized extinction rate after the potential for a rescue effect. This results in a new form of equation 4 which is:

$J_i = C_i / \{C_i + [(1 - C_i)*E_i]\}$ Eq 8

Once again, the C_i and E_i formulas from equations 4 and 5 are substituted into equation 8 and after algebraic reduction this becomes:

$J_i = 1 / (1 + e' / S_i^2 A_i^x)$ Eq 9

Where $e' = ey'^2$, again produced through algebraic reduction and combining these two parameters. The drawback to the use of this e' combination is that extra data is required to separate the two e and y' parameters. This is done by collecting data about observed population turnover events between years, and using this to numerically iterate the value of y'. To do so Hanski defined the formula:

$T = \Sigma\ (1-C_i)\ E_i*p_i + C_i(1 - p_i)$ Eq 10

Where T is the number of observed turnover events. With substitution of the C_i and E_i expressions, from equations 4 and 5, this becomes:

$T = \Sigma\ [1/(S_i+y'^2)] * [S_i^2(1-p_i) + (e'* p_i/A_i^x)]$ Eq 11

The known T value, observed p_i , calcuated S_i, and the values of e' and x from solving equation 9 are put into this equation, leaving only the final step of iterating the value of y'. After using the formula $e'=e*y'$ to obtain the value of e, all required parameters of the IFM model are then known and the metapopulation dynamics may be iterated.

Other metapopulation modeling methods exist, such as matrix models (Ackakaya, 2000) and turnover models (Tuck and Possingham, 1994; Sjogren-Gulve and Ray, 1996). Although these models contain more parameters, they may not produce better results, despite costing more time and effort to conduct (Hokit *et al.*, 2001). As the purpose of this study was to test the use of area versus 'effective area' scaled by quality in metapopulation theory, and since these alternative methods assume many of the same functions but with greater complexity, I decided to use the simpler IFM model. Further description of the IFM model may be found in Hanksi (1994) and Moilanen and Hanski (1998), while some modifications used in this study are described in the *Methods* section below.

The purpose of this paper is to outline a process by which the two approaches of habitat quality and metapopulation analyses may be combined and used to assess the roles of individual patches within a metapopulation. Until recently, the IFM model has been used specifically for assessing persistence of the overall metapopulation without considering the role of individual patches within this network. Metapopulation capacity analysis ((Hanski and Ovaskainen, 2000, Ovaskainen and Hanski, 2003, Ovaskainen 2003) extends metapopulation analyses to deal with precisely this issue. Individual patches are weighted for their importance in the network based on their respective contribution to the pool of immigrants that (re)colonize other patches (C_i), and also weighted by their own persistence/resistance to extinction as a viable population in their own right (E_i).

Specifically, I used this method to model the patch occupancy of *Erynnis propertius* (Scudder and Burgess, 1870), a species of rare butterfly found in coastal British Columbia, Canada. First I test the validity of applying metapopulation analysis, in comparison with linear regression models (Chapter 2) that do not include structural assumptions about metapopulation dynamics. I then use a modified version of the IFM (Hanksi, 1994), to account for variation in habitat quality in each patch due to flower abundance. Metapopulation capacity analysis is then used to determine the relative importance of individual meadows contributing to the butterfly metapopulation. Assessment of how the change to the quality of each meadow affects this contribution was performed by means of matrix models and sensitivity analysis following the metapopulation capacity framework. This procedure demonstrates how factors affecting patch occupancy for a species may be assessed, given both the role of habitat quality and the role of metapopulation effects, within a framework based on the larger scale provided by metapopulation theory.

METHODS

STUDY AREA

Location and Context

The general study area has a Mediterranean-type climate due to the mitigating influence of the ocean keeping temperatures relatively warm for such northerly latitudes, and the influence of two mountain ranges that cause a double rainshadow effect, producing dry weather. This region of biogeoclimatic oddity is defined as the Coastal Douglas Fir zone (Fuchs, 2001) and it covers Southeast Vancouver Island, British Columbia, and includes the Southern Gulf Islands. In Canada, Garry oak (*Quercus garryanna*) ecosystems are the driest and most rare subsection of this rare ecotype, and they exist as a patchy network within a matrix composed primarily of Douglas fir (*Pseudotsuga menzesii)* forest.

The study was conducted in a Garry oak meadow network located on Mount Maxwell, Saltspring Island. This network has remained largely undisturbed by anthropogenic actions such as building houses and roads, is large in size, and is relatively isolated from other Garry Oak meadows (Appendix A, Figures A.1 and A.2, from Mitter and Lea, 2004; Figure 3-2). The meadow network was approximately 25 km^2 in area, and has been designated as a protected area to preserve the Garry oak meadows.

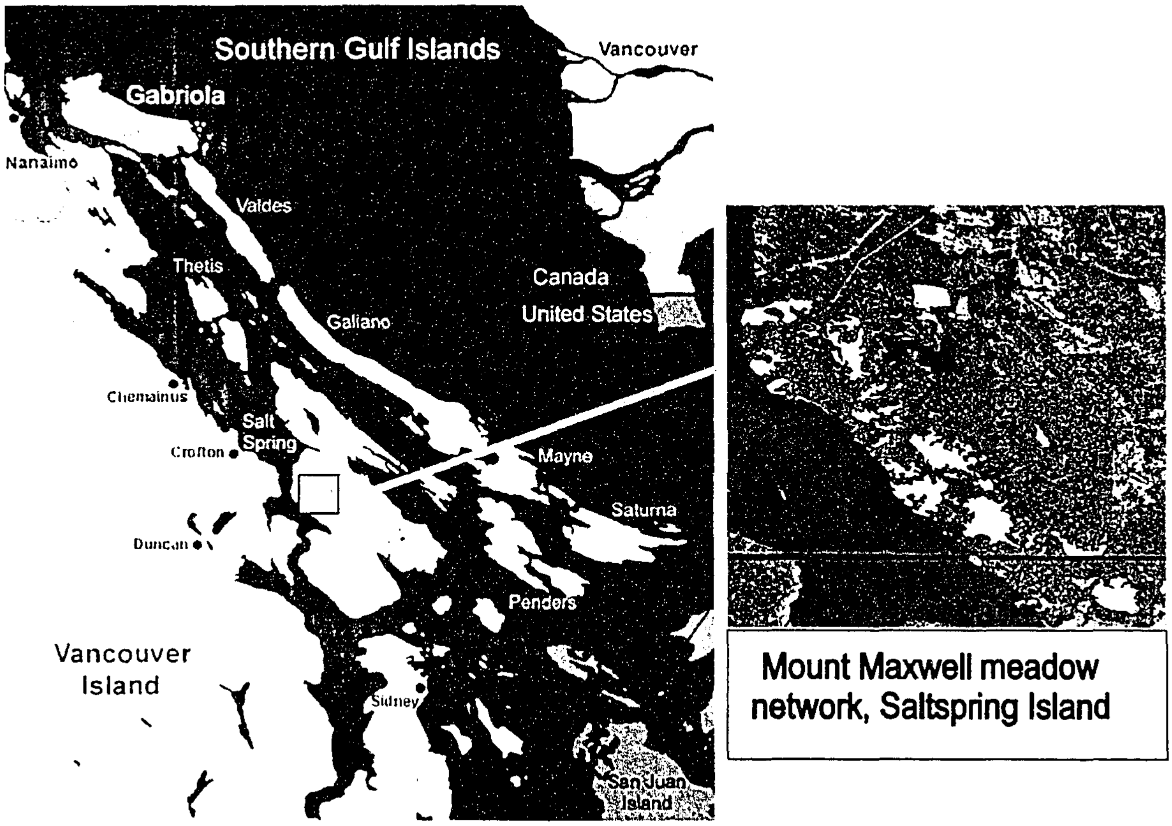

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Figure 3-2: Map of study site location showing regional context of the Mount Maxwell study site near Vancouver, British Columbia, and location of meadows at this study site.

Butterfly species

The Propertius Duskywing (*E. propertius*) was chosen based on a general pilot survey for Lepidoptera distribution conducted during the summer of 2001. It was also chosen because results from past studies to evaluate the degree of host specificity for this species found it was obligately monophagous on Garry oak (*Q. garryanna*), and as such is mostly restricted to Garry oak meadows (Guppy and Sheppard, 2001).

DATA COLLECTION

Habitat Quality

As discussed in the Introduction, habitat quality can change the 'effective area' of a patch for a species, and may be a better surrogate measure of population size than is area alone. Local measures of habitat quality have been found to be important factors in distributions of other butterfly populations in this region (Hays, 2000). A given meadow may be large, but if it is of poor quality it will not support as large a population as a smaller meadow of high quality. In this study, 'habitat quality' was integrated by making effective patch area dependent upon cover/availability of general floral abundance (this combination is described further below and in the section *Methods/Metapopulation model*).

Flower Abundance

Flower availability is related to habitat use by butterflies since these resources provide food for the adults. A subjective, categorical abundance estimate was made for cover of each flowering plant species during a survey (see Appendix B for species list), according to the rough scale in Table 3-1. For each meadow, the sum of the cover levels assigned to all flowers was calculated, producing an index of average flower abundance for each survey.

Table 3-1: Categorical abundance class divisions as recorded for each flowering plant species in flower at the time of each survey.

Categorical abundance class	Floral abundance class definitions [observed in the surveys]
0	0% – none
1	0.5 % – trace
2	3 % – sparse
3	20% – moderate
4	50% – abundant
5	80% - very apparent / ubiquitous

Butterfly surveys

Surveys for *E. propertius* were conducted on sunny days during March-August 2002 and 2003, along randomly located 'belt' transects (Sparrow *et al.*, 1994) of 20m width (10m on each side of the observer, ~400 transects in each year). Each site was visited up to five times during and until the end of the butterfly flight season, or until *E. propertius* was observed. Presence of an individual *E. propertius* was assumed to mean that there was a reproducing population present. Data were collected in two years in order to allow turnover events to be used to estimate α, the species flight ability parameter (Chapter 2). This avoids having to estimate the species dispersal ability parameter (α) along with the other IFM model parameters from only one year of presence/absence data (see *Methods/Data collection-Patch Size and Isolation* for additional information). With two years of data the estimate of the time-process parameter for dispersal ability can be more reliably estimated from the spatial pattern data, since one turnover time period was observed. With only one year of data the results are less reliable (Verboom and ter Braak, 1996; Gosselien, 1999). Having two years of data also allows estimation of the 'rescue effect' form of the IFM model (Hanski, 1994).

Patch Size and Isolation

Habitat patches in each network were delineated using 1:10,000 orthorectified digital airphotos of each network as a base layer, and tracing them using the program ARCVEIW 3.2/8.1/9.x (ESRI, 1996). These boundaries were ground-truthed in the field, and patch areas were determined using the 'calculating areas' script for ArcMap 9.x (produced by ESRI, 2004). Patch-specific connectivity measures for each meadow were calculated by the formula for S_i, as described in Eq.2.

Although the S_i connectivity estimate is more complex than nearest neighbour analysis, it has been found that composite measures such as this are often more accurate in defining spatial connectivity and produce better results in modelling exercises (Moilanen and Nieminen, 2002). Distances between patches (d_{ij}) were measured in kilometres using the 'Real Centroid' and 'Distance Matrix of Point Features' extensions from ESRI for ARCview 3.2 (written by P. Zsolt, 2003, and H. Maoh, 2001, respectively). Flight ability of the species of interest is estimated by the parameter α, estimated by using two consecutive years of data to identify newly colonized patches from which to measure distance to the nearest occupied neighbour. This follows a conservative assumption that the nearest occupied neighbour was the origin of the successful colonists. A nonlinear regression model was fit using the formula $P = \exp(-d\alpha)$, where P is the proportion of newly colonized patches to uncolonized empty patches in each 100m distance class, and d is the distance to the nearest occupied patch (Hokit *et al.*, 1999).

Regression Submodel Defining Variables with an Effect on Habitat Quality

To define the relative importance of individual patches and how their quality affects their role in a practical example, I first examined the extent to which habitat quality correlates to the patch occupancy of *E. propertius*. I ran a logistic regression to examine the effects of flower abundance, patch area and patch connectivity (S_i) on patch occupancy (Chapter 2). The fit of each explanatory variable was assessed by means of the p-values and percent deviance explained in the model, and by the coefficient of effect size +/- SE for each variable. Flower abundance was found to have a significant correlation with patch occupancy (Chapter 2), and was used to modify the metapopulation model to account for the effect of floral availability on habitat quality.

Metapopulation Model

The metapopulation approach differs from a regression approach because each patch may potentially contribute immigrants to others, which accounts for the dynamic effect of patches on each other through their spatial arrangement, their area and the dispersal ability of the species. As was observed in Chapter 2, additions to the 'effective' amount of habitat available in any given patch may occur due an increase in flower availability, in turn affecting the butterfly population size in that patch. This is likely caused by increased food availability, and as a result, there should be a greater chance of local extinction in a patch with less adult food, due to lower carrying capacity and population size. Such a patch will also provide fewer emigrants.

Based on the IFM, I produced a probability of individuals from a given patch colonizing other nearby patches, wherein this probability decreases with increasing distance from the source patch, and increases with increasing source patch/population size. To produce this probability required reformulation to allow splitting of the patch specific colonization probability (C_i)

$$C_i=1/\{1+[y'/\Sigma\, p_j \exp(-d_{ij}\alpha)A_j]^2\} \qquad \text{Eq 12}$$

into component parts, the (C_{ij}) values:

$C_{ij}=1/\{1+[y'/p_j \exp(-d_{ij}\alpha)A_j]^2\}$ Eq 13

These partial colonization probabilities (C_{ij}) represent the respective contribution of each patch j to the colonization probability of patch i, and are dependent on patch area of the contributing j patch through the patch connectivity measure (defined by α, patch j areas, and distance; see equation 3), and the factor y', that describes the colonization ability of a species. If the partial contributions are summed, they result in C_i, the sum total colonization probability for a given patch i.

In order to build in habitat quality factors I changed this formula further to allow habitat quality to vary (Hanski, 1994). Good quality will make the 'effective area' of a patch larger, while low quality will make the 'effective area' smaller. The 'area' term in the IFM model is meant as a surrogate for population size and so it is logical to change this term in the model, making it partially dependent on the effect of the flower availability on patch quality.

$C_{ij}=1/\{1+[y'/p_j \exp(-d_{ij}\alpha)A_j \cdot Q_j]^2\}$ Eq 14

Quality (Q_i) of a given patch was represented using the probability of occupancy given the observed level of flower abundance, as obtained using the effect size coefficient from the logistic regression of patch occupancy and flower abundance. In the regression, the coefficient associated with flower abundance was found to be $\beta=0.0203$, and an intercept of -2.7. Based on these values, the probability of patch occupancy associated with the level of the continuous flower abundance factor is given by:

$P_{\text{flowers}} = e^{[-2.7 + (0.0203*\text{flowers})]} / 1 + e^{[-2.7 + (0.0203*\text{flowers})]}$ Eq 15

This probability was calculated for each meadow, and then used to adjust the area into effective area ,through the Q_j adjustment for patch quality, based on the actual level of this quality variable in the given patch.

In addition to adjusting the colonization function (C_i) to account for habitat quality, I also used the IFM model to produce patch-specific extinction probabilities (E_i) with an adjustment for habitat quality, modifying the formula of Eq 3 into:

$E_i = e / (A_i \cdot Q_i)^x$ Eq 16

A transformation similar to that described above for the C_{ij} probabilities, changing patch areas into effective area by means of a quality factor, was used in this case as well. The predicted incidences (J_i) from the modified IFM model were fit to the data, and the fit of this model compared to the results of a simple linear regression by means of AIC (Burnham and Anderson, 1998). The modified IFM was compared to the fit of a simple regression model that looked only for linear main effects and interaction effects of the same variables. Since these models were non-hierarchical they were compared by means of Akaike weights (ω_i, Burnham and Anderson, 1998; Johnson and Olmand, 2004).

The IFM model is a simple metapopulation model with few parameters, and because of this a further test is warranted to make sure the system follows the assumption that it is at a quasi-stationary equilibrium. This test uses the present patch occupancy as a description of the equilibrium occupancy state. If it is not at equilibrium, use of this model may result in erroneous conclusions. For example, the current patch occupancy may reflect a slow long-term decline rather than fluctuations around a quasi-stable state. In order to assess whether this key assumption was valid, I enumerated the number of turnover events occurring as either extinctions or colonizations. I then compared these two observed numbers of turnovers of each type against one another to determine if they were significantly different. If so, this would imply that the metapopulation was not at a quasi-stable equilibrium state (Clinchy, 2002). If the metapopulation is stable, the matrix analysis may continue.

Matrix Analysis

To assess the importance of each meadow within the network, the output of the metapopulation model equations defining its role in contributing to colonizations and extinctions were placed into a matrix format. The colonization probability values of C_{ij} from each patch i to all other patches j, and the patch-specific persistence probability $1/E_i$

(inverse of extinction probability) are calculated and put into a large square matrix ($\mathbf{A_P}$), representing the contributions of each patch to colonization and persistence, given the *present* meadow quality. This matrix was of the form:

$$\mathbf{A_P} = \begin{bmatrix} 1/E_{P_1} & C_{P_{12}} & . & C_{P_{1n}} \\ C_{P_{21}} & 1/E_{P_2} & . & C_{P_{2n}} \\ . & & . & . \\ C_{P_{n1}} & C_{P_{n2}} & . & 1/E_{P_n} \end{bmatrix}$$

This $\mathbf{A_P}$ matrix is linear and based on an assumption that the E_i and C_{ij} values it contains are time invariant. It represents the metapopulation dynamics of the species in that specific patch network because the E_i and C_{ij} values are produced directly from the species specific dispersal parameter, and patch quality and patch spatial arrangement data specific to that network of patches. The values I created for this matrix are based on the current distribution of flowers in each patch network, through the effect of flower availability on the 'effective area' (Equations 14 and 16 – pgs 110 and 111, in Methods section). This matrix is used as a basis for sensitivity and prospective analyses of the role of each patch in the network.

A measure of the 'metapopulation capacity' may be obtained by deriving the dominant eigenvalue (λ_1) of the matrix $\mathbf{A_P}$ through matrix population model analysis (Caswell, 2001). The dominant eigenvalue usually represents the effects of fecundity and survival of each life stage on the 'population growth rate' (Leslie, 1945), but in this case it has a different meaning. The dominant eigenvalue (λ_1) in this case relates to the colonization C_{ij} and persistence E_i of individual populations within the metapopulation. In this new use of matrix analysis, the dominant eigenvalue is termed λ_M, and is called the 'metapopulation capacity' (Hanski and Ovaskainen, 2000). Metapopulation capacity represents the overall landscape structure of the specific network of patches under scrutiny because the individual terms in the matrix are based on the C_{ij} and E_i formulas and thus contain information about the amount of habitat in each patch, the species dispersal and colonization ability, and the geometric configuration of the habitat patches.

Application of this method to metapopulations effectively allows assessment of the importance of C_{ij}, the colonization output (Ovaskainen and Hanski, 2003; relates to the role of emigrants from this patch in colonizing other patches, analogous to the reproductive output of a given life stage) and E_i, the population persistence (analogous to life stage survival) in a given patch i in terms of its contribution to the metapopulation. The matrix may be used for iterating dynamics of the butterfly populations across a collection of sites that form a metapopulation by multiplying the matrix $\mathbf{A_P}$ by a column vector $\mathbf{N_P}$ which represents the abundances of butterflies in the meadows:

$$(N_{P_{t+1}} = A_P * N_{P_t}).$$

A sensitivity analysis ($\delta\lambda / \delta a_{ij}$, Caswell, 2000) was then performed to assess the relative contribution of the different a_{ij} values of the matrix to the dominant eigenvalue, λ_M, producing a new matrix of sensitivity values, $\mathbf{A_S}$. Elements of this sensitivity matrix are defined:

$$\mathbf{A_S} = \begin{bmatrix} \lambda / \delta a_{11} & \lambda / \delta a_{12} & . & \lambda / \delta a_{1j} \\ \delta\lambda / \delta a_{21} & \lambda / \delta a_{22} & . & \lambda / \delta a_{2j} \\ . & . & . & . \\ \delta\lambda / \delta a_{i1} & \delta\lambda / \delta a_{i1} & . & \lambda / \delta a_{ij} \end{bmatrix}$$

Perturbation analysis (Caswell, 2001, section 9.1.6, Eq 9.38, pg.218) was then done to examine the effect of hypothetical losses and increases of flower abundance on λ_M. Elasticity analysis (Caswell, 2000) was *not* used, because I was interested in the additive change in λ_M associated with a change in a_{ij} values. Using proportional changes, as produced by elasticity analysis, would bias the later stages of my analysis by basing the elasticity of each meadow on a proportional scale. Elasticity analysis was thus not comparable across meadows in terms of changes induced in each meadow, and precludes comparison of relative merit of different management actions that would each cost a certain amount to implement per unit area, not by proportion of meadow covered. Sensitivities are thus a more realistic expression for use in this instance, given the limited resources and cost of implementing real-world restoration/management actions.

The perturbation analysis requires two other matrices to assess differences in output related to the hypothetical changes in the state of the flower resources. In the first matrix, $\mathbf{A}_R$, the C_{ij} and E_i data were adjusted to hypothetically represent a state of all meadows having lower quality due to less flower availability (equations 9 and 11). To do this I followed the same method as that used to produce the square matrix $\mathbf{A}_P$, but adjusted the quality data used in the underlying IFM metapopulation model to assume that there were very few flowers in any of the meadows (as if all plants had failed to flower that year). This has an effect on the C_{ij} and E_i values and thus the new $\mathbf{A}_R$ matrix contained different C_{ij} and E_i values than the original $\mathbf{A}_P$ matrix that was based on the real present meadow quality. In the adjusted dataset used to produce the $\mathbf{A}_R$ matrix, flower abundance in each meadow was set at 0, representing a hypothetical loss of the flowers due to poor weather conditions, overgrazing, or invasion of an unusable or non-flowering weed (Figure 3-3.a). I also made a similar adjustment to a second matrix, $\mathbf{A}_A$, wherein I adjusted the meadow quality data in the underlying metapopulation model assuming that all the meadows had a high level of flower abundance in them (a high overall average flower abundance in a meadow could result from several species being highly abundant, many species being at a sparse to moderate abundance, or some combination of these two). This would represent a hypothetical 'good year' for the flowers, removal of grazing, removal of the unusable weeds, or revegetation activities boosting populations of the flowering plants (Figure 3-3.b).

These two matrices, $\mathbf{A}_R$ and $\mathbf{A}_A$, thus contain the same type and format of information as in the matrix $\mathbf{A}_P$, but were produced by modifying the underlying metapopulation model data slightly. The individual entries in each of these two matrices were subtracted from the corresponding entries in the original matrix $\mathbf{A}_P$, producing two new matrices of data, $\mathbf{A}_{RH}$ and $\mathbf{A}_{AH}$, representing the differences produced by the hypothetical removals and hypothetical additions of flowers in the meadow quality relative to the current quality. For example, $\mathbf{A}_P - \mathbf{A}_R = \mathbf{A}_{RH}$:

$$\begin{bmatrix} 1/E_{P_1} & C_{P_{12}} & . & C_{P_{1i}} \\ C_{P_{21}} & 1/E_{P_2} & . & C_{P_{2i}} \\ . & . & . & . \\ C_{P_{i1}} & C_{P_{i2}} & . & 1/E_{P_{ii}} \end{bmatrix} - \begin{bmatrix} 1/E_{R_1} & C_{R_{12}} & . & C_{R_{1i}} \\ C_{R_{21}} & 1/E_{R_2} & . & C_{R_{2i}} \\ . & . & . & . \\ C_{R_{i1}} & C_{R_{i2}} & . & 1/E_{R_{ii}} \end{bmatrix} = \begin{bmatrix} 1/E_{RH_1} & C_{RH_{12}} & . & C_{RH_{1i}} \\ C_{RH_{21}} & 1/E_{RH_2} & . & C_{RH_{2i}} \\ . & . & . & . \\ C_{RH_{i1}} & C_{RH_{i2}} & . & 1/E_{RH_{ii}} \end{bmatrix}$$

The individual elements in the 'difference' matrix $\mathbf{A}_{AH}$ ($\mathbf{A}_P - \mathbf{A}_A = \mathbf{A}_{AH}$) were all negative, since the addition of flowers increased persistence and colonization probabilities in the matrix $\mathbf{A}_A$ relative to the matrix $\mathbf{A}_P$. These were all converted to absolute values, as I was primarily interested in the magnitude of the differences, as I already knew the direction of change that changing the underlying data would induce.

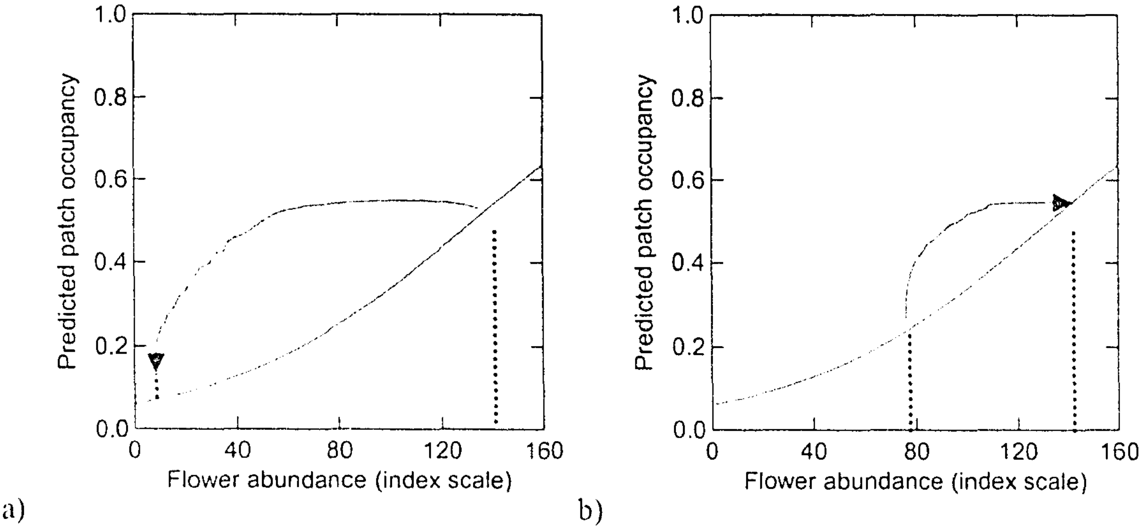


Figure 3-3: Predicted patch occupancy of *E. propertius* as a function of flower availability: a) hypothetical drop in patch occupancy due to loss in local flower availability in a patch, b) hypothetical increase in patch occupancy due to an increase in local flower availability. Recalculation of the Incidence Function Model colonization function for each patch was based on hypothetically changing the underlying patch area data based on meadow quality in relation to flower abundance. Model coefficients used for this modification were obtained from *E. propertius* patch occupancy in relation to flower abundance in the Mt Maxwell network in 2002 (this was the weakest effect and so the most conservative estimate of the effect of flower availability on patch occupancy).

Each difference matrix was separately multiplied by the sensitivity matrix to obtain the Hadamard product ($\mathbf{A}_{RH} \circ \mathbf{A}_{S}$ and $\mathbf{A}_{AH} \circ \mathbf{A}_{S}$) giving the element by element multiplication product as for a standard prospective analysis ($\delta \lambda_M / \delta$ Flowers = Σ ($\delta \lambda_M / \delta a_{kl}$) * ($\delta a_{kl} / \delta$ Flowers) =; Caswell, 2001, pgs 218, Eqn.9.38). Using this method allows the overall metapopulation capacity (λ_M) to be broken down into the component parts contributed from each meadow to the metapopulation. This may then be summed by meadow in order to rank the importance of each meadow to the metapopulation as well.

Results of the sensitivity analysis, $\mathbf{A}_S$, were produced with Mathematica, and prospective analyses were done using MS Excel. The sensitivity and prospective analyses results were summed by meadow to produce values for each meadow representing the cumulative importance of persistence of that meadow and colonizations from that meadow to all other meadows within the network. These sets of sums were imported into ARCview 3.2 (ESRI, 1996) and mapped to identify where management actions may have the greatest impact by virtue of boosting contribution of immigrant colonists within the metapopulation.

The prospective analysis weights the meadow sensitivity by the magnitude of the difference between hypothetical and current meadow quality. Essentially, this prospective analysis method helps determine which management actions are realistic, given potential changes that may be brought about, rather than relying on subjective judgments based only on the simpler sensitivity analysis method (Caswell, 2000).

RESULTS

Model Fit

Flower abundance has a positive effect on patch occupancy by the butterfly *E. propertius* (Figure 3-4). There was also a positive effect of both patch area and connectivity on occupancy by *E. propertius* (Table 3-2; Figure 3-5.a and b; Chapter 2 tables 2-4.3, 2-5.3; Appendix C, Table C.3). Most meadows had a relatively low abundance of flowers (<30 on the abundance index; Figure 3-6) and these meadows were least likely to contain *E. propertius*.

The IFM model produced a substantially better fit to the data than did the logistic regression model with the same terms, when compared by means of AIC (Table 3-2). This implies that the inclusion of connectivity and the assumptions of an 'Allee effect' and a 'rescue effect' provides a better explanation of occupancy than did the simpler linear models. Given the better fit of the IFM model, which assumes spatial structure is important, it is reasonable to conclude that some form of metapopulation effects are occurring. The version of the IFM including flowers provided the best fit model to the data (Table 3-2), demonstrating strong evidence for the importance of including this habitat quality measure, as well as putting it in a spatial context, for predicting butterfly occurrence. Results show that increasing availability of flower resources increased the 'effective area' of patches, demonstrating that nonlinear models that make use of the structure of a well-tested theory can provide a better alternative to simple linear regression models (Table 3-2).

Table 3-2: Comparison of 'best fit' linear regression model for occupancy by *E. propertius* with the equivalent IFM model using the same data. Nonlinear regression with the IFM model fits the data best. As such there is virtually no support for alternative models (as measured by the Akaike weight - ω_i) that use only linear regression to explain patch occupancy, and little support for the model lacking habitat quality measures. Data are from Mt. Maxwell in 2003.

Model form	Residual deviance / Null deviance	AIC	ΔAIC	ω_i
Nonlinear regression: Eqn. 5.2, with flowers (Q_i)	16.5/159.6	17.5	0	0.74
Nonlinear regression: Eqn. 5.2	18.5/159.6	19.6	2.1	0.26
Logistic regression: *Ai + Sij + flowers*	115.8/159.6	123.3	105.8	$7.86e^{-24}$
Logistic regression: *Ai + Sij*	129.1/159.6	134.7	117.2	$2.63e^{-26}$

NOTE: *Ai*= Patch area, *Sij* = Connectivity.

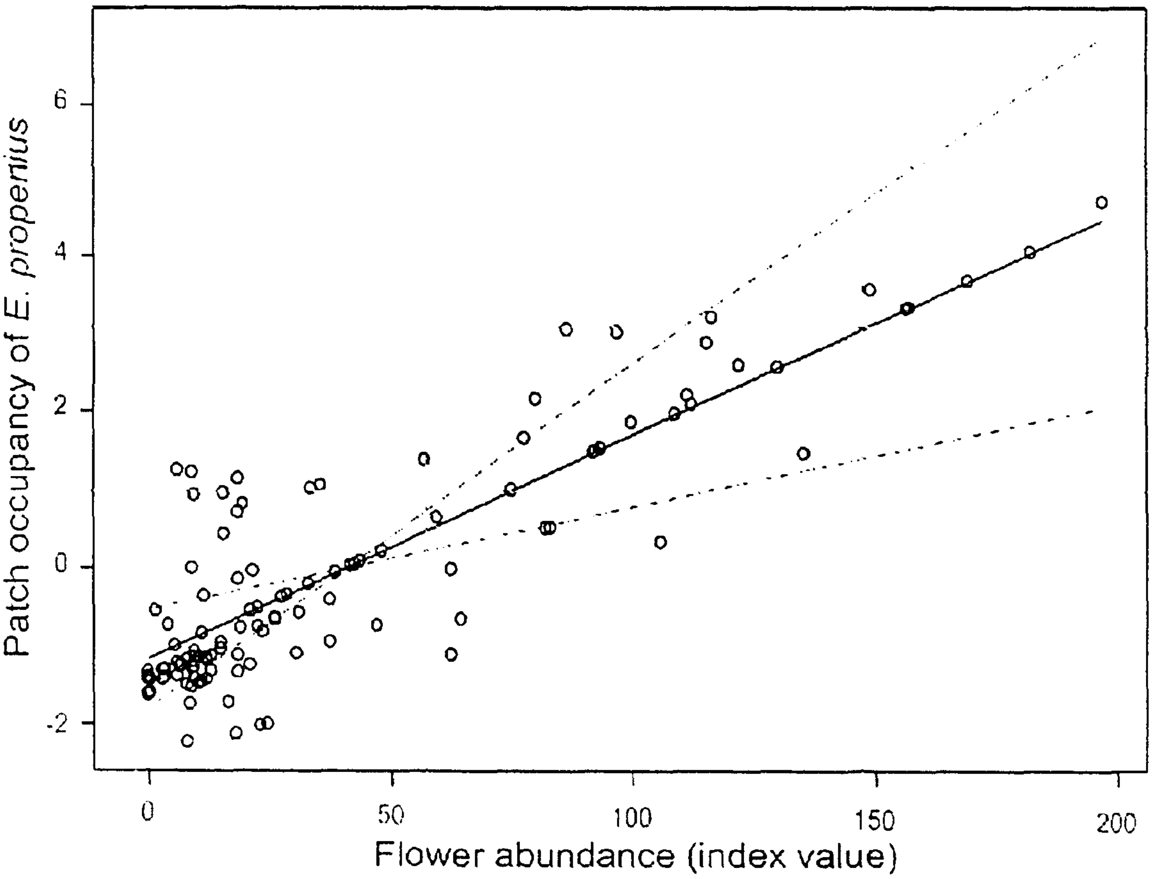
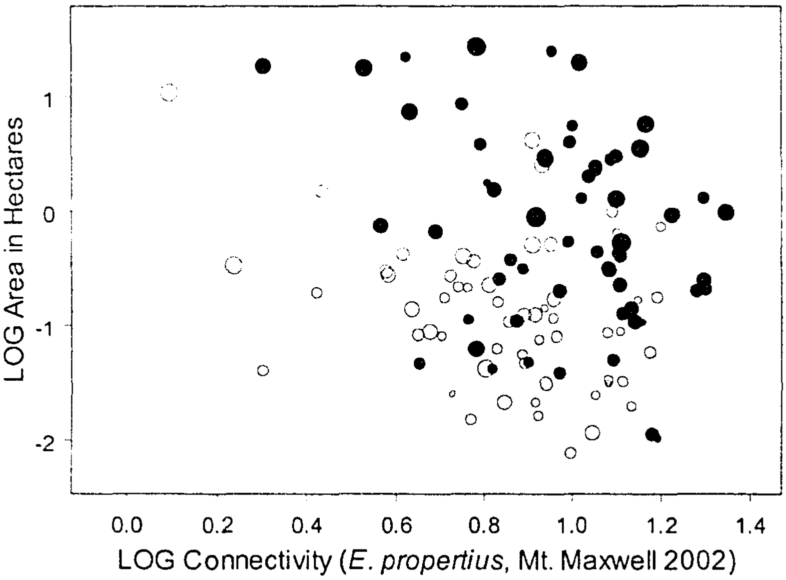
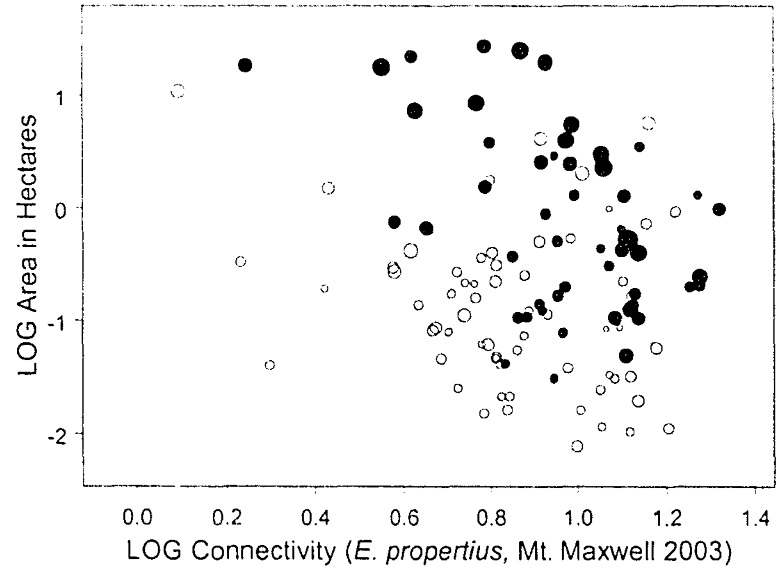


Figure 3-4: Best fit GLM model of effect of increasing availability of the general floral resources on patch occupancy of the butterfly *E. properties* for Mt. Maxwell 2002. The coefficient for flowers in this model was 0.0206 +/- 0.008 SE. The equivalent model averaged coefficient for flowers across all candidate models for Maxwell 2002 was almost identical, at 0.0203 +/- 0.00796 SE.



a)



b)

Figure 3-5: Patch occupancy by *E. propertius* as a function of increasing area and connectivity. Larger points represent sites with greater flower abundance, and filled circles are sites where *E. propertius* was present. Data are from a) Maxwell 2002, and b) Maxwell 2003.

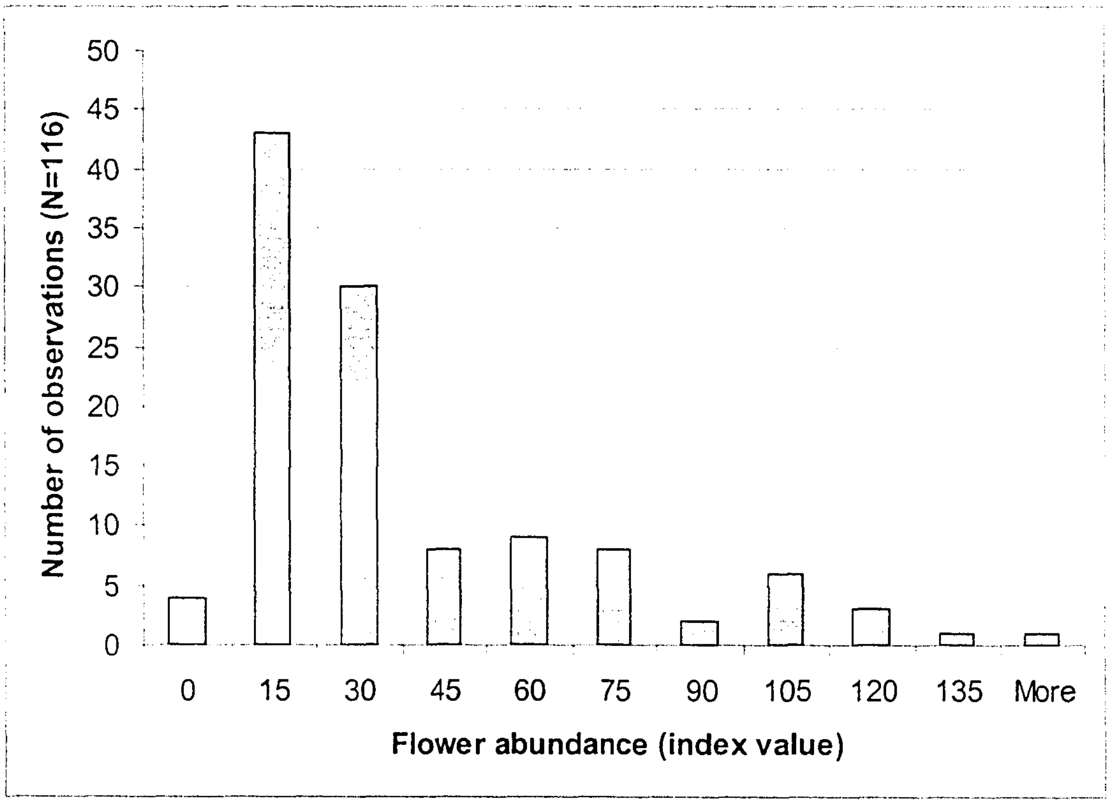


Figure 3-6: Frequency distribution of flower abundance in the Mt Maxwell meadows in 2002. The average flower abundance in a meadow was 32, and most meadows (66.4%) contain a flower abundance lower than level 30.

Assumption of Equilibrium

There were 9 colonization events and 16 extinction events between 2002 and 2003 in the Mt. Maxwell network. There was no significant difference between these two turnover rates ($\chi^2_{0.05,1}=1.96$, $p=0.18$), implying that the current state can be considered to be within the bounds of a quasi-stationary equilibrium state, and that use of the metapopulation model was valid.

Sensitivity Analysis

Meadows differed in their sensitivities to changes in colonization and persistence probabilities, as estimated from the transitions matrix generated using the IFM model. A detailed meadow-by-meadow discussion is not warranted, however, those meadows that were centrally located (Figure 3-7) were more important to the overall metapopulation, likely because they were the most well-connected. In addition, the larger meadows that, by virtue of their size, tend to produce more emigrants, are also in the center of the network. One of these large central meadows had the highest sensitivity value and could thus be considered the 'most important' in the metapopulation. Interestingly, some of the smaller, more centrally located, and well-connected meadows were found to provide greater contribution to the metapopulation importance than did many of the larger meadows (Figure 3-7). These smaller meadows had the highest sensitivity values, implying that they may be key 'stepping stones' in the network.

Prospective Analysis of Loss of Flower Abundance

The two prospective perturbation analyses resulted in predictions that help define which patches would impact the butterfly metapopulation most if there were a change in flower abundance. The prospective analysis for the effect of flower loss defines sites where loss of flowers would have the most detrimental effect on the butterfly metapopulation. Reduction in flowers has a greater effect if it occurs in the central meadows (Figure 3-8). This is because these meadows had both a high sensitivity *and* a large potential for drop in flower abundance. The large effect on the butterfly metapopulation from loss of the flowers at these sites occurs because they are some of the highly sensitive key interconnection points in the butterfly metapopulation, *and* because they are currently relatively undisturbed, with relatively high flower abundance. The meadow that had the highest sensitivity (meadow #44) was also predicted to be of greatest importance for protection from further flower loss, though the relative ranking of other meadows shifted when comparing the prospective and sensitivity analysis. This meadow is also heavily invaded on the southwest side by Scotch broom, which has been found to have dramatically negative effects on cover of native flowering plant species (Erickson, 1996; Parker *et al.*, 1997), and butterfly habitat use at a local within patch scale (Hays *et al.*, 2000). Since flower abundance is the most important predictor of occupancy by the butterflies, and broom negatively influences the flower abundance, meadow #44 may be a good site from which to remove this weed before further adverse impacts on the flowering plants occur at this location and potentially reduce butterfly habitat. Several other large and centrally located meadows (#39 and #42), and to a lesser degree several smaller meadow (#1, #3, #6, and #103) were also predicted to be good candidates for preventative efforts aimed at conserving the current level of flower abundance (Figure 3-8).

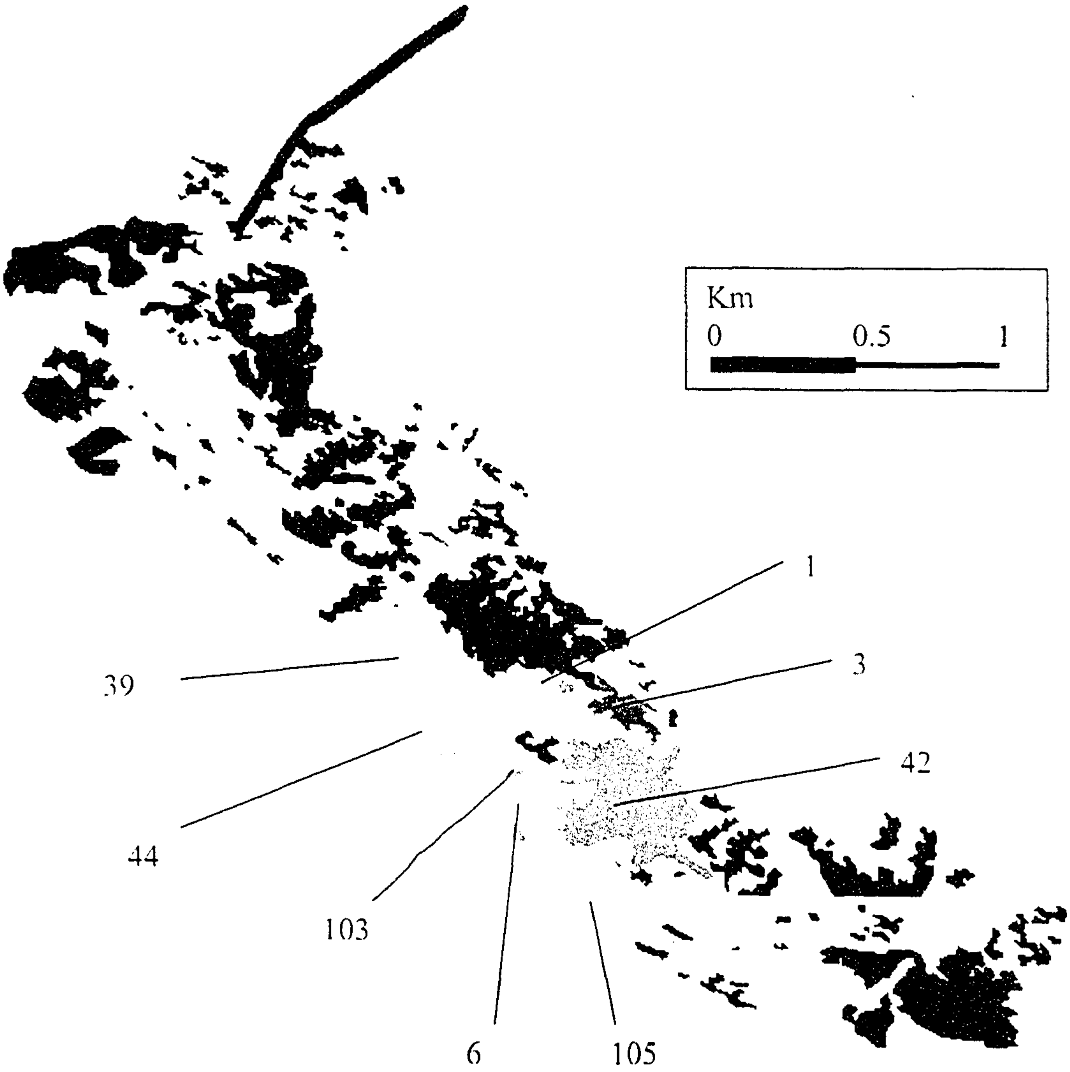


Figure 3-7: Mapped sum of matrix sensitivities values for each meadow of the Mount Maxwell network – Lighter shading represents those meadows where a change in colonization probability or extinction probability would cause the greatest change in the metapopulation capacity, λ_M.

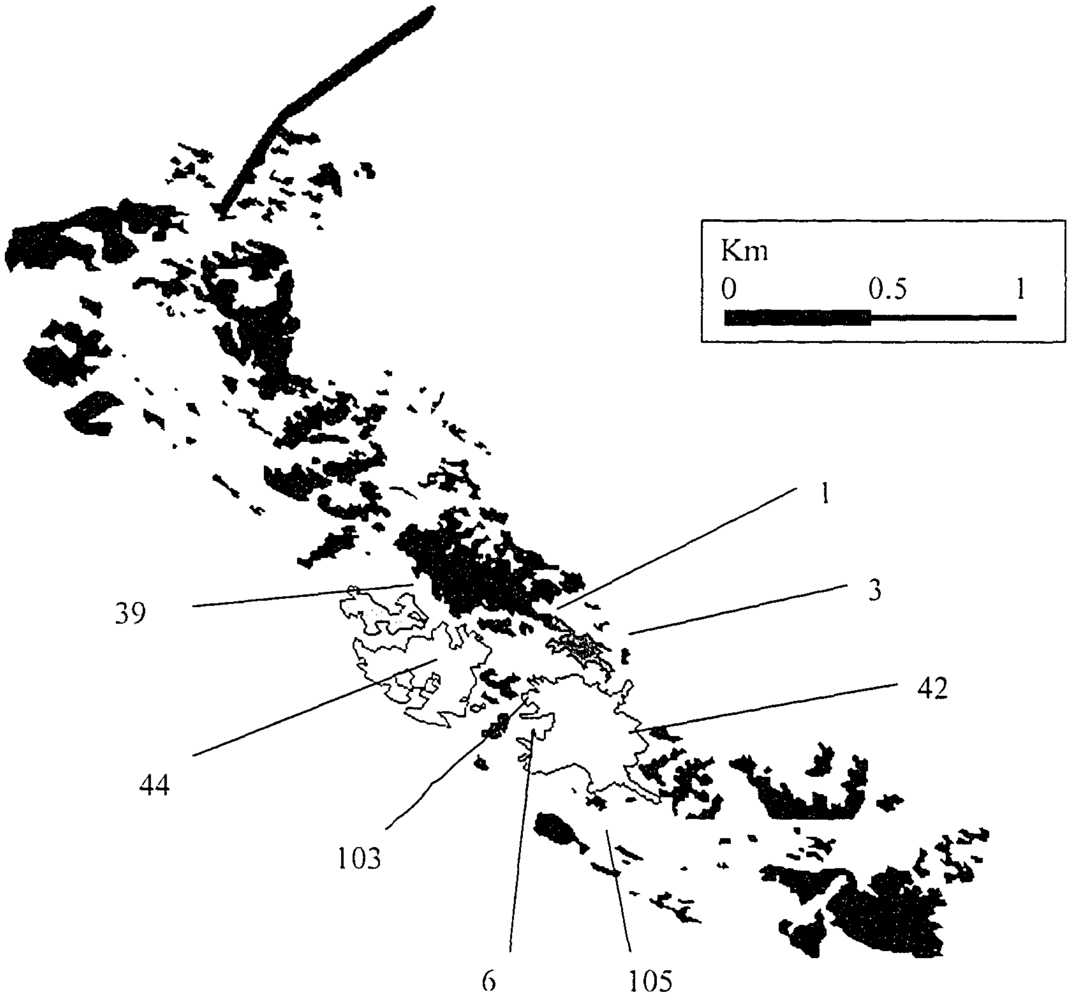


Figure 3-8: Mapped sum of matrix values for each patch with regard to projected changes due to loss/removal of flowers – Represents meadows where a change in colonization probability or extinction probability due to loss of flower abundance would cause the largest loss in the metapopulation capacity, λ_M.

The high importance ranking of large and central meadows in this prospective analysis relative to the high ranking of smaller stepping stone sites in the sensitivity analysis is due to the greater potential for loss of carrying capacity in populations located in the larger meadows. The results highlight the difference between sensitivity analysis, which looks at only the role of connectivity, area, and current meadow quality in determining meadow importance to the metapopulation, versus prospective analysis, which also considers the effect of hypothetically changing (in this case lowering) quality.

Prospective Analysis of Increased Flower Abundance

Increasing the abundance of flowers produced somewhat different results than did flower removal (compare Figure 3-9 with Figure 3-8). Meadows with the highest potential increase were again those meadows in the central part of the network, but the rankings of these meadows differed. Again, meadow #44, with the extremely high sensitivity value, was the most important in terms of addition of flowers as well. Given the known negative influence of broom on flowering plants (Erickson, 1996; Parker *et al.*, 1997), this implies that removal of broom and subsequent revegetation at this site would be the most beneficial action for the overall butterfly metapopulation. Interestingly, one of the smallest meadows turned out to be next most important in terms of the effect of increasing flower abundance. This meadow (#103) was relatively dry and rocky which may account for the low value it currently has as a reservoir of adult butterfly food (implied by the high value in Figure 3-9), but it is in a strategic location within the meadow network, and likely acts as a key stepping stone (Figure 3-7). Additions of flowers to this site should thus boost the overall connectedness of the network for less effort than doing the same elsewhere. Several other large meadows that are also centrally located (#39 and #42) were predicted to have strong effects if flowers increase. Both meadows have high broom cover and may be poor in flower abundance as a result. In order to improve the viability of the overall butterfly metapopulation, these meadows and meadow #44 would be the most important ones for habitat enhancement. Comparing reduction to the addition of flowers, shows that, for *E. propertius*, the most important meadows in which losses of flowering plants should be prevented differ somewhat from those in which it would do the most good to enhance flowering plant abundance. Meadow #44 was ranked very highly by both analyses and as such seems to be the most important meadow with regard to both considerations.

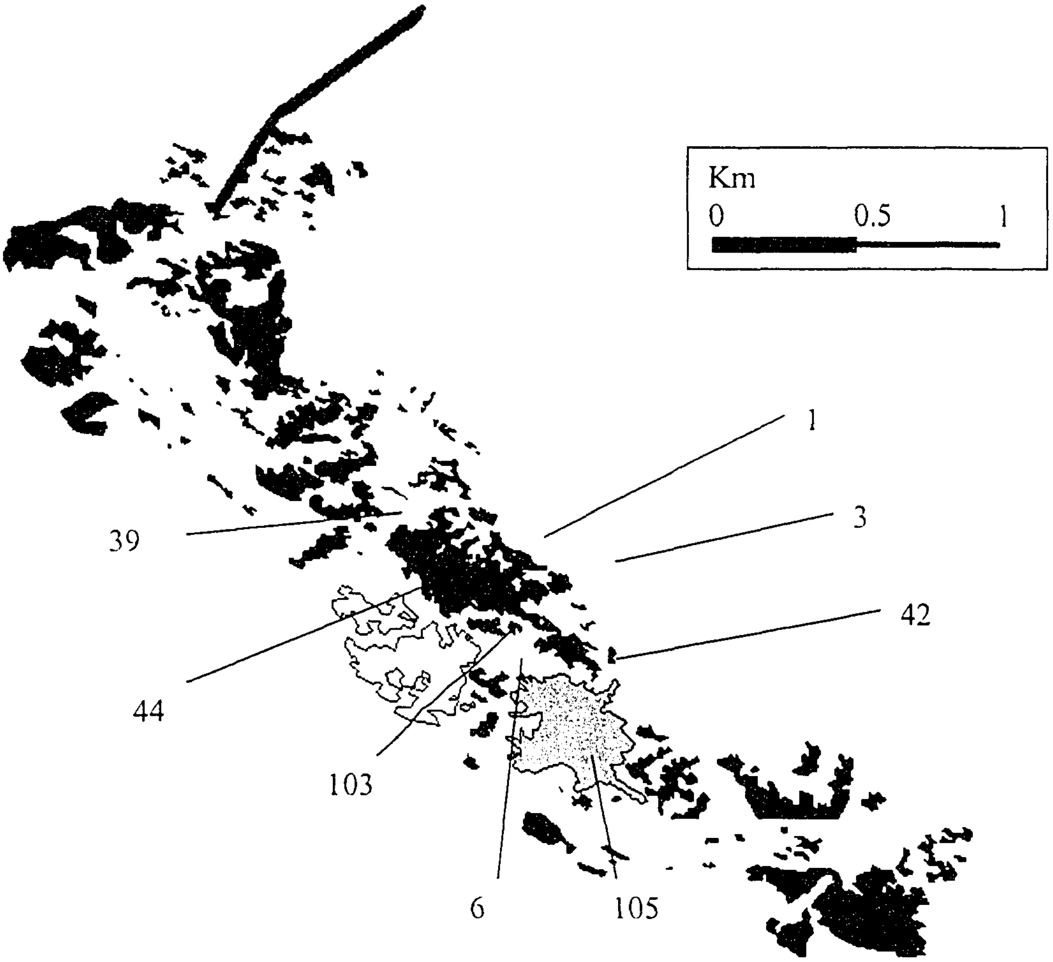


Figure 3-9: Mapped sum of matrix values for each patch with regard to projected changes due to increase in flowers - Represents meadows where a change in colonization probability or extinction probability due to increased flower abundance would cause the largest loss in the metapopulation capacity, λ_M.

DISCUSSION

Two applied questions were asked of this analysis; 1) in which meadows would loss of the important adult flower resources have the most detrimental impact for the overall metapopulation, and 2) in which meadows would the enhancement of flower resources have the most beneficial impact? The answers are provided by the sum of each column *i* in the prospective matrices. This sum represents the total contribution of meadow *i* to the overall metapopulation, given the magnitude of the treatment under consideration. For example a meadow may have a high sensitivity due to its' large area and its' high connectedness within the landscape. However, it may already have abundant flowers in it, and so, it is not possible to 'treat' or 'improve' the meadow any further. In contrast, a meadow currently with low abundance of flowers and a high sensitivity will result in a large product in the final $\Delta\lambda$ / Δflowers index, since it had both a high Δa_{ij} from change in the hypothetical level of flowers, and a high sensitivity due to its relatively large influence in the metapopulation. Neither the large difference alone, nor the large sensitivity alone, are particularly important; it is the *product* of the two that must be large. Based on this model, we can prioritize which meadows are most important in the metapopulation.

Nectar sources are generally known to be the most important food source for adult butterflies, although there are example of butterflies' nectaring at other food sources such as dung, rotting fruit, sap, aphid honeydew, and carcasses (Pivnick and MacNiel, 1987; Boggs, 1997). Flowers play an important role in the biology of butterflies, as Murphy (1983) and Boggs (1997) both found that females with greater access to nectar produce more and better quality eggs. Immigration of *Parnassius smintheus* adults was highest into sites with high availability of flowers (Matter and Roland, 2002), implying that movement is in part a response to flower abundance. In Chapter 2, I found that flower availability was an important determinant of patch occupancy by *E. propertius*. Since connectivity was also identified as important, a metapopulation model, including variable flower availability, was tested and found to produce better results in predicting patch occupancy than did models without metapopulation structure or without adjusting the metapopulation model to account for habitat quality.

The relatively strong correlation of *E. propertius* with flowers in the regression meant that the amount of improvement, or loss, need not be large to have a large effect, since the effect of changing the flower abundance was strongly positive over the range of values observed at Mt. Maxwell (it was not 'topped out' until approximately a flower index value of 300 [Figure 3-10.a], which was double the highest observed value, [Figure 3-10.b]). A similar positive effect of flowers on patch occupancy was observed to occur in the cases of two other butterfly species, *C. ladon* and *I. mossii* ssp. *mossii* (Chapter 2) and on habitat selection by another butterfly species *Parnassius smintheus* (Matter and Roland, 2002). Given this common result of the importance of abundance of floral food resources for adult butterflies, the type of analysis presented here is directly applicable to other butterfly or pollinator species.

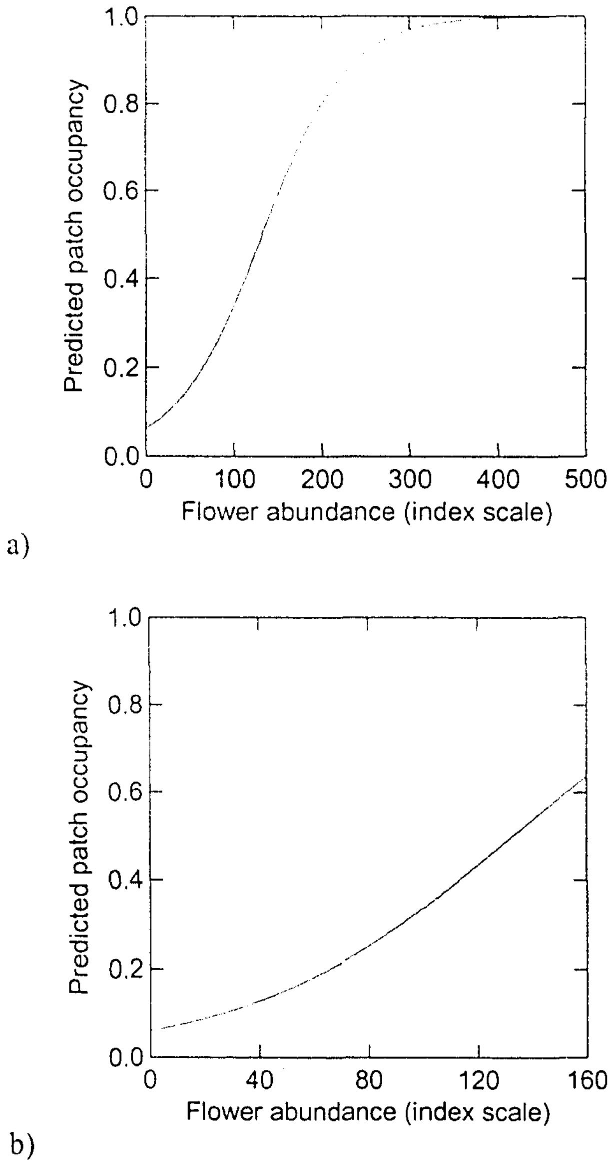


Figure 3-10: Predicted patch occupancy of *E. propertius* as a function of flower availability, based on model coefficients for *E. propertius* patch occupancy in the Mt Maxwell network in 2002: a) predicted occupancy rate for full range of occupancy probability, b) Predicted occupancy rate within the range of observed values for flower abundance at the Maxwell site in 2002.

The results of the hypothetical projection analysis are quite simple, based as they are on a relatively uncomplicated regression analysis of patch occupancy, floral abundance and meadow connectivity, the implicitly observed migration ability of *E. propertius*. It is important to note that the Mt. Maxwell meadow network is something of an anomaly in that both the largest and the most connected meadows are found in the center of the network. The most sensitive meadows for *E.propertius* are these meadows as well. Of course, predictions form the model are landscape specific, and the results may be much less intuitive in another meadow network. For example, meadows with the highest sensitivities may not be all clumped in the center of the network if the patch arrangement is different, and several very small meadows may play a key 'stepping stone' role, as observed for some of the Mount Maxwell meadows in the sensitivity analysis (Figure 3-7). In addition, if the distribution of the resources is not matched to the sensitivities (as was observed here), and the sensitivities are all relatively equal, sites projected to have the most impact in a management plan may not be found simply by using the results of only a sensitivity analysis (Caswell, 2000). This is because using sensitivities alone does not account for the real world feasibility of changing the habitat quality. For example, a sensitivity analysis may demonstrate that changing the number of emigrants produced by a meadow has a very high sensitivity value, a nice mathematical result, until you realize that there may be no practical way to do so. The prospective analysis allows a manager to define what is possible within the bounds of the prospective analysis, and use this to 'screen' through which of the high sensitivities are most pragmatically modified.

This approach could also be used to determine if there is a subset of patches that provide nearly the same metapopulation capacity as the whole set. This would be very useful for the purpose of reserve design, where resources are only sufficient for a part of the patch network (Hanski and Ovaskainen, 2000; Tuck and Possingham, 2000). Such an analysis could also be used to assess which populations of a metapopulation of a pest or a weed is that which most influences the metapopulation (highest rank in the prospective analysis), and thus where to potentially implement control measures. The method could be extended to apply to use with taxa such as fish or amphibians, in order to define which sites should be restored in order to achieve the greatest overall benefit at a scale larger than simply the local site. The field of restoration biology is quite large (Schultz and Crone, 1998; Feist *et al.*, 2003; Leon-Cortes *et al.*, 2003; Wirth and Pyke, 2003) but currently lacks a framework by which to assess the neglected question of *where* restoration actions should occur.

In this study, large improvements in the model fit would most likely occur if the area term were replaced by a more exact measure of the resources available in the patches, such as the availability of food, shelter and/or mates. In terms of butterfly biology specifically, Dennis *et al.* (2003), made an exhaustive summary of factors that might be added to a metapopulation model, including; perching sites, predator exposure, wind levels, and pupation sites. In the case of *E. propertius,* patch occupancy is strongly correlated with abundance of the hostplant, *Q. garryanna* (Tables 2-4.3 and 2-5.3). Although this was almost as strong a correlation as that with the flower availability, I did not include it here, since effectively changing this factor in the real world would be difficult, time consuming, and costly due to the effort required to plant and grow the oak seedlings

The availability of flowers is strongly influenced by the cover of invasive weeds, including Scotch broom (Hays *et al.*, 2000; Parker *et al.*, 1997). Broom is a densely growing shrub and it shades out smaller flowering plant species (Williams, 1981; Waterhouse, 1988; Zielke, 1996; Ussery, 1997; Ussery and Kraanitz, 1998), and by doing so reduces adult butterfly nectar food availability by decreasing flower abundance (Hays *et al.*, 2000). Given the general importance of flower availability for butterflies found in this study (Chapter 2) and other studies of butterflies (Schultz and Dlugosch, 1999; Matter and Roland, 2002; Fred, 2004), and the known negative effect on these resources from spread of broom, it seems prudent to stop spread of it as soon as possible and to prevent further colonization of new meadow "habitat islands". This would have the dual benefit of preserving rare plant populations in the Gary oak ecosystem and benefiting the butterflies.

Negative effects of broom were not observed to occur strongly by this study (Chapter 2), likely because the scale at which the effect is occurring is at both larger (decrease in patch effective area affects metapopulation) and smaller (local area within a patch) scales than the patch measurement (presence/absence in each given patch) recorded here. There may be less use of a subsection of a meadow with dense Broom, but the butterflies may still continue to use the remaining un-degraded part of the meadow. Loss of habitat may not affect presence/ absence, but may affect absolute population size, and in turn could have a metapopulation level effect. For example, in studies of the difference in resolution power between presence/absence versus abundance studies, it has been noted that population losses of up to 50-60% may not be noticed as they do not affect the presence/absence surveying results (Strayler, 1999). One way to deal with this problem would be to stratify sampling within each meadow (Figure 3-11). This would require a mixed-model statistical approach to determine the effect of habitat quality, which would potentially be more accurate than simply using the patch average.

Another improvement would be to test for an effect of habitat quality on the extinction and colonization rates by looking at the turnover events (Sjogren-Gulve, 1991; Sjogren-Gulve and Ray, 1996; Fleishmann *et al.*, 2002). For example, Matter and Roland (2002) found positive correlations of flower availability with butterfly immigration into a patch, implying that sites with higher flower abundance will also be more readily colonized. If habitat variables such as percent cover of weeds, or incursion by forest were also quantified, then the effect of these factors may be examined and/or tested experimentally for correlations with extinction and colonization. Following the method of Sjogren-Gulve and Ray (1996), this was done for one turnover of generations for *E. propertius*, (Hallstrom, in prep./unpublished data). It appears that the spread of the weed Scotch Broom has a negative impact on the colonization events, but not on extinction events. These results could be used to modify the colonization and extinction functions separately (or the immigration and emigration rate parameters of a model with different structure), rather than assuming that they are both affected equally through changes in patch 'effective area' by a given habitat quality factor such as Broom or flowers.

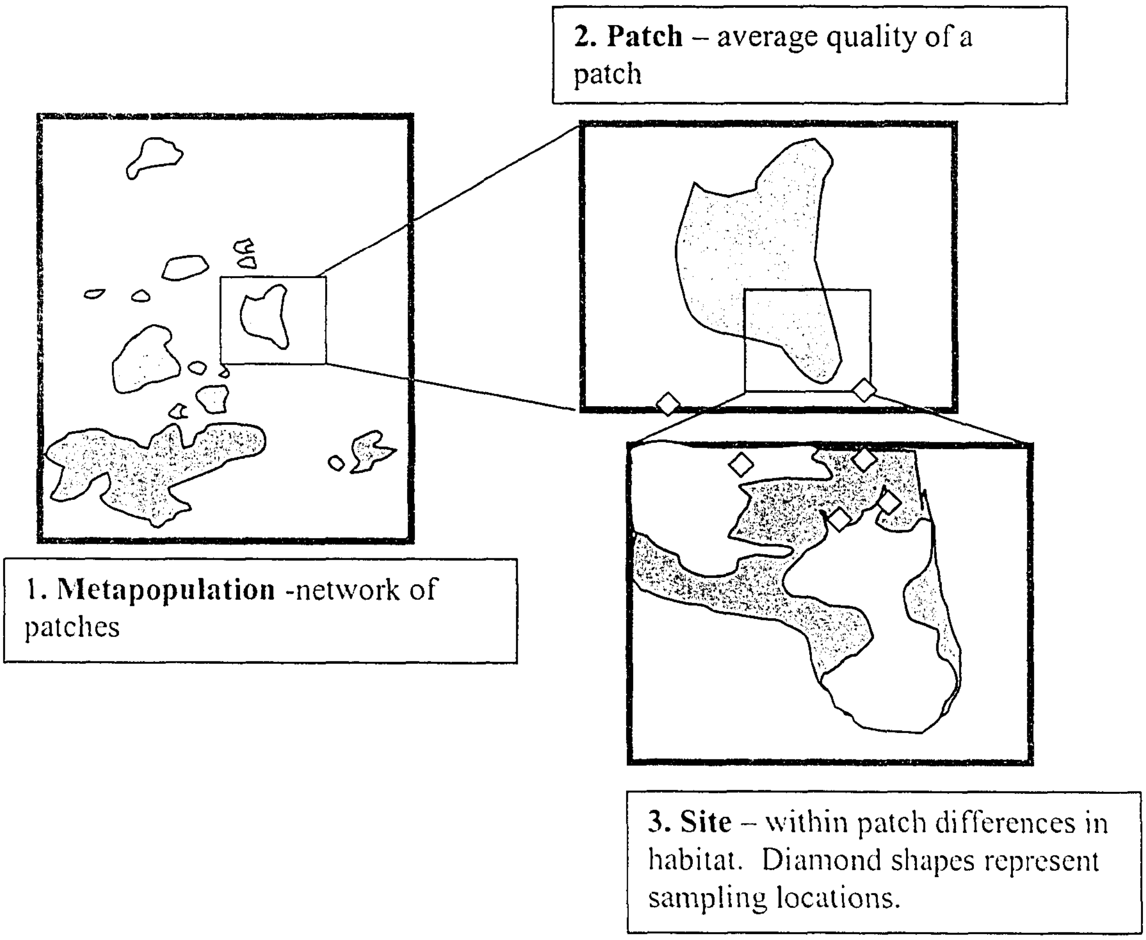


Figure 3-11: Scales of measurement that may affect the distribution of a species, and the outcome of results in metapopulation analyses. This study examined the top two levels of 1) metapopulation and 2) patch, by averaging habitat data obtained at the lowest level 3) site. Dark gray represents suitable habitat, light gray represents another category of habitat quality, such as degraded areas due to forest ingrowth, overgrazing, or invasion of a weed.

In the current study there was no account made for effects of intervening 'matrix' type, although this has been shown to be an important factor for other butterflies (Roland *et al.*, 2000; Rickets, 2001), and further improvements may be possible through inclusion of intervening 'matrix' habitat quality in the model. This may not be an important factor for all species, however, as a species may use diffuse resources, or the resources may be highly ephemeral in nature (Roslin, 2000). In this event it would be better to use a different modeling approach that allows the patch location and quality to vary with time (Wahlberg *et al.*, 2002; Berec and Konvicka, 2004).

This study demonstrated how to make use of nonlinear models and metapopulation capacity analysis to assess the importance of individual meadows in a network of habitat patches, and how to determine the effect on the metapopulation of changes in this network due to loss of or addition of habitat within the original patches of the network. It is one of the first studies to make applied use of the metapopulation capacity matrix analysis method to look at the impact of changing habitat quality on the metapopulation dynamics of a species. As well, it is the first study of which I am aware to use prospective analyses to project what effect changes in habitat quality would have on a metapopulation of a species of interest. Like other analyses (Jonsen, 2001; Wahlberg, 2002; Stockhausen and Lipcius, 2003; Berec and Konvicka, in press), this method will allow biologists to extend the use of metapopulation level analyses into the management realm.

LITERATURE

Akçakaya, H.R. 2000. Population viability analyses with demographically and spatially structured models. Ecological Bulletins 48:23-38.

Amarasekare, P. 1998. Allee effects in metapopulation dynamics. American Naturalist 152:298-302

Allee, W.C. 1938. The Social lives of animals. W.W. Norton and Co. New York.

Begon, M., J.L. Harper and C.R. Townsend. 1996. Ecology: Individuals, populations and communities. Blackwell, Cambridge, Massachusetts.

Berec, L., and M. Konvicka. 2004. Living in a dynamic landscape: forest management and conservation of an endangered woodland butterfly, (*Parnassius mnemosyne*). Journal of Applied Ecology IN PRESS.

Brommer, J., and M. Fred. 1999. Movement of the Apollo butterfly *Parnassius apollo* related to host plant and nectar plant patches. Ecological Entomology 24:125-131.

Brown, J.H. and A. Kodrick-Brown. 1977. Turnover rates in insular biogeography: effect of immigration and extinction. Ecology 58:445-449.

Burnham, K.P., and D.R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer, NY.

Caswell, H. 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. Ecology, 81(3): 619–627.

Caswell, H. 2001. *Matrix population models: construction analysis and interpretation.* Sinauer Assosc. Sunderland, MA.

Clinchy, M., D.T. Haydon, A.T. Smith. 2002. Pattern does not equal process: what does patch occupancy really tell us about metapopulation dynamics? American Naturalist 159(4): 351-362.

Crone, E., D. Doak, and J. Pokki. 2001. Ecological influences on the dynamics of a field vole metapopulation. Ecology 82(3): 831–843.

Dennis, R.L.H., and H. T. Eales. 1997. Patch occupancy in *Coenonympha tullia* (Lepidoptera: Satyridae): habitat quality matters as much as patch size and isolation. Journal of Insect Conservation 1: 167-176.

Dennis, R.L.H., Shreeve TG, and H. Van Dyck. 2003. Towards a functional resource-based concept for habitat: a butterfly biology viewpoint. Oikos 102(2): 417-426

Diamond, J.M. 1975. Assembly of species communities. IN *Ecology and evolution of communities* (Cody ML and JM Diamond, eds.), pp 342-444. Harvard University press, Cambridge.

Ellis, B. J. Mills, J. Childs, M. Muzzini, K. Mckee Jr., D. Enria, and G. Glass. 1997 Structure and floristics of habitats associated with five rodent species in an agroecosystem in central Argentina. Journal of Zoology-London 243:437-460.

ESRI. 1996. ARCview 3.2 User's Guide. ESRI, Redlands, CA, USA

Feist, B., E.A. Steel, G.R. Pess, and R.E. Bilby. 2003. Influence of scale on salmon habitat restoration priorities. Animal Conservation 6(3): 271-282.

Fleishmann, E., C. Ray, P. Sjogren-Gulve, C. Boggs, and D. Murphy. Assessing the roles of patch quality, area, and isolation in predicting metapopulation dynamics. Conservation Biology 16(3): 706-716.

Fred, M. 2004. Influence of resource distribution and abundance on population structure and dynamics of *Parnassius apollo.* PhD thesis, 118pp., University of Helsinki, Finland.

Fuchs, M. 2001. Towards a recovery strategy for Garry Oak and associated ecosystems in Canada. Environment Canada, Canadian Wildlife Service, Franzen Print Communications Ltd.

Gosselien F. 1999. Test of the mathematical assumptions behind the 'incidence function' estimation process of metapopulation dynamic parameters. Mathematical Biosciences 159: 21-32.

Guppy, C., and J. Sheppard. 2001. Butterflies of British Columbia. Royal British Columbia Museum Press, Victoria, BC.

Hanski, I. 1994. A practical model of metapopulation dynamics. Journal of Animal Ecology. 63:151-162

Hanski, I. 1999. *Metapopulation Ecology*. Oxford University Press. Oxford.

Hanski, I., and O. Ovaskainen. 2000. Metapopulation capacity of a fragmented landscape. Nature 404:755-758

Hays, D.W., A.E. Potter, C.W. Thompson, and P.V. Dunn. 2000. Critical habitat components for four rare south Puget Sound butterflies. Report prepared for Washington Department of Fish and Wildlife, and The Nature Conservancy of Washington, Seattle.

Hokit, D.G., B.M. Stith, and L.C. Branch. 2001. Comparison of two types of metapopulation models in real and artificial landscapes. Conservation Biology 15(4): 1102-1113.

Hokit, D.G., B.M. Stith, and L.C. Branch. 1999. Effects of landscape structure in Florida scrub: a population perspective. Ecological Applications 9(1):124-134.

Jonsen, I.D., R.S. Bourchier, and J. Roland. 2001. The influence of matrix habitat on *Apthona* flea beetle immigration to leafy spurge patches. Oecologia 127:287-294.

Johnson, J., and K. Olmand. 2004. Model selection in ecology and evolution. Trends in Ecology and Evolution 19(2):101-108.

Krauss, J., I. Steffan-Dewenter, and T. Tscharntke. 2004. Landscape occupancy and local population size depends on host plant distribution in the butterfly *Cupido minimus*. Biological Conservation IN PRESS.

Leon-Cortes, J.L., J.L. Lennon, and C.D. Thomas. 2003. Ecological dynamics of extinct species in empty habitat networks: the role of habitat pattern and quantity, stochasticity and dispersal. Oikos 102(3): 449-464.

Leslie, P.H. 1945. On the use of matrices in population mathematics. Biometrika 33:183-212.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America. 15:237-240.

Lewis, M. and P. Kareiva. 1993. Allee dynamics and the spread of invading organisms. Theoretical Population Biology 43:141-158.

Matter, S.F., and J. Roland. 2002. An experimental examination of the effect of habitat quality on the dispersal and local abundance of the butterfly *Parnassius smintheus*. Ecological Entomology 27:308-316.

Matter, S.F., and J. Roland, A. Moilanen, and I. Hanski. 2004. The migration and survival of *Parnassius smintheus*: Effects of the habitat matrix for individual butterflies. Ecological Applications. IN PREP

Macarthur, R.H., and E.O. Wilson. 1967. *The theory of Island biogeography*. Princeton University Press, Princeton.

Mitter, K., and T. Lea. 2004. Historical Garry oak ecosystems of the Cowichan Valley and Saltspring Island. 1:50,000 map. Biodiversity Branch, BC Ministry of Water Land and Air Protection. Victoria, BC.

Moilanen, A., and I. Hanski. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. Ecology 79(7):2503-2515

Moilanen, A., and M. Nieminen. 2002. Simple connectivity measures in spatial ecology. Ecology 84, 1131-1145.

Ovaskainen, O., and I. Hanski. 2003. How much does an individual habitat fragment contribute to metapopulation dynamics and persistence? Theoretical Population Biology 64:481-495

Ovaskainen, O. 2003. Habitat destruction, habitat restoration and eigenvector-eigenvalue relations. Mathematical Biosciences 181:165-176

Parker, I.M.,W.S. Harpole, and D. Dionne.1997. Plant community diversity and invasion of the exotic shrub *Cytisus scoparius*: Testing hypotheses of invasibility and impact. IN *Ecology and conservation of the South Puget Sound prairie landscape* (P.V. Dunn, and K. Ewing, eds.), pp.149-162, Seattle: The Nature Conservancy Press.

Price, M., R. Goldingay, L. Szychowski, and N. Waser. 1994. Managing habitat for the endangered Stephens' kangaroo rat (*Dipodomys stephensi*):Effects of shrub removal. American Midland Naturalist 131:9-16.

Ricketts, T.H. 2001. The matrix matters: effective isolation in fragmented landscapes American Naturalist 158: 87-99.

Roland, J., and P.D. Taylor. 1997. Insect parasitoids respond to forest structure at different spatial scales. Nature 386: 710-713.

Roland, J., N. Keyghobadi, and S. Fownes. 2000. Alpine *Parnassius* butterfly dispersal: effects of landscape and population size Ecology 81:1642-1653.

Roslin, T. 2000. Dung beatle movements at two spatial scales. Oikos 91:323-335.

Scheiman, D., E. Bollinger, and D. Johnson. 2003. Effects of leafy spurge on grassland birds. Journal of Wildlife Management 67(1):115-121.

Schultz, C.B., and E.E. Crone. 1998. Burning prairie to restore butterfly habitat: A modeling approach to management tradeoffs for the Fender's blue. Restoration Ecology 6: 244–252.

Schultz, C.B., and K.M. Dlugosch. 1999. Nectar and hostplant scarcity limit populations of an endangered Oregon butterfly. Oecologia 119:231-238.

Sjogeren-Gulve, P. and C. Ray. 1996. Using logistic regression to model metapopulation dynamics: large scale forestry extirpates the pool frog. Pages 111-137 in D.R. McCullough, editor. Metapopulations and wildlife conservation. Island, Washington, DC.

Sjogeren-Gulve, P. 1991. Extinction and isolation gradients in metapopulations: the case of the pool frog (*Rana lessonae*). Biological journal of the Linnean Society 42:135-147.

Sparrow, H.R., T.D. Sisk, P.R. Ehrlich, and D.D. Murphy. 1994. Techniques and guidelines for monitoring neotropical butterflies. Conservation Biology 8: 800-809.

Strayler, D.L. 1999. Statistical power of presence-absence data to detect population declines. Conservation Biology 13(5): 1034-1038.

Thomas, J.A. 1994. Why small cold-blooded insects pose different conservation problems to birds in modern landscapes. IBIS 137: S112-S119.

Thomas, J.A., N.A.D. Bourn, R.T. Clarke, K.E. Stewart, D.J. Simcox, G.S. Pearman, R. Curtis, and B. Goodger. 2001. The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. Proceedings of the Royal Society of London SERIES B 268:1791-1796.

Tuck, G. and H. P. Possingham. 1994. Optimal harvesting strategies for a metapopulation. Bulletin of Mathematical Biology 56:107-127

Tuck, G.N. and H. P. Possingham. 2000. Marine protected areas for spatially structured stock. Marine Ecology Progress Series 192:89-101.

Ussery, J.G. 1997. Managing invasive plant species in Garry oak meadow vegetation communities: a case study of Scotch Broom. MSc Thesis, Simon Fraser University, Vancouver, BC.

Ussery, J.G., and P.G. Kraanitz. 1998. Control of Scot's Broom (*Cytisus scoparius* (L.) Link.): the relative conservation merits of pulling versus cutting. Northwest Science 72(4): 268-273.

Verboom, J. and C.J.F. ter Braak. 1996. On deducing time parameters from spatial patterns: a critique on Hanski's 'practical metapopulation model'. IN *Fragmented populations: between theory and application in landscape planning*, (J Verboom ed.) pp 93-118. DLO Institute for Forestry and Nature Research (IBN_DLO), Wageningen, Netherlands.

Wahlberg, N., T. Klemetti, and I. Hanski. 2002. Dynamic populations in a dynamic landscape: the metapopulation structure of the marsh fritillary butterfly. Ecography 25:224-232

Walker, R.S., A.J. Novarro, and L.C. Branch. 2003. Effects of patch attributes, barriers, and distance between patches on the distribution of a rock-dwelling rodent (*Lagidium viscacia*). Landscape Ecology 18: 187-194.

Waterhouse, BM. 1988. Broom (*Cytisus scoparius*) at Barrington tops, New South Wales. Australian Geographical Studies 26:239-248.

Wiens, J.A. 1997. Metapopulation dynamics and landscape ecology. Pp. 43-62 In *Metapopulation Dynamics: Ecology, Genetics and Evolution* (I. Hanski and M. Gilpin, eds.). Academic Press, New York.

Williams, P.A. 1981. Aspects of the ecology of broom (*Cytisus scoparius*) in Canterbury, New Zealand. New Zealand Journal of Botany 19:31-43.

Wirth, T.A., and D.A. Pyke. 2003. Restoring forbs for sage grouse habitat: fire, microsites, and establishment methods. Restoration Ecology 11(3): 370-377.

Zielke, K., J.O. Boateng, N. Caldicott, and H. Williams. 1996. Broom and Gorse in British Columbia: a forestry perspective problem analysis. Silviculture Branch, Ministry of Forests, Victoria, BC.

CHAPTER 4

General Conclusion

RESULTS AND DISCUSSION SUMMARY FOR CHAPTER TWO

Logistic regression found that the explanatory variables of connectivity and flower abundance had consistently positive effects of all three species studied (Chapter 2). Hostplant density also had a positive effect on occupancy by *Incisalia mossii* ssp *mossii* and *Erynnis propertius*, in half the models for each species, but was not strongly related to occupancy by *Celastrina ladon*, showing a positive effect in only one instance. The effects of patch area were as common, occurring in 4/10 models (as did hostplant effect), but were not as strong as those of hostplant density, explaining less of the total model deviance (Tables 2-5.1, 2-5.2, and 2-5.3). Area had a positive effect for two species (*I. mossii* ssp *mossii* and *E. propertius*), but was less consistent in the case of the third species, *C. ladon* where there was a positive effect in one year but a negative effect in another instance. The weed Scotch Broom was found to have no biologically meaningful effect on occupancy of either *I. mossii* ssp *mossii* or *C. ladon*, though this habitat attribute was positively associated with occupancy by *E. properties.*

The consistent positive effects from hostplant and nectar food sources are not surprising given the primary role of these food sources in defining the survival of each of these species. Since connectivity had a strong positive influence on patch occupancy in all three species and the scale of separation between patches in similar to the scale of dispersal limitation for each species as defined by their dispersal kernels (Chapter 2, Chapter 3) and dispersal of similar species (Bidwell, 1995; Fuchs, 2001; Gutierrez et al, 1999), this implies that a metapopulation effect is occurring and determining the distribution of populations of these species. Patch area was likely a significant predictor of patch occupancy since larger sites are more likely to contain heterogeneities that allow some buffering of populations against changing conditions (Kindvall, 1996), and because the population is larger at a larger site (Begon et al, 1996), and thus more resilient to stochastic catastrophic events (Hanski, 1994). In the case of the species *C. ladon*, for which area was not a significant predictor, this could be due to the ability of the host plant of this widespread butterfly species to exist at low densities in the conifer forest, thus allowing *C. ladon* to survive in a more continuous manner across the landscape rather than being confined to discrete habitat patches as are the other two species with more restricted hostplant ranges. As well, the weak overall predictive power of patch area is likely due to the fact that it does not account properly for between patch variation in habitat quality. The attribute of hostplant density explained species occurrence as well or better than the patch area, and flower abundance was a much better predictor than patch area, being the best of those variables tested. Overall, host plants, flowering plants, and patch connectivity explained the largest part of the variance in the occurrence data for all three species. The importance of the connectivity variable is likely related to metapopulation effects, with the more colonizations observed to occur in years when the connectivity measure was also of significance as a predictor of patch occupancy. This implies that connected sites were more likely to be colonized, while the host plant and flower plant variables relate to the response of the butterflies to quality of the sites.

The inconsistency of the results for effect of Scotch broom have several possible explanations. First, in hindsight, the haphazard nature of the butterfly transect sampling to observe presence/absence of populations in each meadow was not the best method possible for definition of the effect of this weed on butterfly habitat use. A mixed model approach incorporating both within and between habitat patch effects would have been preferable since this would have defined the role of the habitat quality more precisely, given that neither broom, nor hostplants, nor flowers cover a given meadow equally but instead grows in varying density at different locations within a patch.

RESULTS AND DISCUSSION FOR CHAPTER THREE

The results of the logistic regression were subsequently used to build a predictive IFM metapopulation model for *E. propertius*, which placed the habitat quality of each patch into a spatial context. To begin, a basic IFM including only patch area and isolation was compared to the fit of the logistic regression and found to provide a much better fit to the data (Chapter 3). When this IFM model was modified to include a measure of nectar plant availability, there was a further improvement in the fit of this model. These results further support the implication that metapopulation effects are occurring, and that habitat quality is playing a significant role in the metapopulation dynamics.

Sensitivity analysis showed that at the current level of flower availability certain smaller meadows located in the interstities between larger meadows were playing a key role in the metapopulation as 'stepping stones'. Extension of this analysis into a prospective analysis determined where changes in the local habitat quality, as measured by flowering plant availability, would have the greatest impact on the butterfly metapopulation. This method allowed predictions to be made of where this effect of changing flowering plant availability would have the greatest impact on the metapopulation in terms of both losses and additions to the flowering plant levels in each meadow (Chapter 3). Specific ranking of each meadow could be done with this method, but given that limited resources will likely be available, picking the top few sites where management actions will have the most benefit is probably more worthwhile.

These results are interesting because by allowing both habitat quality and patch connectivity to both be assessed simultaneously, this method provides a significant improvement over the current method of assessing the roles of either habitat quality or patch connectivity in isolation from each other. Thus, in a broad sense, this type of model is likely to prove useful in many other applications ranging from defining which patches to treat for pest management at a metapopulation scale, to designating marine reserves to maximize fisheries catches, and conservation of endangered species existing in a network of discrete habitat patches.

CONCLUSIONS

The regression analysis found flower abundance to be one of the strongest variables with an effect of the butterfly patch occupancy of all three species (Chapter 2). This effect was not surprising given the abundant literature describing the importance of nectar availability for butterflies (Matter and Roland, 2002; Fred, 2004; Schultz and Dlugosch, 1999). Hostplants were found to be the best predictor of species distributions for the rarest butterfly species *I. mossii*, and this appears to be the strongest driver of rarity among the butterfly species in this study.

The sensitivity analysis and prospective analyses proved useful in allowing both the habitat quality and metapopulation effects to be simultaneously accounted for in assessing the role of individual patches. The most important meadow site in terms of both loss and addition of nectar flower availability in the metapopulation analysis was meadow #44, and it is recommended that this site be the focal point of conservation and restoration efforts aimed at improving butterfly habitat in the Mt. Maxwell meadow network. Given limited resources, this is a good point at which to start, until further resources possibly become available at a later date. As well, this meadow site and the adjacent meadow #39 and #42 are at the front edge of an expansion of the weed Scotch broom on Mt Maxwell. Given that many other studies of floral composition have found that this plant negatively impacts the native flower species (Erickson, 1996; Ussery, 1997 and 1998; Hays et al, 2000), restoration efforts aimed at removing this plant will likely have a dual benefit for both the plants and butterflies that rely on them. Both the native plants and the butterflies are likely to benefit from removal of this weed at these particular sites and following up with revegetation efforts and suppressive treatments to inhibit it from becoming reestablished. This is likely to be the single most effective method for boosting flowering plant populations in these meadows, and will have the added benefit of stopping or slowing the advance of this weed into these and other meadows where it would reduce native plant populations and negatively affect the butterflies.

LITERATURE

Begon, M., M. Mortimer, and D.J. Thompson. 1996. *Population ecology: a unified study of animals and plants*. Blackwell Science Ltd. Cambridge.

Bidwell, A.D. 1995. Karner Blue butterfly (*Lycaeides melissa samuelis*) dispersal and habitat disturbance at Fort McCoy military reservation, Wisconsin. M.S. thesis, University of Wisconsin, Stevens Point.

Erickson, W. 1996. Classification and interpretation of Garry oak (*Quercus garryanna*) plant communities and ecosystems in southwestern British Columbia. MSc thesis, University of Victoria.

Fred, M. 2004. Influence of resource distribution and abundance on population structure and dynamics of *Parnassius apollo*. PhD thesis, 118pp., University of Helsinki, Finland.

Fuchs, M. 2001. Towards a recovery strategy for Garry Oak and associated ecosystems in Canada. Environment Canada, Canadian Wildlife Service, Franzen Print Communications Ltd.

Gutierrez, D. C.D. Thomas, and J.L. Leon-Cortes. 1999. Dispersal, distribution, patch network and metapopulation dynamics of the dingy skipper butterfly (*Erynnis tages*). Oecologia 121:506-517.

Hanski, I. 1994. A practical model of metapopulation dynamics. Journal of Animal Ecology 63: 151-162.

Hays, D.W., A.E. Potter, C.W. Thompson, and P.V. Dunn. 2000. Critical habitat components for four rare south Puget sound butterflies. Report prepared for Washington Department of Fish and Wildlife, and The Nature Conservancy of Washington, Seattle.

Kindvall, O. 1996. Habitat heterogeneity and survival in a bush cricket metapopulation, Ecology 77:207-214.

Matter, S., and J. Roland. 2002. An experimental examination of the effect of habitat quality on the dispersal and local abundance of the butterfly *Parnassius smintheus*. Ecological entomology 27:308-316.

Schultz, C.B., and K.M. Dlugosch. 1999. Nectar and hostplant scarcity limit populations of an endangered Oregon butterfly. Oecologia 119:231-238.

Ussery, J.G. 1997. Managing invasive plant species in Garry oak meadow vegetation communities: a case study of Scotch Broom. MSc Thesis, Simon Fraser University, Vancouver, BC.

Ussery, J.G., and P.G. Kraanitz. 1998. Control of Scot's Broom (*Cytisus scoparius* (L.) Link.): the relative conservation merits of pulling versus cutting. Northwest Science 72(4): 268-273.

APPENDIX A: Large scale regional maps

Figure A.1: Map of historical distribution of Garry oak ecosystems in the study region (used with permission from Mitter and Lea, 2004 – see Chapter 3 literature cited for details).

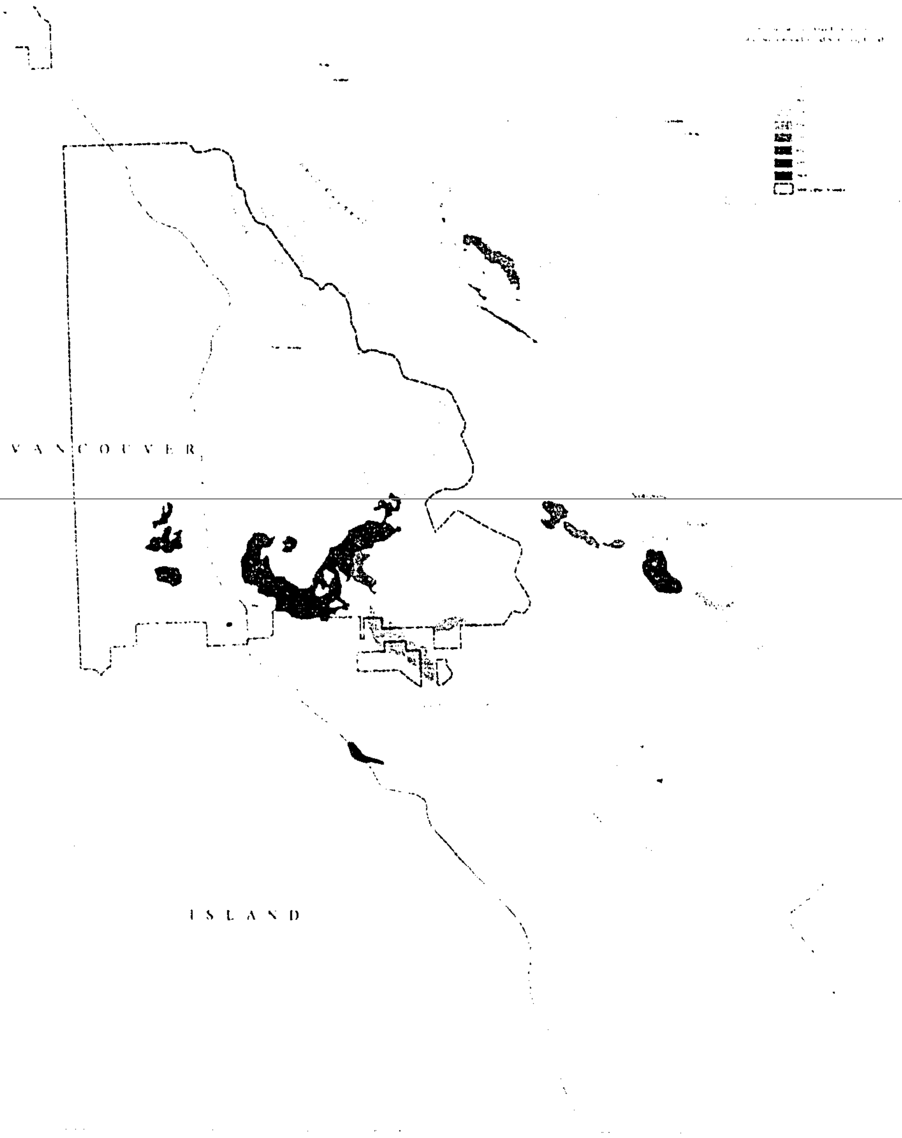
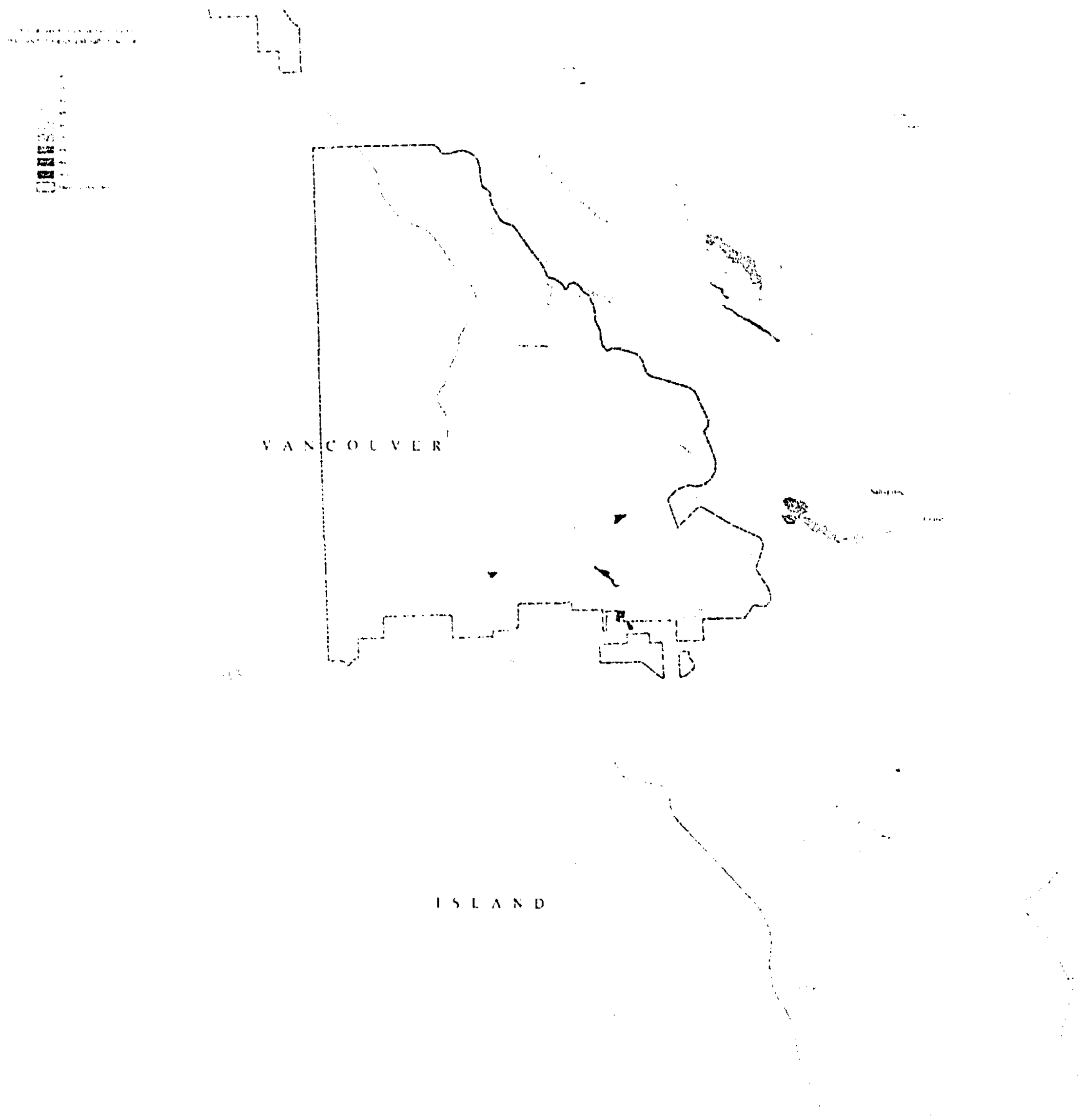


Figure A.2: Map of historical distribution of Garry oak ecosystems in the study region (used with permission from Mitter and Lea, 2004 – see Chapter 3 literature cited for details).



APPENDIX B: list of flower species observed. Species marked with a * were commonly observed.

_Holodiscus discolor_*
_Rumex acetosella_*
_Sedum spathulifolium_*
_Geranium molle_*
Ranunculus occidentalis
_Taraxacum officinale_*
_Achillea millefolium_*
_Veronica beccabunga americanum_*
_Lotus microanthus_*
_Medicago lupulina_*
_Vicia sativa_*
_Trifolium wormskjoldii_*
_Trifolim repens_*
_Erodium cicutarium_*
_Collinsia parviflora_*
_Lupinus polycarpus_*
Cammassia quamash
Zygadenus venenosus
_Alluim acuminatum_*
Allium cernuum
Brodieae hyacinthine
Brodieae coronaria
Erythromuim oregonum
Fritillaria lanceolata
_Dodecatheon hendersonii_*
Claytonia sibirica
Viola adunca
_Cytisus scoparius_*
Lomatium utriculatum
_Mimulus guttatus_*
_Cerastium arvense_*
_Plectris congesta_*
Plectris macrocera
Castilleja miniata (hispida?)
_Gaultheria shallon_*
Lonicera ciliosa
Lonicera hispidula
_Vaccinuim parvifolium_*
Fragraria chiloensis
_Galium trifolium_*
Rubus parviflorus
_Silene vulgaris_*
Goodyeria oblongifolia
Heiracium spp*
Balsamorhiza deltoides
_Rosa nutkana_*
Matricaria discoidea
Epilobium angustifolium
Sambucus racemosa
Cornus nuttallii
Orobanche uniflora
Arabis spp*
Prunus spp
_Moneses uniflora_*
Delphinium menziesii
_Denathe sarmentosa_*
_Madia sativa_*
Linanthus bicolor
Ulex europaeus
Ribes sanguineum
_Lithophragma parviflorum_*
_Capsella bursa-pastoris_*
_Thlaspi arvense_*
_Linaria vulgaris_*
Malus fuscs
_Anaphalis margaritacea_*
_Haplopappus hallii_*
_Lactuca muralis_*
_Cirsum arvense_*
Crataegus douglassii
Urtica dioica
Satureja douglassii
_Prunella vulgaris_*
_Lychnis coronaria_*
Linnea borealis
Leucanthemum vulgare
Oemleria cerasiformis
Opuntia fragilis
Aquilegia formosa
_Digitalis purpurea_*

APPENDIX C: Top GLM model coefficients and SE values used to produce AIC / model averaging results. Three tables, Table C.1 for *I. mossii* ssp. *mossii*, Table C.2 for *C. ladon* and Table C.3 for *E. propertius*.

Table C.1: Set of the top GLM models for each site-year of data for the butterfly species *I. mossii* ssp. *mossii,* with deviance explained/null deviance, df / null df, ΔAIC, Akaike weights (ω_i; (Burnham and Anderson, 1998), and model coefficients with standard errors (SE). Results are for surveys in both 2002 and 2003, and for only the Maxwell Mountain network due to the lack of data from Maple Mountain network for this species.

Model structure	**Deviance/ null dev.**	**Df / null df**	**ΔAIC**	ω_i	β_{NULL} (SE)	β_{BROOM} (SE)	β_{SEDUM} (SE)	$\beta_{CONNECT}$ (SE)	β_{AREA} (SE)	β_{FLOWER} (SE)	$\beta_{S\cdot B}$ (SE)	$\beta_{B\cdot F}$ (SE)
Maxwell 2002												
1. S + F + log(B) + log(A)	19.1 / 34.7	110 / 114	0	0.52	**-7.57 (2.63)**	-0.526 (0.273)*	0.109 (0.063)*	-	**1.331 (0.586)**	0.028 (0.016)*	-	-
2. S + F + log(B) + log(A) + C + B:S	18.1 / 34.7	108 / 114	0.8	0.35	**-6.77 (2.64)**	-0.33 (0.316)*	-0.099 (0.436)	-1.037 (5.71)	**1.31 (0.621)**	0.0256 (0.0154)*	-0.0503 (0.0951)	-
3. S + F + log(B) + log(A) + C	19.0 / 34.7	109 / 114	3.5	0.09	**-7.69 (2.73)**	-0.521 (0.272)*	0.0641 (0.064)*	1.22 (5.59)	**1.372 (0.635)**	0.028 (0.016)*	-	-
Maxwell 2003												
1. C + S	52.9 / 68.1	113 / 115	0	0.46	**-3.265 (0.511)**	-	**0.0889 (0.0352)**	**15.616 (5.03)**	-	-	-	-
2. C + S + F	52.6 / 68.1	112 / 115	1.3	0.24	**-3.45 (0.616)**	-	**0.08261 (0.0368)**	**14.81 (5.142)**	-	0.00451 (0.0075)	-	-
3. C + S + F + B	52.5 / 68.1	111 / 115	2.9	0.11	**-3.48 (0.627)**	-	**0.0371 (0.0371)**	**14.49 (5.244)**	-	0.00762 (0.0076)	-	-
4. C	58.2 / 68.1	114 / 115	3.7	0.07	**-2.812 (0.409)**	-	-	**14.07 (4.77)**	-	-	-	-
5. C + S + F + B + A	52.3 / 68.1	110 / 115	113 / 115	0.06	**-3.471 (0.627)**	-0.0128 (0.0283)	**0.069 (0.0371)**	**13.683 (5.465)**	-0.0451 (0.107)	0.0059 (0.0084)	-	-
Maple 2002												
NOT ENOUGH DATA	-	-	-	-	-	-	-	-	-	-	-	-
Maple 2003												
NOT ENOUGH DATA	-	-	-	-	-	-	-	-	-	-	-	-

NOTE: S=*S. spathulifolium* density, F=Nectar flower cover, B=Scotch Broom cover, A=Area in Hectares, C=Connectivity. All models implicitly contain an intercept (β_0). Coefficients (β_i's) are printed in the table in the same order as they appear in the model structure description column. Coefficients with an asterisk have χ^2 probabilities ≤0.10, coefficients printed in boldface type have χ^2 probabilities ≤0.05.

Table C.2: Set of the top GLM models for each site-year of data for the butterfly species *C. ladon*, with deviance explained/null deviance, df / null df, ΔAIC, Akaike weights (ω_i; (Burnham and Anderson,1998), and model coefficients with standard errors (SE). Results are for surveys in both 2002 and 2003, and for both Maple and Maxwell networks.

Model structure	**Deviance/ null dev.**	**Df / null df**	**ΔAIC**	ω_i	β_{NULL} (SE)	β_{BROOM} (SE)	$\beta_{HDISCOLOR}$ (SE)	$\beta_{CONNECT}$ (SE)	β_{AREA} (SE)	β_{FLOWER} (SE)	β_{HB} (SE)	$\beta_{BR\ FLWR}$ (SE)	$\beta_{H\ FLWR}$ (SE)	$\beta_{H\ AREA}$ (SE)
Maxwell 2002														
1. B + O+ F+ S + B:H	126.5 / 156.3	109 / 114	0	0.33	**-2.132 (0.51)**	-0.0265 (0.0249)	0.0181 (0.0151)*	**0.52165 (0.172)**	-	**0.01471 (0.0064)**	**0.01184 (0.0053)**	-	-	-
2. B + O+ F+ S + B:H + B:F	124.3 / 156.3	108 / 114	0	0.33	**-1.991 (0.52)**	-0.0706 (0.051)	0.0175 (0.015)*	**0.5014 (0.171)**	-	**0.01195 (0.0066)**	**0.0122 (0.0051)**	0.00143 (0.0011)	-	-
3. B + O+ F+ S + B:H + B:F + F:O	122.7 / 156.3	107 / 114	0.5	0.26	**-1.74 (0.56)**	-0.079 (0.053)	-0.00284 (0.0226)	**0.5035 (0.174)**	-	**0.003654 (0.0094)**	**0.01248 (0.0051)**	0.00165 (0.0011)*	0.000738 (0.0006)	-
2. B + O+ F+ S + A + B:H + B:F + F:O	122.7 / 156.3	106 / 114	2.8	0.08	**-1.752 (0.57)**	-0.079 (0.053)	-0.00271 (0.0227)	**0.5052 (0.175)**	0.00417 (0.048)	**0.003672 (0.0094)**	0.0125 (0.0051)	0.00163 (0.0012)*	0.000738 (0.0006)	-
Maxwell 2003														
1. B + F + log(A) + S + B:F + O:F	124.6 / 159.6	109 / 115	0	0.66	**-1.381 (0.57)**	0.04017 (0.024)	-	**0.3939 (0.11)**	**0.35 (0.15)**	0.0026 (0.009)	-	**-0.00108 (0.0005)**	**0.0096 (0.0043)**	-
2. B + F + log(A) + S + log(O) + B:F + O:F	124.5 / 159.6	108 / 115	2	0.24	**-1.386 (0.58)**	0.04 (0.024)	**0.0156 (0.124)**	**0.3912 (0.112)**	**0.35 (0.15)**	0.0028 (0.009)	-	**-0.00108 (0.0005)**	**0.0092 (0.0052)**	-
3. B + F + log(A) + S + log(O) + B:F + O:F + B:O + O:A	122.3 / 159.6	106 / 115	4.2	0.08	**-1.456 (0.61)**	0.078 (0.042)	**0.117 (0.2)**	**0.3737 (0.112)**	**0.32 (0.19)**	0.0033 (0.01)	-0.0291	**-0.00119 (0.0005)**	0.00922 (0.0059)*	0.0223 (0.08)
Maple 2002														
1. F + O + A + O:A	75.5 / 111.6	85 / 89	0	.50	**-0.353 (0.45)**	-	-0.02234 (0.0163)	-	-1.318 (0.348)	**0.0855 (0.022)**	**0.07255 (0.0228)**	-	-	-
2. S + F + O + A + O:A	74.7 / 111.6	84 / 89	1.1	.29	**-0.688 (0.6)**	-	-0.02285 (0.0166)	0.151 (0.171)*	-1.26 (0.351)	**0.08231 (0.0222)**	**0.071635 (0.0238)**	-	-	-
3. B + S + F + O + A + O:A	74.2 / 111.6	83 / 89	2.4	.15	**-0.643 (0.61)**	-0.0104 (0.014)	-0.0245 (0.017)	0.21 (0.193)*	-1.23746 (0.351)	**0.08062 (0.0224)**	**0.07402 (0.0255)**	-	-	-
4. B+ S + F + O + A + O:A + B:F	74.0 / 111.6	82 / 89	4.4	.06	**-0.63 (0.61)**	-0.0010 (0.019)	-0.02364 (0.0173)	0.2196 (0.197)*	-1.1971 (0.371)	**0.07628 (0.0255)**	**0.07258 (0.0276)**	0.00029 (0.0008)	-	-
Maple 2003														
1. log(B) + log(F) + log(O) + S	81.8 / 124.4	85 / 89	0	0.76	**-5.942 (1.42)**	-0.3282 (0.098)*	**0.3085 (0.14)**	**1.619 (0.473)**	-	**0.9955 (0.347)**	-	-	-	-
2. log(B) + log(F) + log(O) + S + A	80 / 124.4	84 / 89	2.5	0.22	**-6.319 (1.51)**	-0.3618 (0.104)*	**0.3436 (0.1038)**	**1.808 (0.516)**	**0.18 (0.12)**	**0.9527 (0.3446)**	-	-	-	-
3. log(B) + log(F) + log(O) + S + A + A:O + B:F + O:B + O:F	72.1 / 124.4	80 / 89	6.8	0.03	**-6.762 (2.67)**	-1 0828 (0.432)*	**-0.1104 (0.663)**	**2.158 (0.618)**	**0.44 (0.33)**	**0.6717 (0.7334)**	0 01964 (0 057)	**0.2248 (0.1172)**	0.2241 (0.2195)	-0.108 (0.14)

NOTE: H=*H. discolor* density, F=Nectar flower cover, B=Scotch Broom cover, A=Area in Hectares, C=Connectivity. All models implicitly contain an intercept (β_0). Coefficients (β_i's) are printed in the table in the same order as they appear in the model structure description column. Coefficients with an asterisk have χ^2 probabilities ≤ 0.10, coefficients printed boldface have χ^2 ≤ 0.05.

Table C.3: Set of the top GLM models for each site-year of data for the butterfly species *E. propertius,* with deviance, df, ΔAIC, Akaike weights (ω_i), and coefficients with standard errors (SE). Results are for 2002 and 2003, and Maple and Maxwell networks.

Model structure	Deviance/ null dev.	Df / null df	ΔAIC	ω_i	β_{NULL} (SE)	β_{BROOM} (SE)	$\beta_{Q\ Garryana}$ (SE)	$\beta_{CONNECT}$ (SE)	β_{AREA} (SE)	β_{FLOWER} (SE)	β_{HR} (SE)	$\beta_{BR\ FLWR}$ (SE)	$\beta_{OAK\ FLWR}$ (SE)	$\beta_{OAK\ AREA}$ (SE)
Maxwell 2002														
A + S + F + O + O:A	110 9 / 156.3	109 / 114	0	0.55	-2.704 (0.67)	-	**-0.00339 (0.0026)**	**0.1837 (0.061)**	**0.0766 (0.126)**	**0.0206 (0.008)**	**0.00606 (0.003)**	-	-	-
A + S + F + O + B + O:A	109.5 / 156.3	108 / 114	0.6	0.41	-2.814 (0.7)	0.023 (0.0198)*	**-0.00329 (0.0025)**	**0.1864 (0.063)**	**0.0352 (0.135)**	**0.0202 (0.008)**	**0.006 (0.003)**	-	-	-
Maxwell 2003														
1. O + S + A + F + O:A + O:F	67.3 / 159.6	109 / 115	0	0.34	**-4.562 (1.1)**	-	**0.0083 (0.0064)**	0.1977 (0.086)*	**-0.7164 (0.649)**	**0.0285 (0.025)**	-	-	-0.00019 (0.0001)*	**0.074 (0.025)**
2. O + S + A + F + O:A	69.8 / 159.6	110 / 115	1.21	0.19	**-4.093 (1.0)**	-	**0.0006 (0.0045)**	0.1866 (0.084)*	**-0.8795 (0.715)**	**0.0202 (0.008)**	-	-	-	**0.0814 (0.0272)**
3. O + S + A + F + B+ O:A + O:F	67.3 / 159.6	108 / 115	1.25	0.18	**-4.566 (1.1)**	-0.00311 (0.0312)	**0.00828 (0.0064)**	0.1989 (0.087)*	**-0.7044 (0.662)**	**0.02853 (0.01)**	-	-	-0.00019 (0.0001)*	**0.0742 (0.0251)**
4. O + S + A + F + B + O:A + O:F + B:F + B:O	64 7 / 159.6	106 / 115	1.18	0.19	**-4.814 (1.17)**	-0.01071 (0.0498)	**0.00693 (0.0062)**	0.2174 (0.095)*	**-0.6302 (0.584)**	**0.03606 (0.013)**	0.0008 (0.001)*	-0.0008 (.0011)	-0.00025 (0.0001)*	**0.0746 (0.025)**
5. O + S + A + F + B + O:A	69.7 / 159.6	109 / 115	2.48	0.10	**-4.107 (1.08)**	-0.00664 (0.0317)	**0.00055 (0.0044)**	0.1897 (0.085)*	**-0.856 (0.724)**	**0.0203 (0.009)**	-	-	-	**0.0819 (0.0273)**
Maple 2002														
1. log(F) + log (O)	63.9 / 93.7	89 / 91	0	.35	**-5.85 (1.29)**	-	**0.6553 (0.1919)**	-	-	**0.8685 (0.281)**	-	-	-	-
2. log(F) + log (O) + A	63.9 / 93.7	88 / 91	1.8	.14	**-5.756 (1.33)**	-	**0.6387 (0.2032)**	-	0.0293 (0.127)	**0.8447 (0.296)**	-	-	-	-
3. log(F) + log (O) + A + A:O	61.4 / 93.7	87 / 91	1.3	.18	**-5.5 (1.36)**	-	**0.4972 (0.2264)**	-	-1.944 (1.68)	**0.9451 (0.322)**	-	-	-	0.4535 (0.402)*
4. log(F) + log (O) + A + S A:O	59.4 / 93.7	86 / 91	1.1	.20	**-5.89 (1.48)**	-	**0.578 (0.2404)**	-0.7507 (0.643)	-2.246 (1.782)	**0.3542 (0.354)**	-	-	-	0.514 (0.426)*
5. log(F) + log (O) + A + S + B + A:O	59.1 / 93.7	85 / 91	2.3	.11	**-5.99 (1.51)**	**-0.00914 (0.353)**	**0.654 (0.2799)**	-0.7374 (0.622)	-2.25 (1.786)	**1.087 (0.353)**	-	-	-	0.511 (0.427)*
Maple 2003														
1. log(B) + log(A)	66 7 / 99.4	90 / 92	0	0.69	**-2.2 (0.40)**	**0.0311 (0.011)**	-	-	**0.278 (0.139)**	-	-	-	-	-
2. log(B) + log(A) + log(F)	66.1 / 99.4	89 / 92	2.1	0.24	**-2.1 (1.42)**	**0.38 (0.145)**	-	-	**0.675 (0.222)**	**0.303 (0.393)**	-	-	-	-

NOTE: O=Oak density, F=Nectar flower cover, B=Scotch Broom cover, A=Area in Hectares, C=Connectivity. All models implicitly contain an intercept (β_0). Coefficients (β_i's) are printed in the table in the same order as they appear in the model structure description column. Coefficients with an asterisk have χ^2 probabilities ≤0.10 and coefficients printed in boldface type have χ^2 probabilities ≤0.05.