University of Alberta

The spatial dynamics of *Aphthona* flea beetles on the invasive weed, leafy spurge.

by

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

in

Environmental Biology and Ecology

Department of Biological Sciences

Edmonton, Alberta

Fall 2002

University of Alberta

Library Release Form

Name of Author: Ian David Jonsen

Title of Thesis: The spatial dynamics of *Aphthona* flea beetles on the invasive weed, leafy spurge

Degree: Doctor of Philosophy

Year this Degree Granted: 2002

27 Banks Ct, Dartmouth,
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Date: 29/09/2002

University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled "The spatial dynamics of *Aphthona* flea beetles on the invasive weed, leafy spurge" submitted by Ian David Jonsen in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Environmental Biology and Ecology.

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For Peter John Jonsen, 1936-1999

Abstract

Few weed biocontrol studies focus on how spatial processes influence the outcomes of biocontrol agent introductions. Using a spatially explicit approach, I quantified and explored the roles that *Aphthona* flea beetle dispersal may play in the successful biocontrol of the invasive weed, leafy spurge. The studies presented are examples of how a spatially explicit perspective can enhance understanding of processes that are important to weed biocontrol systems.

Components of *Aphthona* dispersal were quantified using manipulative and observational field studies on landscapes with different matrix habitats. Key results from dispersal studies indicated that movement rates and immigration probabilities differ according to the type of landscape on which releases are made but that these effects differ between closely related biocontrol agent species. Even for species where dispersal differs little between landscape types, patterns of incidence on spurge patches were different between landscape types, albeit at a slightly broader scale.

Habitat-beetle density interactions assessed over a 3-year period, indicated that fine-scale habitat preferences changed between years but explained surprisingly little of the observed variation in beetle densities. Only *A. lacertosa* densities were correlated with declines in spurge density between the first and second years of the study but in the third year, spurge densities recovered to near original levels and beetle densities declined markedly over much of the landscape.

A spatially explicit simulation model revealed that emigration rates and movement ability can have antagonistic effects on release persistence and failure to consider dispersal will produce misleading predictions regarding release establishment. A more realistic model, parameterized with much of the empirical data presented in this thesis and incorporating landscape-mediated dispersal, illustrated that landscape structure had minor influence on *Aphthona lacertosa* population dynamics and impact on spurge patches. This finding appears to depend on the characteristics of the particular landscape on which the dynamics are played out; biocontrol agent population sizes and impact on spurge decreased as landscapes became more restrictive to dispersal. These results suggest that landscape-dispersal interactions can have important implications for the success of weed biocontrol introductions and should be considered when planning classical weed biocontrol programmes.

Acknowledgements

Much of my field work would not have been possible without the assistance of the following people: Jeff Rau, Stephanie Erb, Jeremy Fox, Tia Fox, Linda van Heek, Nicole Humble, John Kean, Jim Tailfeathers, Monte Thomson, and Ray Wilson. I also thank Monte Thomson for designing and building contraptions that actually worked and Ray Wilson for showing me the real way to drive a 4x4 off-road; Monte showed me the wrong way.

I thank my thesis committee for their encouragement and advice and, in particular, my co-supervisors, Rob Bourchier and Jens Roland, for giving me the freedom to pursue my own interests and the insight to bring me back to issues related to weed biocontrol and insect population dynamics.

Extra-curricular, lab activities were a welcome diversion and I thank Stephanie Erb and Shannan Little for their organizational skills and Vanessa Carney, Mike Crowe, Kendra Grams, Jeff Rau, Kevin Staley, and Ray Wilson for their participation. A special thanks also goes to the LRC soccer team and lunch-time soccer crowd for more wholesome, although not necessarily less dangerous, diversions.

Jens' lab: Corina Brdar, Sherri Fownes, Brian van Hezewijk, Nusha Keyghobadi, Steve Matter, April Mitchell, and Chris Schmidt, all helped make my time in Edmonton enjoyable and were excellent conference companions.

I am grateful to Ransom Myers, who generously provided financial support, space, and a computer during the last stages of writing my thesis at Dalhousie University, Halifax, NS.

Financial support from an NSERC PGS B scholarship, a W. H. Johns Graduate Fellowship and a Graduate Tuition Supplement from the University of Alberta, and through the Agriculture and Agri-Food Canada Research Affiliate program are all gratefully acknowledged.

Finally, I thank my wife, Nicole, for keeping me focused, for always believing in me, and for untold sacrifices.

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General Introduction

My research explores the role of dispersal in the successful biological control of an invasive weed, Leafy Spurge (*Euphorbia esula* L.), by *Aphthona* (Coleoptera: Chrysomelidae) flea beetles. Compared to traditional weed biocontrol studies that tend to focus on fine-scale (*i.e.*, within-patch) factors that contribute to agent establishment and impact (Kirby *et al.* 2000; Jacobs *et al.* 2001; Sheppard *et al.* 2001), I take a relatively novel approach that draws on the disciplines of metapopulation biology and landscape ecology. Specifically, I explore how dispersal-landscape interactions can influence the population dynamics of *Aphthona* beetles, which, in turn, will affect the beetles' ability to control leafy spurge.

Dispersal is a critical, yet poorly understood, component of animal population dynamics. The process of dispersal can be broken down into three components: (1) emigration from natal sites; (2) movement through unsuitable (or marginal) habitat; (3) immigration to or colonization of suitable habitat. Successful dispersal does not occur unless an animal accomplishes all three

components and reproduces thereafter (Fahrig and Merriam 1994). Each of the three components has the potential to influence animal population dynamics through a variety of mechanisms; I discuss some of these, presently. My thesis focuses primarily on how movement through unsuitable habitats can affect population dynamics but, as will be seen throughout, all three components are closely linked.

Weed biocontrol

Weed biocontrol was first conducted in Canada in 1950 when the beetle *Chrysolina hyperici* (Forster) was introduced from England to control St. Johnswort (*Hypericum perforatum*, L.) (Julien and Griffiths 1998). Since that time a total of 94 biocontrol agents has been introduced and released on 20 weed species in Canada (Julien and Griffiths 1998). As an alternative to pesticide use, weed biocontrol is economically viable in areas such as rangeland, where pesticide application often is not. Furthermore, invasive weeds such as leafy spurge and spotted knapweed (*Centaurea maculosa*, Lamarck) generally form thick, monoculture stands thus competitively excluding native plants (Hirsch and Leitch 1998; Sheley *et al.* 1998). Estimates of costs to ranchers and associated businesses of not controlling these weeds can range from 10's to 100's of millions of dollars (US) per year over a single and 4 state region, respectively (Leistritz *et al.* 1992; Hansen *et al.* 1997). Although developing a biocontrol program against a weed can be expensive (*i.e.,* several million dollars), the returns generally are more cost effective for end users than equivalent investments in pesticides (Harris 1979; Harris 1991).

The most common method of biocontrol of introduced weeds is classical biocontrol. This approach involves the importation and release of natural enemies of an introduced weed from that weed's native range. Usually, releases of relatively small numbers of a biocontrol agent are conducted in localized areas where a dramatic increase in the agent's population size (*i.e.,* an outbreak) may occur. If an outbreak density is reached, the biocontrol agent may be able to reduce the density of the target weed. This approach to biocontrol has been referred to as 'applied population dynamics' (Murdoch and Briggs 1996) because researchers attempt to select for or create conditions that will maximize the chances of agent establishment and eventual outbreak. A second phase of this kind of release strategy is to have the agent disperse and locate other areas colonized by the target weed.

Although classical biocontrol can be thought of as applied population dynamics, the majority of weed biocontrol research does not link well with current population theory (Kareiva 1996). This

may be due to the need for biocontrol researchers to address system-, species-, or even location-specific problems for which general theory may be of little use. I argue, however, that current population theory which focuses on spatial interactions combined with a conceptual framework for studying animal movement, can be brought to bear on an important issue in classical weed biocontrol – assessing the importance of dispersal from initial release sites and colonization of new weed patches on the overall ability of a biocontrol agent to control its target weed.

Recent studies utilizing ecological theory as a guide to address problems in weed biocontrol (*e.g.*, McEvoy *et al.* 1993; Grevstad 1996; McEvoy and Coombs 1999; Sheppard *et al.* 2001) represent a starting point from which the field may develop into a more predictive, applied science (Kareiva 1996). Improving the predictive ability of weed biocontrol research will improve the ratio of successful to failed biocontrol programmes against weeds and may reduce some of the potential risks associated with classical weed biocontrol (Simberloff and Stiling 1996; Louda *et al.* 1997).

Below, I provide a brief introduction to the relevant population theory and landscape ecology. I then point out how these fields may contribute to weed biocontrol research and conclude this introduction with a brief outline of my thesis.

Population dynamics

The notion that animal populations fluctuate but generally persist over the long-term has been of interest to researchers for over a hundred years (Hutchinson 1978). Over the years numerous models have been proposed to explain how populations are regulated (*e.g.*, Lotka 1925; Nicholson and Bailey 1935; Andrewartha and Birch 1954). Turchin (1995) argued that populations are regulated by density-dependent mechanisms and that many hotly debated exceptions to this 'rule' arise mainly from inadequate data or inappropriate analytic methods (Turchin 1995; Ray and Hastings 1996). However, until more empirical evidence is gathered to support Turchin's (1995) arguments, the debate about how populations are regulated is likely to continue. Regardless, important questions for empirical ecologists are to determine the biological mechanisms that underlie population regulation and persistence. These questions revolve around factors that influence births, deaths, immigration, and emigration.

Key factors influencing birth and death processes have been studied for years and are now relatively well understood for a variety of organisms (Royama 1992 and references therein).

However, an understanding of the importance of immigration and emigration on population dynamics has lagged behind. This was partly due to the difficulty of studying dispersal processes directly and partly due to the inability of earlier population models (*e.g.,* the original Nicholson-Bailey model) to address the influence of spatial structure on population dynamics (Andrewartha and Birch 1954). Andrewartha and Birch recognized that organisms were heterogeneously distributed in space and that this could stabilize population fluctuations. Although their work was widely ignored for many years, Andrewartha and Birch set the stage for a new field of population dynamics – Metapopulation dynamics – that focuses on the broad-scale interactions between groups of populations separated in space.

As empirical evidence accumulated ecologists began to realize the influence dispersal might have on population dynamics and community structure (Huffaker 1958; den Boer 1968; MacArthur and Wilson 1967). Levins (1970) visualized animal populations comprised of subsets or local populations that individually had a high probability of extinction but collectively (as a metapopulation) promoted regional persistence of a species. This new class of population models emphasized the roles of colonization, extinction, and asynchronous dynamics of local populations on metapopulation persistence in a spatially implicit way. A spatially implicit population model does not account for the absolute locations of populations, nor does it usually account for variations in population size.

Metapopulation ecologists have developed Levins' ideas and placed them in a more spatially explicit framework (Pulliam 1988; Harrison 1991; Hanski 1994) so that models now account for the size and spatial arrangement of local populations (Hanski 1994, 1998). Furthermore, current theoretical models suggest that dispersal may have a greater role in metapopulation dynamics than Levins originally envisioned, via mechanisms such as the rescue effect (Brown and Kodric-Brown 1977). A rescue effect prevents local populations from going extinct by increasing local population size through immigration. These ideas have generalized the metapopulation concept so that many forms of population structure are now recognized (Harrison and Taylor 1997). Still, difficulties remain in exploring how habitat spatial structure influences population dynamics (Kareiva 1990), partly because studies are often conducted at inappropriately fine-scales (May 1994) and partly because dispersal is still treated phenomenologically in many population studies (Kareiva and Wennergren 1995). Below I argue that tools exist to begin mechanistically incorporating the spatial dynamics of dispersal into metapopulation research.

Landscape ecology

Landscape ecology focuses primarily on quantifying the structure of landscapes – the composition and configuration of habitat patches on landscapes – and determining how this structure influences ecological processes across different spatial scales (Turner 1989; Wiens *et al.* 1993). Central to this theme is the idea that landscapes are organism-scaled, not human-scaled (Wiens 1989; Turner 1989). Thus, landscape ecology provides a framework to study spatial structure, how ecological processes shape it, and how organisms respond to it (Dunning *et al.* 1992; Taylor *et al.* 1993; Wiens *et al.* 1993).

Determining when landscape structure does and does not influence population processes is an important contribution that landscape ecology can make to understanding metapopulation dynamics (Kareiva and Wennergren 1995; Wiens 1997). The body of research on the movement responses of animals to differences in landscape features has grown steadily (Crist *et al.* 1992; With 1994*a*; Wiens *et al.* 1997; With *et al.* 1997; Pither and Taylor 1998; Jonsen and Taylor 2000; Roland *et al.* 2000; Matter *et al. in review*). These studies demonstrate that differences in either (or both) the composition and configuration of landscapes influences connectivity – the ability of animals to move through a landscape. Furthermore, congeners or even conspecifics may respond very differently to landscape structure depending on their behavioural or physiological states (Crist *et al.* 1992; With 1994*b*; Taylor and Merriam 1995). Thus connectivity is a function of both the structure of the landscape and also of the behavioural, morphological, or physiological state of an individual (Taylor *et al.* 1993; With *et al.* 1997). This idea of landscape connectivity can be generalized to encompass processes such as dispersal between local populations. At this population level, connectivity between local populations may still be influenced by landscape structure, individual differences in behaviour, morphology, or physiology, but may also be influenced by local population processes such as density-dependent emigration (Albrechtsen and Nachman 2001; Travis and French 2002).

Although few studies show directly how connectivity may influence population dynamics (but see Fahrig and Paloheimo 1988; Moilanen and Hanski 1998), several provide compelling circumstantial evidence that such links do exist (Fahrig and Merriam 1985; Kareiva 1987; Roland and Taylor 1995, 1997; With *et al.* 1997). The next step towards a synthesis of landscape ecology and metapopulation dynamics will be to determine under what conditions accounting for landscape structure enhances our understanding of metapopulation dynamics (Wiens 1997). Although metapopulation theory has become tremendously diversified since Levins' classic

model (1970), in some ways it is still analogous to the island biogeography theory of MacArthur and Wilson (1967) because local populations are usually viewed as 'islands in a sea of inhospitable habitat'. Landscape ecologists suspect otherwise; the connectivity of local populations may be strongly influenced by the composition and configuration of the landscapes on which local populations are embedded. This synthesis of landscape ecology and metapopulation theory potentially has great benefit for applied ecological research such as weed biocontrol.

Application to weed biocontrol

The current trend in population dynamics is to incorporate spatial structure in analytical and conceptual models of how populations function. However, many weed biocontrol studies are conducted at small spatial (*i.e.,* using potted plants or small garden plots) or short temporal scales (*i.e.,* one growing/breeding season) and are incapable of exploring many of the processes that influence broader-scale population dynamics (Kareiva and Wennergren 1995; May 1994). Often there are good reasons to conduct experiments at these small spatial and/or short temporal scales but an over-reliance on such experiments, particularly because they are cheap and simple to conduct, runs the risk of failing to capture some of the important details of the study system (*e.g.,* Callaway *et al.* 1999).

Landscape ecology and metapopulation dynamics potentially have much to offer to weed biocontrol theory and practice. Landscape ecology provides useful tools for studying the interactions between animals and spatial structure, while metapopulation dynamics has a solid base of theory from which predictions can be generated and tested in biocontrol systems. Weed biocontrol is conducted on real landscapes and biocontrol agents interact not only with their host plant but also with the broader landscape surrounding host plant patches. Often these landscapes are vastly different in habitat composition, spatial structure, and phenology compared to that in the agent's native range. Predictions regarding the ability of biocontrol agents to disperse and colonize (or immigrate) to new weed patches may not be a straightforward function of the distance between patches, which is how current metapopulation theory generally deals with dispersal. These interactions between spatial structure and dispersal may have important consequences for population establishment and growth that, in turn, may affect herbivore impact on host plants.

Releases of weed biocontrol agents generally are conducted over large areas that encompass a range of infestation levels of the "target" weed. The goal of these releases is to establish agent populations and have them grow and propagate throughout landscapes containing weed populations. In virtually all cases, purposeful release of agents wherever weed populations are located is impossible both logistically and economically and so biocontrol practitioners must rely on the agents to disperse, colonize, and reduce weed populations in areas where no releases have been conducted. It is, therefore, of critical importance to understand how biocontrol agent populations propagate from initial release locations and what implications dispersal – landscape interactions (*i.e.,* connectivity) have on successful control of target weeds. These issues form the unifying thread that ties together the different chapters of my thesis.

Thesis outline

I have divided my thesis into 5 data chapters. This general introduction and a general methods section, where I provide a description of the study system and the main study area, precede these chapters.

In Chapters 1 and 2, I use a combination of experiments and a survey to quantify the components of *Aphthona* dispersal and to explore how an exogenous factor, landscape structure, and an endogenous factor, wing morphology, can influence dispersal. Landscape structure has been shown to influence various movement behaviours (Crist *et al.* 1992; Jonsen and Taylor 2000) and the dispersal success (Pither and Taylor 1998; Roland *et al.* 2000; Rickets 2001) of a variety of insects. It is, therefore, reasonable to assume that similar effects may occur for insect biocontrol agents. In Chapter 1, I use a mass mark-recapture experiment to provide a straightforward illustration of how landscape structure, *vis-à-vis* the type of unsuitable (matrix) habitat present, can influence the immigration of *A. nigriscutis* and *A. lacertosa* to patches of their host plant, leafy spurge. In Chapter 2, I follow-up on the analysis presented in Chapter 1 by augmenting the data presented there with additional data to quantify movement rates through the two matrix habitats. I then present an experiment to assess whether or not *A. lacertosa* emigration rates are density-dependent. In addition to hypothesized consequences for population regulation (Denno and Peterson 1995, Ruxton 1996), density-dependent emigration may have practical consequences for the establishment of biocontrol agent releases and it is, therefore, of interest to determine whether such mechanisms exist. Finally, the realization of specific dispersal patterns ultimately depends upon the physical capabilities of individual insects. I end Chapter 2 with a

comparison of wing morphologies of *A. lacertosa* individuals collected at original release sites and at sites 200 m (or more) away, on two different landscape types.

Few weed biocontrol studies quantify, either with experimental or observational data, the relationship between year-to-year changes in host plant density and biocontrol agent density. Furthermore, there are very few studies that quantify how this relationship plays out in a spatial setting where host plants are patchily distributed and their quality, as viewed by different biocontrol agents, may be variable (for one example, see Huffaker and Kennett 1959). Even simple issues such as the rate of spread of biocontrol agents from initial release locations are rarely quantified. In Chapter 3 I document the spatial dynamics, over a 3-year period, of *A. lacertosa* and *A. nigriscutis* on a single, intensive-study landscape containing numerous spurge patches interspersed with shrub and grass matrix habitats. I relate *Aphthona* densities sampled on this landscape to a variety of habitat attributes to determine the extent to which habitat features influence beetle distributions. I then correlate year-to-year changes in leafy spurge densities and patch sizes to *Aphthona* densities to infer whether the two species are having the desired effect on their host plant.

Experimental studies that illustrate direct cause and effect links between dispersal patterns and population dynamics can be extremely difficult to design both because of the broad spatial extent over which dispersal can occur and because multiple generations must be followed to determine population outcomes following dispersal events. Simulation models offer a viable alternative to an experimental approach, when both spatial (dispersal) and temporal (population change) processes are of interest. In Chapters 4 and 5 I develop simulation models to explore how dispersal influences population processes that are relevant to weed biocontrol.

Recent interest in developing general guidelines for optimal biocontrol agent release sizes (Memmott *et al.* 1996; Grevstad 1999; Shea and Possingham 2000) has focused on how temporally scaled population and environmental processes influence the probability of establishment (persistence) of biocontrol releases. These studies ignore the potential influence of spatial processes such as dispersal that are known to affect population persistence (Brown and Kodric-Brown 1977; Fahrig and Merriam 1985). In Chapter 4, I use a simple simulation model to explore the interactions between environmental stochasticity, Allee effects, and dispersal on the persistence of biocontrol agent releases.

In Chapter 5 I use an empirically based simulation model to test the hypothesis, suggested in Chapter 1, that landscape structure – dispersal interactions influence biocontrol agent population dynamics and, therefore, influence impact on target weeds. I parameterize the model using data presented in Chapters 1, 2 and 3 and run the model on the landscape studied in Chapter 3 (see Fig. G.1).

My thesis concludes with a general discussion where I summarize the key results from each of the chapters, describe how they may influence the practice of weed biocontrol, and suggest future avenues for combining a 'spatial perspective' with more traditional approaches to studying the population processes that are relevant to weed biocontrol.

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General Methods

Study system

Leafy spurge (*Euphorbia esula*, L.) is an introduced, perennial weed that invades uncultivated land and displaces native plants by forming large, dense patches. Spurge is native to Eurasia but currently can be found throughout much of Canada and the Northern United States (Best *et al.* 1980; Watson 1985). However, its greatest impact as a pest species occurs on rangeland in the Great Plains states and the Prairie provinces (Watson 1985).

New spurge infestations are established from dispersed or dormant seeds and have a distinct spatial patchiness which can gradually coalesce into large, continuous stands via clonal spreading. Leafy spurge's extensive and highly persistent root system enables it to survive grazing and many herbicide treatments. New shoots develop from numerous root buds which in turn arise along almost any portion of the root system (Selleck *et al.* 1962; Messersmith *et al.* 1985). These life

history features make leafy spurge both an extremely aggressive invader of rangeland and an extremely difficult weed to control.

Over the past 20 years a variety of biocontrol agents have been released to control leafy spurge. Several Lepidopteran (*Hyles euphorbia*, *Lobesia euphorbiana*, and *Minoa murinata*), Dipteran (*Pegomya curticornis*, *P. euphorbiae*, and *Spurgia esula*) and Coleopteran (*Aphthona cyparissiae, A. czwalinae, A. flava, A. lacertosa, A. nigriscutis*, and *Oberea erythrocephala*) species have been released (McClay *et al.* 1995). The most successful control to date has been achieved by *Aphthona* (Coleoptera: Chrysomelidae) flea beetles, in particular *A. nigriscutis* Foudras and *A. lacertosa* (Rosch). The other three *Aphthona* species are much less common in my study area.

Both *A. nigriscutis* and *A. lacertosa* are univoltine in Canada (Maw 1981; Gassmann 1990); adults emerge in mid- to late June and feed on leafy spurge foliage. Females lay eggs in the soil near leafy spurge stems and after eclosion the larvae move through the soil and begin feeding on leafy spurge roots and root hairs. Beetles over winter as larvae and pupate in mid- to late May. Although the adults can completely defoliate the ramets (Maw 1981), this damage appears to have little effect on plant survivorship. Larval feeding, however, can damage the plant's root system and limit water and nutrient uptake (Hansen *et al.* 1997) and this appears to have much greater effect on plant survivorship (Harris 1984). Of all the insect taxa released on leafy spurge, *O. erythrocephala* (Coleoptera: Cerambycidae) is the only other insect that attacks roots but it has failed to achieve widespread establishment in Alberta (McClay *et al.* 1995).

Study area

The majority of the empirical research presented in this thesis was conducted on the Blood Indian Reserve, located SW of Lethbridge, AB (49°29'N, 113°11'W). An immigration experiment (Chapters 1 & 2) and field collections of beetles for morphological measurements (Chapter 2) were collected at a variety of sites located throughout the Blood Reserve and in the Oldman River valley in the city of Lethbridge. The remainder of the work (Chapters 3 & 5) was conducted on an intensive-study landscape located on the Blood Reserve, near the St. Mary's Reservoir (49°22'N, 113°3'W; Fig. G.1).

The intensive-study landscape is a large area of rangeland bounded by the St. Mary River to the South and East and by crop fields to the North and West (Fig. G.1). A complex network of

coulees (gulleys created by soil erosion from water run-off) dominate the landscape and the majority of spurge patches are located along the sides and bottoms of these coulees or on the large, low flat adjacent to the river (Fig. G.1, at middle-left bottom). Spurge patches are heterogeneous in size and fine-scale habitat (*i.e.,* habitat features within spurge patches), which ranges from nearly complete spurge cover, grass-spurge or shrub-spurge mixtures, to predominantly bare ground. In addition to the spurge patches, the landscape is composed of a matrix (habitat unsuitable for *Aphthona* beetles) of predominantly grassland with shrub patches (mainly *Salix* spp. and *Prunus* spp.) interspersed along the coulees. Nearly all of the landscape was subjected to heavy grazing by cattle during all three years of the study.

Aerial photographs (Alberta Environment, 1:10 000 scale) of the study landscape were scanned at 600 dpi and these images were ortho-rectified (using ER Mapper 6.0 – Earth Resources Mapping, Inc.) to remove distortion resulting from the planar representation of highly undulating terrain. A coordinate system (UTM, Zone 12) was associated with the ortho-rectified images by geo-referencing with a series of GPS landmarks and the images were then merged to produce a single, high-resolution image of the entire intensive-study landscape (using ER Mapper 6.0). Shrub and grass patches were easily discerned and were digitized as polygons from the image using ArcView 3.1 (ESRI, Inc.). Spurge patches were mapped *in situ* by walking along the perimeters of the patches with a Trimble™ Ag132 dGPS unit (Trimble Navigation Ltd.). Patch sizes for spurge and shrub habitats were calculated from the combined GPS and digitized data using ArcView 3.1 (ESRI) and nearest-neighbour distances (edge-to-edge) among spurge patches were calculated using Analysis Extension 1.3 for ArcView (SWEGIS).

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Figure G.1. Air photo-mosaic of the intensive-study landscape showing the coulees (erosional gulleys) and spurge patches (blue) embedded in a grass-dominated matrix. Shrub patches are generally found on the East- and North-facing slopes of the coulees (an example is indicated by the white arrow). Note the crop fields bordering the landscape to the north (top) and south of the river (bottom).

Chapter 1

The influence of matrix habitat on *Aphthona* flea beetle immigration to leafy spurge patches[†]

1.1 Introduction

Dispersal between local populations has long been recognized as a potentially important influence on local population dynamics and broader-scale population persistence (Andrewartha and Birch 1954; den Boer 1968; Levins 1970; Brown and Kodric-Brown 1977; Pulliam 1988). Current theory has expanded upon Levins' (1970) original ideas about metapopulation dynamics and placed them in a more spatially explicit framework (*e.g.,* Hanski 1994) so that models now account for the size, spatial arrangement of local populations and the potential 'rescue effect' of immigration prior to population extinction (Hanski 1994, 1998; Stacey *et al.* 1997). These enhancements have generalized the metapopulation concept so that many forms of population structure are now recognized (Harrison and Taylor 1997). However, difficulties remain in exploring how both population structure and landscapes influence population dynamics (Kareiva

[†] Originally published as: Jonsen ID, Bourchier RS, Roland J (2001) The influence of non-habitat on *Aphthona* flea beetle immigration to leafy spurge patches. Oecologia 127:287-294

1990), primarily because dispersal is a difficult process to measure and model, especially on complex landscapes (Kareiva and Wennergren 1995; Wiens 1997).

Landscape ecologists define landscape spatial structure as the composition and spatial configuration of habitats on a landscape (Dunning *et al.* 1992; Taylor *et al.* 1993). An important question addressed is, "How does landscape spatial structure influence animal dispersal?" Recent studies in this field demonstrate that components of landscape spatial structure such as patch size, patch aggregation and amount of suitable habitat influence the ability of animals to disperse over landscapes (*e.g.,* Wiens *et al.* 1997; Pither and Taylor 1998; McIntyre and Wiens 1999; Jonsen and Taylor 2000). However, less attention has been paid to the effect of unsuitable habitat (hereafter referred to as matrix habitat) on animal movement (but see Kareiva 1985; Åberg *et al.* 1995; Roland *et al.* 2000 for examples).

The type(s) of matrix habitat present on a landscape and their spatial configuration are features that can potentially influence an animal's ability to disperse successfully among patches of suitable habitat (*e.g.,* breeding habitat). Matrix habitat may confer a high mortality risk (St. Clair *et al.* 1999; Zollner and Lima 1999; Hanski *et al.* 2000), physically impede movement (*e.g.,* Crist *et al.* 1992; Johnson *et al.* 1992), have some marginal value as a resource (Fahrig and Merriam 1994; Wiegand *et al.* 1999), or may even facilitate movement (*e.g.,* Matthysen *et al.* 1995; Taylor and Merriam 1995; Pither and Taylor 1998). The first 3 factors may reduce or completely prohibit movement across landscapes (landscape connectivity; sensu Taylor *et al.* 1993), while the latter obviously increases landscape connectivity. Changes in landscape connectivity can influence immigration or colonization probabilities (*e.g.,* Gustafson and Gardner 1996) and thus influence metapopulation population dynamics.

I explore some of these ideas in the context of a weed biocontrol system comprised of an invasive weed, leafy spurge, and two introduced flea beetle species, *Aphthona lacertosa* and *A. nigriscutis*. The practice of biological control has benefited from recent modeling studies (*e.g.,* Rees and Paynter 1997) that seek to identify the vulnerable stages of targeted weeds and predict the effects of various biocontrol strategies (McEvoy *et al.* 1999). However, more studies are required that can generate useful guidelines for practitioners (Shea and Possingham 2000). Because weed biocontrol is conducted on heterogeneous landscapes, I suggest that using a landscape ecology approach to studying population processes will generate new insight into some of the underlying features responsible for successful biocontrol.

An important goal of weed biocontrol is to foster population growth of the control agent on the target weed. The spatial scale at which sufficiently high densities of the control agent are achieved and the method used may be influenced strongly by interactions between the control agent's movement ability/behaviour and landscape spatial structure. For example, the number of releases required to achieve an outbreak and the scale at which those releases are distributed may, in part, be dictated by the movement ability of the biocontrol insect, the degree of isolation among weed patches, and the type(s) of intervening matrix habitat.

Here I compare the influence of two types of matrix habitat (grass versus shrub) on the ability of *A. lacertosa* and *A. nigriscutis* to immigrate to isolated patches of their host plant, leafy spurge. Little is known about the movement abilities of the two species, but the species are reported to differ in their fine-scale habitat preferences. In its native range, *A. lacertosa* is commonly found in moist areas often containing dense leafy spurge or other vegetation (Gassmann 1990). In North America, *A. nigriscutis* establishes best in open, dry areas with low density leafy spurge (Maw 1981; McClay *et al.* 1995). In my study region (S. Alberta, Canada), I also have found *A. nigriscutis* adults on dense spurge patches and on patches embedded in shrubs (*personal observation*). In light of these differences in fine-scale habitat preference, I was interested in determining whether or not the two beetle species have different immigration abilities on the two landscape types. I used a mark-recapture experiment to directly assess how immigration ability differs between species and between sexes on landscapes dominated by either grass or shrub matrix habitat.

1.2 Methods

1.2.1 Study area

I conducted beetle releases on 10 landscapes, 7 located on the Blood Indian Reserve, AB, CAN and 3 in the Oldman River valley, Lethbridge, AB CAN (49°41'N, 112°50'W). Distances between individual landscapes ranged from 1.3 to 29.6 km. Each landscape consisted of a single leafy spurge patch (the 'target' patch) isolated from other patches by at least 600 m in the general direction of the release transect (see 'Experimental design'). In addition, each target patch was embedded in a landscape of either grass-dominated or shrub-dominated matrix habitat that extended at least 400 m away from the target patch. Each grass landscape consisted of a matrix composed of at least 90 % cover of native and introduced grass species. All grass landscapes

were heavily grazed by cattle and contained no shrub cover. Each shrub landscape had a matrix composed of between 60 and 75 % cover of shrubs (predominantly *Salix* spp.) ranging from 1 to 2 m in height. The remaining 25 – 40 % of the matrix was composed of grass and bare ground, however, in all cases the release points and the target patches were embedded in shrub habitat. I selected target leafy spurge patches that were approximately equal in size (grass: 40.58 ± 14.47 m^2, shrub: 44.83 ± 9.86 m^2; mean ± sd) to eliminate a potential confounding interaction between patch size and matrix habitat.

1.2.2 Experimental design

All releases were initiated within the period 14 – 24 July, 1999. *A. nigriscutis* and *A. lacertosa* were collected from 3 'nursery' sites on the Blood Indian Reserve, the latter species was also collected from the Stoney Indian Reserve, AB, CAN (51°09'N, 114°50'W). The releases were designed to compare the influence of two kinds of matrix habitat (grass versus shrub) on the ability of both species to immigrate to isolated leafy spurge patches.

Beetles collected from nursery sites were stored overnight in a rearing cage at 10 °C and provided with freshly clipped leafy spurge stems. Approximately 5 – 6 hours prior to release, beetles were marked with fluorescent powder in groups of between 400 and 450. Beetles were aspirated from the rearing cage and passed into an Erlenmeyer flask containing a tissue liberally dusted with fluorescent powder. Once marked, beetles were aspirated individually into a 250 ml plastic Nalgene® bottle with a mesh lid. This second aspiration allowed us to (1) count the actual number of beetles allotted for each release and (2) to reject individuals that were marked with too much or too little powder (as per Kareiva 1982).

All releases were conducted approximately 1 hour after the last group of beetles was marked (*i.e.*, at ca. 1600 – 1700 hrs). Each of the 10 landscapes consisted of a single target leafy spurge patch into which both beetle species were released in groups of between 400 and 450 (the exact number was noted for each release). These releases in the centre of target patches (0 m) provided expected recapture proportions for each target patch. In addition I also released between 400 and 450 individuals of both species at 100 and 200 m along a transect away from each target patch. These two releases were situated in either grass-dominated or shrub-dominated matrix habitat. The orientation of the release transects relative to the target patches differed among landscapes because I had to ensure that no other leafy spurge patches were closer than the target patch to the

100 and 200 m release points. Initial analyses indicated that release orientation had no significant effect on results and therefore was ignored.

Different colours of fluorescent powder were used to distinguish beetles from each release point (0, 100 & 200 m) on a single landscape. Releases conducted in a grass and a shrub landscape were paired by release date. This approach ensured that releases in grass and shrub landscapes experienced approximately the same initial weather conditions.

After releases, target patches were sampled every 2-3 days over a two-week period. Patches were sampled systematically with a sweep net by walking through the patch along parallel lines spaced approximately 1 m (*i.e.,* 1 sweep net arc) apart. In the field, sweep net contents were carefully extracted into one 1 plastic containers and subsequently placed into a freezer to kill all insect fauna. *Aphthona* beetles were separated from other fauna, inspected for powder marks and sexed under a dissecting microscope at 40 x magnification using both UV and fibre-optic light sources. During initial processing I determined that the fibre-optic light source was adequate to locate even minute powder marks on beetles and so this method was used thereafter. Individual beetles were scored as marked or unmarked and the color of powder – indicating release location – was noted.

Most target patches were occupied by *A. nigriscutis* prior to releases but no patches were occupied by *A. lacertosa*. Occupancy of *A. nigriscutis* prior to releases may have influenced the patch occupancy (immigration to or emigration from) of experimentally released beetles. However, this is unlikely to be important in the context of the experimental design because recaptures of matrix habitat-released individuals were compared only to recaptures of controls and not to recaptures of unmarked beetles. My estimates of immigration ability are likely to be conservative because I can not detect individuals that successfully immigrate to target patches from a distance and subsequently emigrate or die. I therefore assume that these rates of disappearance are similar to those of the control individuals (i.e., individuals released at 0 m, inside target leafy spurge patches).

1.2.3 Statistical analyses

Recapture data were analyzed using quasi-likelihood regression (McCullagh and Nelder 1989) with proportion recaptured as the response variable and SPECIES[1], LANDSCAPE, and RELEASE LOCATION as predictors. I used quasi-likelihood regression because the data were highly under-dispersed. Unlike some other generalized linear models (*i.e.,* Poisson or binomial) which assume a dispersion equal to one, quasi-likelihood models use a dispersion parameter estimated from the data and therefore produce more reliable parameter estimates and significance levels. Because recapture rates were low, data were pooled among the two matrix habitat release distances (100 and 200 m), thus RELEASE LOCATION indicates whether beetles were released in target patches (controls) or in the matrix habitat (grass or shrub). Initial analyses indicated that recaptures of 200-m released beetles were significantly lower (both species) than for those released at 100 m ($F_{1,79} = 7.04$, $p<0.01$), as might be expected. But there were no interactions between SPECIES or LANDSCAPE and RELEASE DISTANCE from the target patch (RELEASE DISTANCE x SPECIES: $F_{1,79} = 0.08$, $p = 0.79$; RELEASE DISTANCE x LANDSCAPE: $F_{1,79} = 0.03$, $p = 0.86$; RELEASE DISTANCE x SPECIES x LANDSCAPE: $F_{1,79} = 0.93$, $p = 0.34$). Therefore, pooling data among the 100 and 200 m release points increased overall recapture rates without significantly altering or obscuring the relationships of primary interest between immigration ability and SPECIES, LANDSCAPE, or RELEASE LOCATION (releases in the target patch versus releases in the surrounding matrix).

Recaptures from individual sample days were pooled over the entire two-week sampling period to eliminate any effect of time on recapture distributions. Differences in sampling effort among target patches were controlled statistically by fitting the covariate SWEEPS in all models before assessing effects of design factors. SWEEPS is the total number of sweep net arcs in each patch over the two-week sampling period. For all analyses, full models (main effects plus all interactions) were fit, including the covariate SWEEPS as the first term of each model. Because the terms of interest are the interactions with the RELEASE LOCATION factor I present only these terms in 'analysis of deviance' tables. Analysis of deviance tables are analogous to ANOVA tables, except that the variance component reported is the deviance rather than the sums of squares (see McCullagh and Nelder 1989 for a full discussion of deviance and generalized linear models).

Subsequent analyses were conducted using SEX as an additional predictor. Due to the design of the experiment it was impossible to sex all individuals prior to release. I therefore estimated sex

[1] Throughout this thesis factors included in statistical models are presented in a SMALL CAPS font.

ratios by dissecting a sub-sample of both species of beetle used in each release (*A. lacertosa* n = 324, *A. nigriscutis* n = 302). These ratios were applied to the numbers of beetle released in each replicate as an estimate of the numbers of male and female beetles released. Subsequent recaptures were separated by sex and recapture proportions were determined for each sex. For this analysis, I fit separate quasi-likelihood models for each species. The response variables are proportion recaptured and the predictors are: SEX, LANDSCAPE, and RELEASE LOCATION.

In order to visualize the nature of significant interactions, I present interaction plots using the mean *relative* proportion of beetles recaptured as the response variable. This measure, although different from the response used in the statistical models, allows us to summarize the important interactions between SPECIES, LANDSCAPE and RELEASE LOCATION in a single graph. The effect of RELEASE LOCATION (beetles released in either target patch or in matrix) is incorporated into the response by dividing the proportion of recaptured beetles released in the matrix by the expected recapture proportion (*i.e.,* the proportion of recaptured beetles released in the target patch).

Due to the relatively broad-scale nature of this experiment, I maximized the numbers of beetles released to ensure sufficient recaptures. By focusing on maximizing recaptures and with a limited number of beetles available, I was able to replicate the landscape treatment 5 times (5 of each matrix habitat type). Based on this replication, an *a priori* alpha level of 0.1 was set for all statistical models.

1.3 Results

A total of 25 956 beetles was released over all 10 landscapes. Table 1.1 presents a summary of the numbers of beetle released and recaptured according to each design factor. Overall recapture rates were very low (3 %) but sufficient to detect effects of experimental treatments.

A. lacertosa had similarly low abilities to immigrate to patches of leafy spurge embedded in both grass- and shrub-dominated LANDSCAPEs, while *A. nigriscutis* was more likely to immigrate to spurge patches on grass-dominated LANDSCAPEs than on shrub-dominated ones (Table 1.2, significant RELEASE LOCATION x SPECIES x LANDSCAPE interaction; Fig. 1.1). Ignoring LANDSCAPE type (shrub vs. grass), there was also an overall difference in immigration ability

between *A. lacertosa* and *A. nigriscutis* (Table 1.2, significant RELEASE LOCATION x SPECIES interaction), suggesting that *A. nigriscutis* is a better overall colonizer of leafy spurge patches than is *A. lacertosa* (Fig. 1.1).

Separate analyses of the effects of SEX (based on estimated sex ratios, see Methods) and LANDSCAPE on immigration probability indicate that *A. lacertosa* males and females had equally low immigration ability on grass- and shrub-dominated LANDSCAPEs (Table 1.3, no significant interactions between RELEASE LOCATION, SEX, or LANDSCAPE; Fig. 1.2). However, *A. nigriscutis* females had a higher immigration ability than males on grass-dominated LANDSCAPEs, whereas males had a higher immigration ability on shrub-dominated LANDSCAPEs (Table 1.4, significant RELEASE LOCATION x SEX x LANDSCAPE interaction; Fig. 1.2).

1.4 Discussion

The experimental design enabled us to assess the connectivity (Taylor *et al.* 1993), here measured as immigration probability, of one dominant (grass) and one less common (shrub) landscape encountered by *Aphthona* beetles released in the study region. I show here that the type of matrix habitat surrounding host patches has a strong influence on the immigration ability of *A. nigriscutis*, while for *A. lacertosa* immigration ability is similar between the two landscape types. I assume released beetles either locate leafy spurge patches embedded in the grass or shrub matrix habitat or perish because both species are specialists on *Euphorbia* spp. (Gassmann 1990; Gassmann *et al.* 1997).

Other studies have demonstrated that the surrounding landscape can influence animal movement behaviours. For example, Jonsen and Taylor (2000), focusing at a similar scale to the current study, showed that Calopterygid damselflies readily move away from streams on completely and partially forested landscapes but not on unforested ones. At a much finer scale (*i.e.*, 2 – 8 m), Kareiva (1985) found a striking difference in host finding ability of two *Phyllotreta* flea beetles between releases conducted in cultivated ground versus goldenrod matrix habitats. While there were no marked differences between the two *Phyllotreta* species, Kareiva's results parallel those presented here for *A. nigriscutis* in that immigration ability was reduced by the taller and structurally more complex matrix habitat (*i.e.*, goldenrod / shrubs versus cultivated ground / grass). At a broader scale (*i.e.*, 1 – 4 km), Åberg *et al.* (1995) demonstrated that habitat isolation

effects for the hazel grouse (*Bonasa bonasia*) were much stronger on a landscape dominated by an agricultural matrix than on one dominated by a logged forest matrix. They suggested that the hazel grouse were reluctant to move across the agricultural matrix but readily moved through the forest matrix. Roland *et al.* (2000) showed a strong negative effect of distance through forest on between-meadow movements of the alpine butterfly *Parnassius smintheus*. This negative effect appears to be due both to a reluctance to enter forest and to reduced rates of movement through forest.

A drawback of mark-recapture experiments of the kind I present here are that they do not allow researchers to determine the behaviours the animals engage in during their travel. Consequently, I am unable to determine the specific mechanism(s) underlying the differential responses of the two *Aphthona* species to the grass versus shrub landscape comparison. Nevertheless, my approach has identified that a difference in immigration ability exists between the two types of matrix habitat studied and between the two flea beetle species. I suspect that the overall difference in immigration ability between the two species may be due a difference in wing size. Despite similar body sizes, *A. nigriscutis* has significantly longer and wider wings than *A. lacertosa* (*personal observation*). These morphological differences are consistent with my results here, suggesting that *A. nigriscutis* is more capable of traversing the 100 to 200-m distances imposed upon beetles in this study. The morphological difference between species does not, however, explain the effect of matrix habitat on immigration. *A. nigriscutis* prefers open and/or grassy spurge patches (Maw 1981; McClay *et al.* 1995) and moves well through grass-dominated landscapes, whereas shrub-dominated landscapes may represent behavioural or physical barriers to its movement (*e.g.,* Crist *et al.* 1992; Johnson *et al.* 1992). In contrast, *A. lacertosa* prefers mesic, shrubby spurge patches (Gassmann 1990) but has equally low immigration rates in both grass- and shrub-dominated landscapes. Regardless of the specific mechanisms involved, an important next step is to determine whether these differences in movement ability, behaviour and/or morphology translate into population-level effects such as lower beetle population incidence on leafy spurge patches embedded in shrub-dominated landscapes.

Initial observations of post-release distributions of *A. lacertosa* and *A. nigriscutis* on the Blood Reserve indicated that *A. nigriscutis* was much more widely distributed on leafy spurge patches, up to ca. 700 m from known release sites, than was *A. lacertosa* (RS Bourchier, *unpublished data*). This is not surprising since, although both species were first widely released in 1997, some localized releases of *A. nigriscutis* were conducted throughout the study region over the past 18

years (McClay *et al.* 1995). Nevertheless, the results here indicate that the higher connectivity of grass landscapes for *A. nigriscutis* than for *A. lacertosa* may also contribute to the observed distribution patterns. Because shortgrass rangeland is the dominant matrix habitat type with shrubs comprising a smaller proportion in the study region, I would expect that a between-species difference in movement ability through grass matrix habitat (Fig. 1.1) would have a stronger effect on broader-scale distribution than any difference in movement through shrub matrix habitat.

The significant interaction between sex and landscape type (Fig. 1.2) for *A. nigriscutis* indicates that females had a larger decrease in immigration ability between grass and shrub landscapes than did males. This difference may reflect oviposition choices made by habitat-seeking females; *A. nigriscutis* prefers open leafy spurge patches in dry, grassy areas over patches in mesic-moist, shrubby areas (Maw 1981; McClay *et al.* 1995). Because only mated females can found new local populations, this interaction between sex and landscape may have important consequences for local demography of *A. nigriscutis* on shrub-dominated landscapes where females have a lower immigration ability.

My experimental design imposed distances of 100 and 200 m over which beetles had to travel in order to immigrate to host plant patches. In the study region inter-patch distances range from tens to many hundreds of metres in both grass- and shrub-dominated habitats. In general, the experimental release distances are not unrealistic of the typical inter-patch distances that beetles may encounter when dispersing from one leafy spurge patch to another. Thus I expect that the experimental results presented here are relevant to the population dynamics of both beetle species in the study region.

1.4.1 Implications for metapopulation dynamics

Differences in overall immigration ability between species and between landscapes have potentially important implications for their population dynamics. Current metapopulation theory suggests that enhanced colonization/immigration can increase the persistence of spatially structured populations (Brown and Kodric-Brown 1977; Hanski 1994, 1998). However, too much dispersal among local populations tends to synchronize local dynamics and may increase the risk of metapopulation extinction (Hastings and Harrison 1994; Gyllenberg *et al.* 1997). Immigration effects on metapopulation dynamics have been demonstrated in various empirical systems (*e.g.*, Holyoak and Lawler 1996; Stacey *et al.* 1997), however, relatively little is known about the

influence of landscape spatial structure, especially the composition of matrix habitat, on immigration rates (Gustafson and Gardner 1996; Wiens 1997). The experimental results indicate that the type of matrix habitat encountered by dispersing individuals can have a profound effect on immigration rates but that these effects may not be consistent among similar species or even between sexes. Roland *et al.* (2000) found a strong effect of distance through forest matrix habitat on between-meadow movements of *P. smintheus* and suggest that such matrix habitat effects on metapopulation dynamics may be magnified when movement is restricted to linear arrangements of suitable habitat and matrix habitat (*e.g.,* mountain ridge tops or riparian habitat). In contrast, Moilanen and Hanski (1998) found little evidence to suggest that landscape spatial structure influenced the metapopulation dynamics of the butterfly *Melitaea cinxia.* However, their study landscape was relatively homogeneous; increased landscape heterogeneity may also contribute to stronger landscape effects on metapopulation dynamics.

1.4.2 Implications for weed biocontrol

My results have implications for weed biocontrol in general and for the leafy spurge – *Aphthona* system, in particular. Much of weed biocontrol is conducted on heterogeneous landscapes that are mosaics of weed patches, native and non-native (*i.e.,* crop land) habitats. Once biocontrol agents are established at initial release sites, biocontrol practitioners are interested in the impact of the agent on target weeds, movement rates of the agent and the ability of the agent to colonize weed patches some distance from initial release points (*e.g.,* Rees 1990; Mays and Kok 1996; Grevstad and Herzig 1997; McFadyen 1998). My results indicate that immigration / colonization of weed patches is dependent upon the type of matrix habitat separating source and destination weed patches. This effect appears to vary between closely related species and between sexes. An important consequence for weed biocontrol is that different release strategies may be required depending on the type of landscape encountered and the biocontrol agent used. Based on this study, I predict that on grass-dominated landscapes, *A. nigriscutis* will be better able to colonize and have impact on spurge patches some distance from initial release locations than *A. lacertosa,* at least at a scale of 100 – 200 m. On shrub-dominated landscapes, however, both species have low colonization abilities and successful biocontrol may only occur when individual releases are conducted at a finer-scale than on grass-dominated landscapes. I am currently exploring these ideas on a large network of leafy spurge patches to determine the extent to which landscape mediated immigration influences within-patch demography of *Aphthona* beetles and, in turn, impact on leafy spurge.

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Table 1.1. Number of beetles released and recaptured (in parentheses) in target leafy spurge patches according to the design factors: RELEASE LOCATION, SEX, SPECIES and LANDSCAPE. Estimated, prior-to-release SEX ratios (see Methods) are provided under the SPECIES column.

SPECIES	RELEASE LOCATION	LANDSCAPE			
		Grass		Shrub	
		♂	♀	♂	♀
A. nigriscutis	Leafy spurge	43 (7)	2114 (238)	45 (7)	2199 (162)
0.0201 ♂, 0.9799 ♀	Matrix	85 (2)	4120 (89)	93 (1)	4556 (3)
A. lacertosa	Leafy spurge	1184 (75)	1198 (68)	1072 (47)	1085 (70)
0.4969 ♂, 0.5031 ♀	Matrix	1853 (6)	1876 (8)	2203 (1)	2230 (4)

Table 1.2. Analysis of deviance table. The response variable is the proportion of *Aphthona lacertosa* and *A. nigriscutis* recaptured in target leafy spurge patches. Beetles were marked, released and recaptured on either grass or shrub LANDSCAPEs. The model is a Quasi-likelihood model fit with binomial errors. Full models (main effects plus all interactions) were fit but only terms including the RELEASE LOCATION factor are presented (see Methods).

Term	df	Deviance	F-value	p(F)
Null	39	2.011		
RELEASE LOCATION	1	0.007	141.541	<0.001
RELEASE LOCATION x SPECIES	1	0.006	0.705	0.408
RELEASE LOCATION x LANDSCAPE	1	0.067	7.463	0.010
RELEASE LOCATION x SPECIES x LANDSCAPE	1	0.070	3.918	0.030
Residual	31	0.289		

Table 1.3. Analysis of deviance table. The response variable is the proportion of male and female *Aphthona lacertosa* recaptured in target leafy spurge patches. Beetles were marked, released and recaptured on either grass or shrub landscapes. The model is a Quasi-likelihood model fit with binomial errors. Full models (main effects plus all interactions) were fit but only terms including the RELEASE factor are presented (see Methods).

Term	df	Deviance	F-value	p(F)
Null	39	2.237		
RELEASE LOCATION	1	1.208	34.928	<0.001
RELEASE LOCATION x SEX	1	0.001	0.021	0.885
RELEASE LOCATION x LANDSCAPE	1	0.006	0.181	0.674
RELEASE LOCATION x SEX x LANDSCAPE	1	0.020	0.283	0.756
Residual	31	0.945		

Table 1.4. Analysis of deviance table. The response variable is the proportion of male and female *Aphthona nigriscutis* recaptured in target leafy spurge patches. Beetles were marked, released and recaptured on either grass or shrub landscapes. The model is a Quasi-likelihood model fit with binomial errors. Full models (main effects plus all interactions) were fit but only terms including the RELEASE LOCATION factor are presented (see Methods).

Term	df	Deviance	F-value	P(F)
Null	39	5.517		
RELEASE LOCATION	1	3.228	64.714	<0.001
RELEASE LOCATION x SEX	1	0.018	0.359	0.553
RELEASE LOCATION x LANDSCAPE	1	0.010	0.192	0.664
RELEASE LOCATION x SEX x LANDSCAPE	1	0.322	3.230	0.053
Residual	31	1.646		

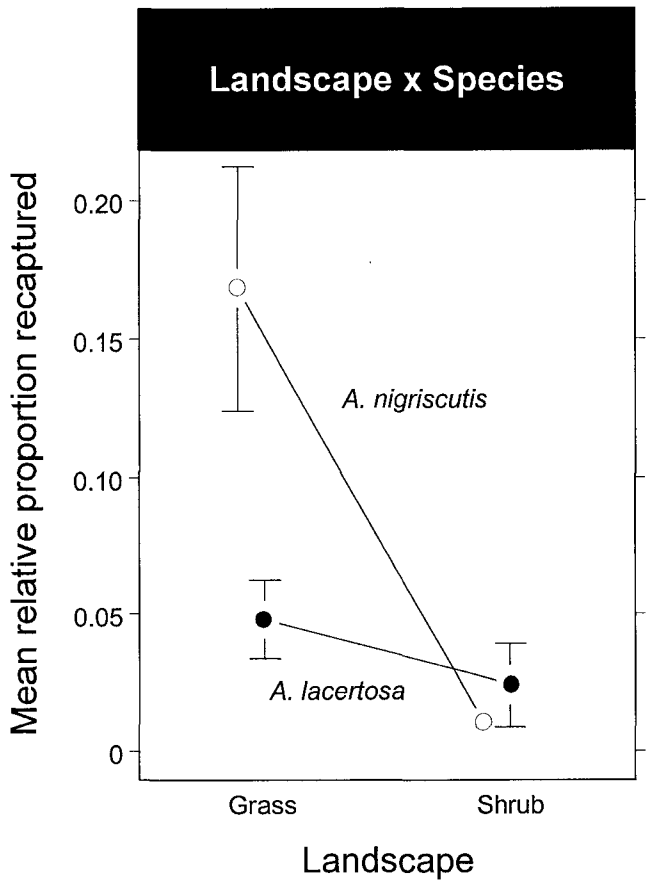

Figure 1.1. Interaction plot of the mean relative proportion of beetles recaptured in target leafy spurge patches embedded in grass and shrub LANDSCAPEs, according to SPECIES. This response incorporates the effect of RELEASE LOCATION by scaling recapture proportions of matrix-released beetles by the expected recapture proportions (beetles released in target patches). Lines indicate direction of trend between means for each combination of the factors LANDSCAPE and SPECIES. Error bars are ± 1 standard error. Pairs of data points in a landscape type are staggered for clarity.

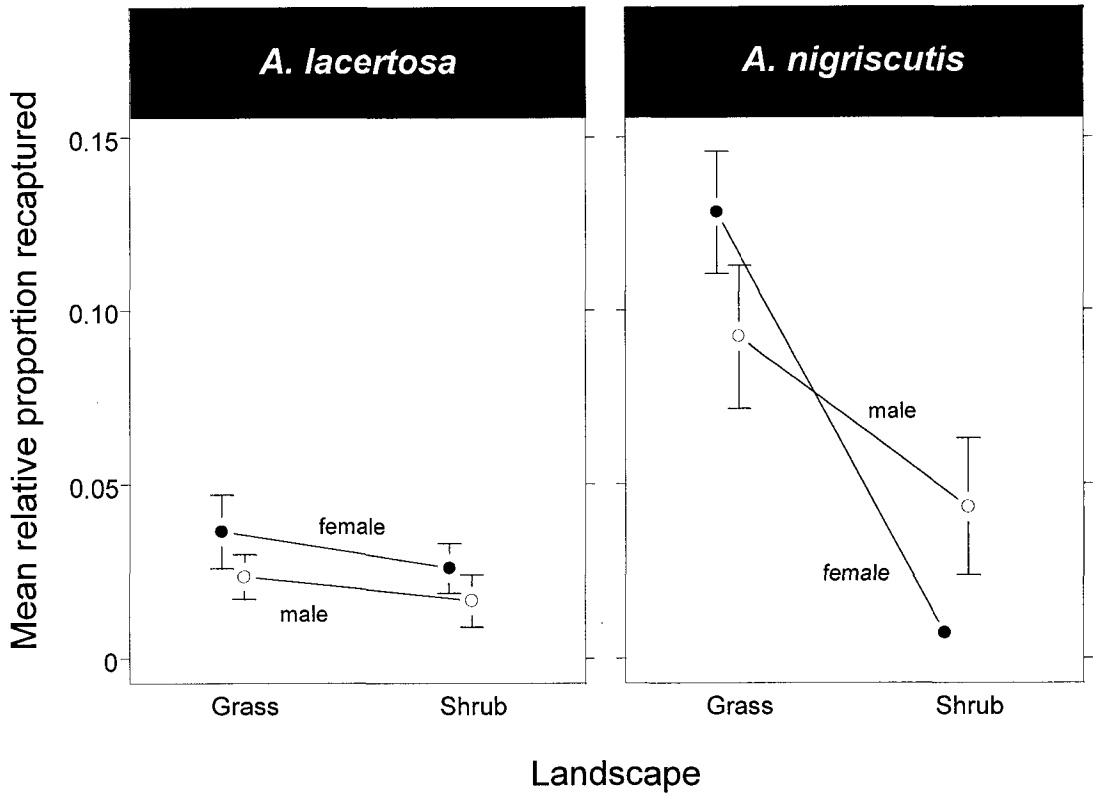

Figure 1.2. Interaction plot of the mean relative proportion of *Aphthona lacertosa* and *A. nigriscutis* beetles recaptured in target leafy spurge patches embedded in grass and shrub LANDSCAPEs, according to SEX. This response incorporates the effect of RELEASE LOCATION by scaling recapture proportions of matrix-released beetles by the expected recapture proportions (beetles released in target patches). Lines indicate direction of trend between means for each combination of the factors LANDSCAPE and SEX. Error bars are ± 1 standard error. Pairs of data points in a landscape type are staggered for clarity.

Chapter 2

Quantifying components of *Aphthona* dispersal and their interactions with wing morphology and landscape structure

2.1 Introduction

The movement to and colonization of unoccupied habitat are important components of the dispersal process that allows populations to persist through time (Andrewartha and Birch 1954; den Boer 1968; Levins 1970; Hanski 1998). Dispersal also is vital to the success of weed biocontrol programmes for which purposeful redistribution of agents is both economically and logistically difficult. For example, high emigration rates from biocontrol agent release sites may reduce population establishment by rendering populations more vulnerable to an Allee effect (Hopper and Rousch 1993; Chapter 4), whereas, very low emigration rates may result in few colonization events and failure of the release to establish at new locations. Furthermore, interactions between movement behaviour, the habitat features present on release landscapes, and individual characteristics such as wing morphology (*e.g.,* Taylor and Merriam 1995) may affect how release populations spread thus reducing or elevating host-patch colonization rates in particular habitats (Andow *et al.* 1990; Chapter 1). Such interactions may even result in selection

against phenotypes (*e.g.,* Hufbauer 2002) not capable of dispersing successfully into new habitat. These scenarios remain largely speculative, however, in part because dispersal is a difficult process to measure in the field.

The overall purpose of the studies presented in this chapter was to quantify some of the key aspects of dispersal for *Aphthona* flea beetles. The documentation of *Aphthona* movement ability provides important baseline information that will aid in prediction of patterns of host-patch colonization and spatial population dynamics. In addition, understanding how biocontrol agents disperse through different kinds of habitat can have practical implications for the way field releases are conducted.

In the first section of this chapter, I use a trial dataset to compare the fit of two models commonly used in the analysis of insect movement – diffusion (Turchin and Thoeny 1993; Turchin 1998) and a negative exponential model (Taylor 1978; Grevstad and Herzig 1997) – to describe movement rates from mark-recapture data. I then use the better fitting of the two models to analyze mass mark-recapture data collected for *A. nigriscutis* and *A. lacertosa* released at different distances from target spurge patches on each of the grass- and shrub-dominated landscapes. In the second section of this chapter, I present field experiments designed to quantify *A. lacertosa* emigration rates from spurge patches and test whether these rates are density-dependent. The results from these first two sections provide movement and emigration rate parameters for a simulation model, presented in Chapter 5, that predicts spatial patterns of *A. lacertosa* colonization and impact on leafy spurge patches. In the final section of this chapter, I compare the body- and wing-size of *A. lacertosa* beetles inhabiting grass- and shrub-dominated landscapes to determine whether morphological differences are related to differences in movement rate and patch colonization on the two landscapes.

2.2 Movement rates

2.2.1 Methods

Aphthona movement through grass and shrub matrix habitats was assessed using field data collected in the experiment presented in Chapter 1. In addition to the distances of 100 and 200 m from release point to target patch presented in Chapter 1, beetles were also released at 300 and 400 m. These latter distances were omitted from the data presented in Chapter 1 because I was

not able to release beetles at the 300- and 400-m distances on all landscapes. Thus inclusion of recapture data from these farther distances in the statistical analysis of immigration rates in Chapter 1 would be problematic. Recaptures from these distances can however be used to model movement distances through grass and shrub matrix habitats.

A wide variety of movement models can be fit to mark-recapture data of the kind I present here (Harrison 1989; Grevstad and Herzig 1997; Turchin 1998). I used an initial trial dataset for *A. nigriscutis* movement through grass matrix habitat, collected in 1998, to determine whether recaptures from different release distances were best modeled by diffusion with settlement or a negative exponential function. Fitting these functions to observed movement distances are two of the most common approaches to describing animal dispersal (Taylor 1978; Turchin 1998) and are relatively simple to implement for mass mark-recapture data.

I used non-linear least squares regression to fit the 1998 *A. nigriscutis* recapture data to a diffusion with settlement model with the form:

$$C(d) = Ad^{-\frac{1}{2}} \exp(-\frac{d}{B}) \qquad (2.1);$$

and a negative exponential model with the form:

$$C(d) = N_0 \delta (2 \tan^{-1} \frac{d}{2\pi}) \exp(-\alpha d) \qquad (2.2).$$

In both models, $C(d)$ is the expected number of beetles recaptured in the target patch expressed as a function of the distances, d, at which different groups of beetles are released from the target. For the diffusion model (Eqn. 2.1 – from Turchin and Thoeny 1993), A and B are parameters fitted to the mark-recapture data. Parameter A is a scale parameter that is proportional to the number of released individuals and the recapture efficiency and parameter B sets the spatial scale of dispersal (see Turchin and Thoeny 1993 for further details). For the negative exponential model (Eqn. 2.2 – from Grevstad and Herzig 1997), N_0 is the number of beetles released at each distance, d, from the target patch and δ is the recapture efficiency (*i.e.*, the proportion of marked beetles in the target patch that actually get recaptured). The term ($2 \tan^{-1} d/2\pi$) adjusts expected recaptures for the differences in the angle subtended by the target patch at each of the release

distances. The parameter α describes the rate of decline in recaptures with increasing distance and its inverse represents the mean dispersal distance attained by each species traveling through grass- or shrub-dominated matrix.

Both models fit the data well (Figure 2.1; see Table 2.1 for parameter estimates) except that Eqn. 2.1 predicted slightly more beetles immigrating to the target patch than was observed for distances beyond 75 m. In comparison, Eqn. 2.2 predicted slightly fewer beetles immigrating to the target than was observed for the closest release distance (10 m) but did a better job of predicting recaptures from the larger distances. I chose to use the negative exponential equation (Eqn. 2.2) to model the 1999 mark-recapture data for both species because of the lower prediction bias at the larger release distances. The model was fit to the 1999 data in a manner similar to that for the 1998 data, but because the 1999 data were collected on 5 replicate landscapes for the grass- and shrub-dominated landscapes each, I fit separate models for the two landscape types and used the means of recaptured beetles from each distance within a landscape type. Note, however, that recapture data from the 300 and 400 m release distances were collected from 3 grass and 2 shrub landscapes, so mean recaptures and standard errors were adjusted for these release distances accordingly.

2.2.2 Results

Results of the negative exponential model fit to the mark-recapture data for each species, not surprisingly, indicate that movement rates through the two matrix types corresponded to the immigration probabilities presented in Chapter 1 (compare α's in Table 2.2 with Fig. 1.1). The difference in movement distances between grass and shrub matrices was greatest for *A. nigriscutis* with a mean movement distance of nearly 100 m in the grass matrix but only 27 m in the shrub matrix, whereas *A. lacertosa* had a mean movement distance of 60 m in the grass matrix and 42 m in the shrub matrix. Unfortunately, I do not have data to assess the bias in model fit at distances smaller than 100 m but data from the 1998 trial data for *A. nigriscutis* moving through grass matrix suggest that the negative exponential model slightly underestimates the number of individuals moving short distances. This is not likely to pose a serious problem because it is the estimation of the number of individuals moving long distances that is more likely to have strong implications for population processes (Turchin 1998).

2.3 Emigration rates

2.3.1 Methods

This experiment was designed to: (1) determine an average rate at which *A. lacertosa* emigrate from spurge patches to be used as a parameter in the simulation model presented in Chapter 5 and (2) to determine if *A. lacertosa* emigration from spurge patches is density-dependent. Density-dependent emigration has been observed for a variety of insects (Denno and Peterson 1995; Herzig 1995) and may have important consequences for the spatial population dynamics of biocontrol agents (Ruxton 1995).

I conducted this experiment in a single, large leafy spurge patch that was experimentally subdivided into 7 pairs of small patches (5 x 5 m each), emigration arenas, within which beetle releases and recaptures were conducted. Leafy spurge was mowed to ground-level in all directions to a distance of at least 15 m from the edge of the patches and so that at least 25 m of mowing occurred between any two pairs of patches (Fig. 2.2). Each pair of patches consisted of one patch into which beetles were released at a known density, and one target patch that was left unoccupied (Fig. 2.2). The distance between release and target patches was small (5 m) to ensure that beetles emigrating from the release patch could easily traverse the intervening unsuitable habitat and colonize the target patch. In addition, aluminium screen fences (1.25 m high) were erected on 3 sides of the release patches to (1) further ensure that emigrating individuals were recaptured and (2) focus emigration in the direction of the target patch (Fig. 2.2). Target patches were swept and fences were monitored visually at regular intervals to recapture dispersing beetles. This design minimized observer influence on beetle emigration by focusing recapture efforts away from the initial release location.

Releases of *A. lacertosa* were conducted at 7 initial densities (200, 400, 800, 1250, 1600, 2000, 3500) over the period of 5 – 8 July, 2001. These beetles had been collected from 2 'nursery' sites on the Blood Indian Reserve and, using an airbrush, were marked with unique colours of Testor's™ model paint for each release density. Although no *A. lacertosa* were present within the experimental area, releasing marked beetles provided the opportunity to observe longer-distance dispersal (*i.e.*, movement between different pairs of patches). Releases were conducted at twilight (2130 – 2200 hrs) when day-time temperatures were lowest. Monitoring for dispersing beetles began the following morning at 0800. Fences were monitored hourly over an 8-hour period for emigrating beetles during the first 2 days post-release but there were very few recaptures (Table

2.3); thereafter, the fences were monitored once daily. Target patches were swept daily and the recaptured beetles from both the fences and target patches were counted and stored for inspection of paint marks and for dissection.

It was of interest to determine whether emigration rates differed between sexes, however, it was not feasible to sex all individuals prior to release so instead, a subset of 300 beetles was reserved for dissection to estimate the sex ratio of the released individuals. There were 154 females and 146 males in the reserved group (1.05 ♀:1 ♂) and so I assume hereafter that the released individuals had a sex ratio of 1:1.

Three to four days following initial releases, recaptures declined to zero. I was unsure whether this was a result of (1) high mortality within the release patch, (2) cessation of dispersal, (3) inadequately low release densities, or (4) a failure of the experimental design to adequately assess beetle emigration. Consequently, a second round of releases was conducted with a modification of the experimental design.

Beetles used for the second round of releases were obtained from Montana and were left unmarked to eliminate the possibility that the marking procedure significantly reduced survival, or otherwise adversely affected behaviour. I also reduced the size of the patches and the inter-patch distance by dividing single 5 x 5 m patches into 4 equal-sized patches (2 x 2 m) with a 1-m strip of unsuitable habitat between each. Fences were then erected around these 4 patches so that they were entirely enclosed (Fig. 2.3). This arrangement reduced the number of emigration arenas down to 4 that could be enclosed by the fencing available. Beetles were then released into the NE patch of each set at 4 different densities: 40, 80, 160, and 240 beetles m^{-2}. The fences and patches were monitored for recaptures as above.

2.3.2 Results

Results from the initial emigration experiment suggest extremely low emigration rates (Table 2.3), however, 3 days following the release, recaptures declined to 0 and remained so for 3 consecutive days. At this point I decided to sweep out the beetles remaining in the release patches to get an estimate of the number of non-emigrating individuals. This estimate was also extremely low (Table 2.3; Number remaining in release patch), suggesting that either the patch and fence design did not capture emigrating individuals efficiently or the released beetles suffered very high

mortality rates shortly after release. The latter scenario may have been precipitated by the marking process but survival trials (conducted in the lab) suggested no significant effect of paint marks on beetle survivorship, over a 45-day period (Fig. 2.4, Cox proportional hazards test: β = 0.022, Wald statistic (1 df) = 0.03, p = 0.87, n = 59).

The second emigration experiment was set up to maximize the probability of beetle recapture following emigration from release patches by completely surrounding the release and target patches with fencing, reducing the distance between release and target patches (Fig. 2.3), and increasing the initial release densities. Recaptures following release were substantially higher (both counts and proportions) than observed in the first experiment (Table 2.4) and continued, albeit at a declining rate, over a 2.5-week period. Based on the 4 releases, the overall average emigration was 0.1686 ± 0.033 (1 se), expressed as a proportion of the total number of beetles released at the start of the experiment. Subsequent dissection of recaptured individuals indicated some subtle differences in numbers of male and female emigrants by release density (Table 2.4) but there were no significant differences between overall means for the recaptures in target patches or on fences (in patch: $t_{6\ df}$ = -0.57, p = 0.6; on fence: $t_{6\ df}$ = 0.28, p = 0.8), or for recaptures irrespective of capture location ($t_{14\ df}$ = -0.15, p = 0.9).

Estimates of emigration rates suggest an increasing trend with increasing release density but the regression model was not significant (Fig. 2.5; slope = 0.0007, se = 0.003, t_{3df} = 0.26). However, the power of the test was miniscule (β = 0.052) and likely represents an extremely conservative estimate of the true relationship between beetle density and emigration rate.

2.4 Wing morphology

2.4.1 Methods

To determine whether *A. lacertosa* wing morphology is related to observed patterns of colonization of new habitat following initial releases, I conducted a survey on spurge patches located in 8 release landscapes in 1999. No releases of *A. lacertosa* in my study area were conducted prior to 1997, therefore by carefully selecting release landscapes that were sufficiently isolated from one another (*i.e.*, > 1 km), I can safely assume that individuals collected from spurge patches some distance from release sites had dispersed, or were the progeny of dispersers, from the nearest release site.

The release landscapes were dominated by either grass or shrub matrix habitats and all were characterized by patchy distributions of spurge habitat. On each landscape, beetles were sampled from the patch containing the original release location and from a haphazard selection of patches that were distributed at various distances from the release location up to a maximum of 600 m. Beetles were sampled from each of these 'distant' patches and from the release location and placed in plastic vials on ice until they could be euthanized for dissection. Beetle collections were conducted over a 1.5-week interval starting on 26 July, 1999.

Collected beetles were stored at -10 °C and dissections were carried out subsequently under a Wild MZ8 dissecting microscope. Individual beetles were affixed to a wax dissection platform and bathed in insect saline. The right wing and tibia were excised from each beetle, washed with distilled water and placed flat onto a microscope slide and left to dry. Beetles were then dissected to determine sex. In cases where the right wing tibia and/or tibia were damaged or missing, the left wing and/or tibia were used. An attempt was made to count eggs or ovarioles in gravid females, however, most of the individuals were stored below freezing for too long a period and had become desiccated. Desiccation is not likely to have affected wing and tibia measurements because these do not rely on the preservation of soft tissues.

Wings and tibias were photographed using a Hitachi HV-C20 digital video camera mounted to a Wild Photomakroskop M400 compound microscope, with a 7x objective lens. A Shotz trans-illumination fluorescent light box was used to back-light the wings and tibias. Images were acquired at a pixel resolution of 120.6 pixels mm^{-1}. Images of wings and tibias were measured using the freeware image analysis package, ImageTool 2.00 (UTHSCSA, 1996). A macro was created to measure the straight-line distance in pixels for leading edge vein length and wing width. The leading edge vein was used instead of total wing length because many wings were missing their distal portions and because the vein had well-defined start and end points to provide as consistent a measurement among different wings as possible. The start and end points used for the measurements are illustrated in Fig. 2.6a. Tibia lengths were measured in a similar fashion with start and end points illustrated in Fig. 2.6b.

Measurement error was estimated by making repeated measurements on a subset of 50 wings and tibias using the procedure described above. Knowledge of the site of origin, DISTANCE from release site, and SEX of each individual was withheld from the measurer and the order of repeat measurements was shuffled by a third party. Of the 50 wings and 50 tibias measured, 3 (6 %)

wings and 8 (16 %) tibias had repeat measurements that deviated more than 10 % (± 0.015 mm) from the original measurement.

2.4.1.1 Statistical analyses

Prior to analyzing the morphological data, I determined whether the incidence of *A. lacertosa* on spurge patches differed as a function of (1) DISTANCE from release sites and/or (2) LANDSCAPE type. The results of this analysis has implications for the analyses of beetle morphology because if no DISTANCE or LANDSCAPE effects were observed for the beetle incidence data, relationships with beetle morphology would be of little importance for dispersal. The wing morphology analyses that follow were performed on beetles collected from the occupied spurge patches used in this patch occupancy analysis. The patterns of beetle incidence as a function of DISTANCE from release site and LANDSCAPE type were analyzed by fitting a Generalized Linear Model (*glm* – McCullagh and Nelder 1989*)* with a Binomial error distribution.

Analysis of wing morphology data was conducted using *glm*'s with Gaussian errors which is equivalent to ANOVA (McCullagh and Nelder 1989). I was interested primarily in the interaction between wing morphology and colonization patterns following biocontrol agent release, however, there likely is a strong allometric relationship between wing size and overall body size which may obscure effects of wing morphology (Wootton 1992; Taylor and Merriam 1995). I, therefore, used the tibia measurements to control statistically for body size prior to assessing other relationships with wing morphology. In addition, two of the factors of interest, SEX and LANDSCAPE, may influence overall beetle size, so controlling for size may actually obscure relationships between wing morphology and the factors of interest! To avoid this problem I first fit a *glm* with the factors of interest, SEX, DISTANCE, and LANDSCAPE (and two-way interactions), to tibia lengths and used the residuals from this model fit as a new body size variable. I then fit this new body size variable to wing lengths and widths, separately, and used the residuals from these model fits as new wing morphology measures corrected for body size. Thus, the final models estimate the effects of SEX, DISTANCE, and LANDSCAPE and two-way interactions on wing length and wing width, each corrected for body size.

The sampling design was highly unbalanced with respect to DISTANCE because local population sizes and patch occupancy generally decreased with DISTANCE from release location. I attempted to account for this by converting DISTANCE from a continuous variable into a factor with 2 levels, near and far from release location, but the design was so biased toward individuals collected at or

close to release locations that the significance of model terms and their parameter estimates would be suspect. I addressed the problem by using only beetles collected at the release location (0 m) and at DISTANCEs greater than 200 m. Using a bootstrap approach, I fit 1000 *glm*'s with randomly selected subsets of the 0-m data and used all the data from DISTANCEs greater than 200 m. Each of the resulting 1000 datasets consisted of 280 observations and were balanced with respect to DISTANCE. This procedure was repeated for all the statistical models fit to the morphological data. The results presented are based on means of the 1000 replicate models.

2.4.2 Results

2.4.2.1 Beetle incidence

In general, *A. lacertosa* incidence on spurge patches declined with increasing DISTANCE but this relationship was complicated by an interaction with LANDSCAPE type (Table 2.5). The incidence of *A. lacertosa* on patches near to release sites was slightly but not significantly higher in shrub-dominated LANDSCAPEs than in grass-dominated LANDSCAPEs. This relationship reversed on patches far from release sites (*i.e.,* > 200 m), where *A. lacertosa* incidence on patches in shrub-dominated LANDSCAPEs was significantly lower than those in grass-dominated LANDSCAPEs (Fig. 2.7). Thus there are significant differences in the distribution of *A. lacertosa* among spurge patches on the two landscape types which suggests that any corresponding differences in beetle morphology (below) represent biologically important trends.

2.4.2.2 Body size

Female *A. lacertosa* were significantly larger than males (Table 2.6) and individuals found on spurge patches greater than 200 m from release sites were significantly larger than those found at release sites, regardless of SEX (Table 2.6). The latter relationship, however, was complicated by an interaction between LANDSCAPE type and DISTANCE from release site (Table 2.6). Beetles collected from spurge patches far from release sites on grass-dominated LANDSCAPEs were significantly larger than beetles collected from similarly distant patches on shrub LANDSCAPEs but there were no size differences among beetles collected near to release sites on either LANDSCAPE type (Fig. 2.8a). This pattern is consistent with the pattern of beetle incidence described above. The sampling distribution of *t*-values for the coefficient describing this interaction suggests that there is a moderate probability (0.28) that the relationship is spurious (Fig. 2.8b).

2.4.2.3 Wing morphology

After controlling for body size, wing length and width both were influenced strongly by SEX and DISTANCE from release site (Tables 2.7 & 2.8). Both of these effects were further complicated by interactions, the former with DISTANCE and the latter with LANDSCAPE type (Tables 2.7 & 2.8). Female *A. lacertosa* collected from patches far from release sites had significantly longer wings than did either males collected from the same patches or individuals collected near to release sites (Fig. 2.9a). There was little difference, however, in male wing size between patches near to and far from release sites (Fig. 2.9a). In addition, beetles found on patches near to release sites on shrub LANDSCAPEs had significantly longer wings than those near to release sites on grass LANDSCAPEs but the opposite was found for beetles on patches far from release sites (Fig. 2.10a). The same relationships were observed for wing widths (not presented), suggesting that the observed relationships are associated with factors acting on overall wing size (area) rather than specific wing morphologies. No non-significant *t*-value estimates were observed for either interaction in any of the 1000 replicate models (Figs. 2.9b & 2.10b), suggesting that neither of the interactions are spurious.

2.5 Discussion

2.5.1 Movement rates

The differences in movement rates through grass- and shrub-dominated landscapes for the two *Aphthona* species illustrate that even closely related, similar sized species can have quite different movement-landscape interactions (*e.g.,* Pither and Taylor 1998; Jonsen and Taylor 2000) that may, in turn, lead to different patterns of colonization of host plant patches (With and Crist 1995). In particular, *A. nigriscutis* host-patch colonization patterns may be especially sensitive to among site differences in the amount of grass and shrub habitat within the vicinity of release sites because this was the species that had the larger magnitude difference in movement rates through grass versus shrub matrix habitat. Interactions of this kind may have an important influence on the success of individual biocontrol releases by enhancing or limiting the rate of spread of an introduced population (Andow *et al.* 1990). These ideas are explored further in Chapter 5.

An implicit assumption of the negative exponential model fit to movement data is that of random movement. That the model fit well to the mark-recapture data suggests that *Aphthona* flea beetles

disperse randomly and colonize spurge patches purely by chance encounters. This would suggest a positive relationship between colonization and host-patch size; however, *A. lacertosa* colonize spurge patches over a broad range of size from < 1 m^2 to > 1000 m^2 (Chapter 3), suggesting that dispersal is in fact not random. Directed movements toward spurge patches may occur at distances less than 100 m, distances that were not included in this experiment but that are typical of inter-patch distances on the landscape studied in Chapter 3. Grevstad and Herzig (1997) illustrated that the chrysomelid beetle, *Galerucella calmariensis*, a biocontrol agent for purple loosestrife, exhibits directed movements toward host-patches at distances of 50 m and less and generally immigrates into host patches already colonized by conspecifics, as does the closely related beetle, *Trirhabda virgata* (Herzig and Root 1996).

Although the specific cues that *Aphthona* flea beetles use to locate host plants are generally unknown, it is suspected that an aggregation pheromone plays a role (P Harris, *personal communication*; Tansy 2001). This pheromone may be used as an aggregation cue by mate-seeking males (*e.g.,* Herzig and Root 1996; Morris *et al.* 1996) or because feeding in aggregations may enhance individual fitness (Peng *et al.* 1992) by overcoming host-plant defences. Regardless, the results presented here suggest that if such pheromones are used by *Aphthona* beetles they are used at finer spatial scales than those typical of movement and host-patch colonization, or they do so in subtle ways that were not detected by the current experimental design.

2.5.2 Emigration rates

I was unable to adequately determine whether *A. lacertosa* emigration rates are density-dependent. Although observed proportions of emigrants do appear to differ among the release densities tested, a regression model fit to these data did not describe the relationship better than did the overall mean emigration rate (Fig. 2.5). Expansion of the second experiment to incorporate more release densities should improve the statistical power to detect a density effect on emigration using a regression analysis. Furthermore, the release densities used in the second experiment were extremely high and might only be relevant to field releases that have achieved 'outbreak' densities. Therefore, a future attempt should include lower density releases that are more representative of typical field situations.

In spite of the inconclusive results, the implications of density-dependent emigration for weed biocontrol warrant discussion. In their review of the prevalence of density-dependent emigration, Denno and Peterson (1995), showed that a number of sap-feeding insects exhibit density-

dependent emigration and that this is most commonly associated with declines in host-plant quality. They suggest that density-dependent emigration may be more prevalent in insects that tend to aggregate and have rapid population growth, features that are shared by *A. lacertosa* and are likely common to many other weed biocontrol agents. Increased biocontrol agent population density combined with declines in host-plant quality are common scenarios in successful weed biocontrol, suggesting that density-dependent emigration may also be a common process in weed biocontrol systems. So what are the benefits of density-dependent emigration for weed biocontrol?

Empirical and theoretical analyses suggest that density-dependent emigration may stabilize population dynamics (Denno and Peterson 1995) by reducing the prevalence of chaotic population fluctuations (Ruxton 1995; Matter 2001) and likely preventing the occurrence of localized population outbreaks. The latter is a feature that, in most cases, is counter to the aims of weed biocontrol – the creation of high density populations of an introduced herbivore to control high densities of an invasive plant. Although the stabilizing effect of density-dependent emigration on biocontrol agent populations may reduce the chance of localized outbreaks occurring, it may also promote persistence over broad, regional scales by increased colonization of unoccupied habitat (Hanski 1998) which would allow more rapid suppression of incipient weed outbreaks (McEvoy *et al.* 1993). In addition, under certain situations density-dependent emigration may help small populations increase more rapidly by reducing loss due to emigration at low densities (cf. Kean and Barlow 2000) and hence improve establishment at release sites. For biocontrol agents whose dispersal is known (or suspected) to be density-dependent, these features suggest that planned releases should be on the small side, assuming demographic stochasticity and Allee effects are minimal (but see Grevstad 1999; Chapter 4). These ideas are speculative but illustrate the potential importance of density-dependent emigration for weed biocontrol and suggest that more empirical exploration for the presence and effects of density-dependent emigration would benefit weed biocontrol research.

2.5.3 Wing morphology

In general, the results from the wing morphology analyses suggest that dispersers on grass landscapes that are successful at locating habitat far from initial release locations – and/or their progeny – tend to be larger and have larger wings (independent of body size) than are individuals that do not disperse, or disperse only short distances. Assuming that larger individuals are energetically more capable of making longer dispersal flights (Anholt 1990; Marden 1994), the

results imply that movement over similarly long distances may be more risky on grass than on shrub landscapes. This hypothesis seems counter to the result from the movement rate analyses, indicating that *A. lacertosa* moved slightly more readily through grass than through shrub landscapes (Table 2.2). However, movement through grass matrix habitat may be more stressful physiologically (*i.e.,* hydro-thermal stress), whereas, movement through shrub matrix habitat may be less stressful but pose a more complex physical barrier to movement (*e.g.,* Crist *et al.* 1992). Thus, the grass matrix would favour more rapid, sustained flights while the shrub matrix would likely reduce movement rates by forcing the beetles to make many stops and detours while negotiating the more complex vegetation structure typical of shrubby habitat (Johnson *et al.* 1992). The end result is that larger beetles making sustained flights through grass matrix habitat may be more likely to survive dispersal than would smaller beetles and may also be more likely to encounter new spurge patches than would beetles taking a more tortuous path in shrub matrix habitat.

It is impossible to know whether differences in wing morphology are even proximately caused by landscape structure (*i.e.,* different landscape types selecting for different morphologies) using the data presented here. An alternate hypothesis may be that beetles inhabiting spurge patches distant from release sites do not have to cope with the same level of intraspecific competition as would be experienced at or near to release sites and, therefore, are able to achieve larger body sizes (Anholt 1991). This alternative seems less likely, however, given the evidence that wing sizes of individuals inhabiting distant patches were generally larger than those of individuals at or near to release sites, even after body-size differences were taken into account. Taylor and Merriam (1995) reached a similar conclusion in their study of damselfly wing morphology in relation to habitat fragmentation; landscape structure selects for, or is associated with, other factors (*e.g.,* microclimatic differences among habitats) that select for different morphologies associated with flight capability.

It remains to be determined whether selection for particular phenotypes is a transient phenomenon related to the initial colonization of unoccupied habitat on different landscapes or whether there will be a lasting founder effect related to wing morphology and the landscapes onto which releases are made. A variety of insects exhibit wing polymorphisms related to habitat persistence, and these polymorphisms arise from a trade-off between maximizing reproductive ability and maintaining the ability to escape from unfavourable conditions (Wootton 1992; Denno 1994). In general, wing polymorphisms represent discrete and drastic morphological responses

associated with habitat stability but it is likely that more subtle differences arise as a function of individuals dispersing through altered or novel environments or landscapes (Taylor and Merriam 1995). In the context of weed biocontrol, introduced agents are released into entirely novel environments, often with host-plant distributions very different from their native range. Therefore, it seems reasonable that selection pressures for particular phenotypes (large wings) already present in the release populations occur frequently and in some cases may be conserved for many generations. Indeed, microevolutionary changes in biocontrol agents have been documented elsewhere (*e.g.,* host specificity shifts; Secord and Kareiva 1996 and parasitoid virulence; Hufbauer 2002). The current study does not represent an adequate test of this hypothesis but neither does it exclude the possibility. Because some of the individuals collected likely were the progeny of original colonizers of distant spurge patches (*i.e.,* collections were made two years following releases of *A. lacertosa* in the study region), the current data suggest that the large-winged phenotype is maintained for at least one or two generations.

2.6 General Discussion & Speculation

The analysis of movement rates presented in this chapter indicate that movement rates for both *Aphthona* species differ between grass- and shrub-dominated landscapes. Statistical analyses of immigration rates (Chapter 1), which are closely linked to the movement rates, indicate that the movement rate differences between landscape types are significant for *A. nigriscutis* but not for *A. lacertosa*. However, a survey of *A. lacertosa* incidence on the two landscape types shows that patches far from release sites on shrub-dominated landscapes are significantly less likely to be colonized by *A. lacertosa* than are patches on grass-dominated landscapes (Fig. 2.7). Combined, these results suggest that even small differences in movement rate between the two landscape types can produce very different patterns of distribution, at least in the short time-frame studied here (*i.e.,* 3 beetle generations).

These differences, even if short-lived, illustrate that in order to predict the extent to which newly released biocontrol agent populations will spread from initial release locations, both the structure of release landscapes and the movement behaviour and/or ability of the agent must be understood. From an operational perspective my results suggest that releases of *A. lacertosa* could be made more efficiently if they are tailored for specific landscape types. For example, in order to achieve similar levels of patch colonization, releases should be made closer together in regions dominated

by shrubby habitat compared to those in regions dominated by grassland. A similar case can be made for releases of *A. nigriscutis* because this species exhibited an even stronger effect of landscape type on movement rate, although it remains unclear how this difference specifically influences patterns of distribution of this species on the two landscape types.

The significant differences in both body and wing sizes of beetles inhabiting spurge patches on grass- versus shrub-dominated landscapes suggest that the two landscape types, or associated factors, select for morphologically different beetles. These differences in body and wing size are consistent with *A. lacertosa*'s pattern of patch colonization on the two landscape types (Fig. 2.7), suggesting that the morphological differences demonstrated here are associated with movement rates and distributions on the two landscape types. I have suggested that the different matrix habitats themselves may select (at least indirectly) for different wing morphologies and body sizes through differences in the risk associated with dispersal. However, the consequences for successful dispersal through the two matrix types are the opposite of what I had expected; immigration and movement rates are higher in the presumably more hostile grass matrix than in the less hostile shrub matrix. This is likely related to how beetles perceive and respond to the different matrix habitat types via behavioural decisions and physiological capabilities (*i.e.,* energy reserves and wing morphology) associated with movement (Åberg *et al.* 1995; Taylor and Merriam 1995; With 1994; Zollner and Lima 1997).

The suggestion that different landscapes 'select' for different body- and wing-size distributions of individuals has an interesting implication for the evolution of biocontrol systems in novel environments. Recent studies of microevolutionary change in host-specificity of biocontrol agents were prompted by concern regarding the safety of planned introductions (McEvoy 1996; Secord and Kareiva 1996; Simberloff and Stiling 1996). However, more subtle and relatively benign changes in host-specificity after introduction may also reduce the effectiveness of biocontrol agents (Hufbauer 2002). It is possible that selection for specific morphologies associated with movement ability can also influence the effectiveness of biocontrol agents by altering population dynamics through changes in patch colonization/immigration rates and these relationships may be further complicated depending on whether or not emigration rates are density dependent (Ruxton 1995; Matter 2001). In addition, if there are strong trade-offs between wing-size and fecundity in females (Denno 1994) selection for individuals with larger wings on certain landscapes may reduce population growth rates and presumably reduce impact on host plant populations. Such

effects are likely difficult to detect because so little is known about the comparative population dynamics of most weed biocontrol agents in their native and introduced ranges.

2.7 Conclusions

In this chapter I quantified several components of dispersal for *A. lacertosa* and compared how some of these components varied between different types of release landscape. The results indicate that even though relatively small differences in movement rate between the landscapes were observed, there were noticeable differences in spurge patch colonization patterns and beetle morphological features associated with dispersal. Combined, these differences suggest complex interactions between habitat structure, movement behaviour, and potential selection for morphologies that facilitate dispersal. Although these explorations do not represent an exhaustive quantification of factors that may influence weed biocontrol agent dispersal, they represent a starting point from which future studies may build. Furthermore, these explorations illustrate that important information regarding dispersal, not usually considered in weed biocontrol programmes, can be gleaned from relatively simple field experiments.

2.8 References

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Table 2.1. Parameter estimates for diffusion and negative exponential models fit to 1998 mark-recapture data for *A. nigriscutis* moving through grass matrix habitat. Parameters were estimated from the empirical data by non-linear least squares regression. All parameter estimates were significant at a Type I error rate ≤ 0.05.

Model	Parameter	Estimate	SE	*t*-value
Diffusion	A	208.3560	7.5323	27.6617
	B	110.5970	20.9261	5.2851
Negative exponential	α	0.0172	0.0028	6.0594

Table 2.2. Mark-recapture data fit to a negative exponential model to determine movement rates for *A. nigriscutis* and *A. lacertosa* through grass and shrub matrix habitats. The model parameter α (movement rate) was estimated using non-linear least squares regression. All values of α were significant at a Type I error rate ≤ 0.05.

Species	Matrix	N_0[†]	δ[†]	Recaptures by distance (m)[†]				α	SE	*t*-value
				100	200	300	400			
A. nig	Grass	431.4	0.12	13.8	4.4	1.67	0.67	0.0101	0.0002	58.65
		23.89	0.16	6.06	2.09	0.88	0.67			
	Shrub	461	0.04	0.4	0.4	0	0	0.0371	0.0054	6.90
		42.82	0.05	0.19	0.19	0	0			
A. lac	Grass	493.5	0.03	4.2	1.0	0.5	0	0.0169	0.0007	25.11
		131.1	0.04	0.84	0.31	0.5	0			
	Shrub	431.4	0.02	1.0	0	0	0	0.0234	0.0005	46.49
		127.8	0.01	0.43	0	0	0			

[†] Values are means (top line) and 1 sd (bottom line) from 5 replicate landscapes
N_0 – Mean number of beetles released at each distance
δ - recapture efficiency

Table 2.3. Number and proportions of recaptured (emigrant) beetles for each release density in the first emigration experiment. Beetles were recaptured in target patches with sweep nets and on fences erected on 3 sides of the release patches (see Fig. 2.2). The final column – number of beetles remaining in release patches – illustrates that most beetles had emigrated or died within 4-6 days following release.

Number released	Density (m^{-2})	Number recaptured (proportion)		Total	Number remaining in release patch
		In target patch	On fence		
200	8	1 (0.005)	0 (0)	1 (0.005)	2
400	16	0 (0)	0 (0)	0 (0)	1
800	32	1 (0.00125)	3 (0.00375)	4 (0.005)	7
1250	50	2 (0.0016)	0 (0)	2 (0.0016)	4
1875	75	1 (0.00053)	4 (0.00213)	5 (0.00267)	6
2500	100	1 (0.0004)	2 (0.0008)	3 (0.0012)	13
3125	125	18 (0.00576)	15 (0.0048)	33 (0.01056)	13
	Mean	3.43 (0.00237)	3.43 (0.00237)	6.86 (0.0047)	

Table 2.4. Number and proportions of recaptured (emigrant) beetles, by sex, for each release density in the second emigration experiment. Beetles were recaptured in target patches with sweep nets and on fences erected to enclose the release and target patches (see Fig. 2.3). The proportion of male and female emigrants is based on the assumption of a 1:1 sex ratio in the released populations (see Methods).

Number released	Density (m^{-2})	Number recaptured (proportion)				Total
		In patches		On fence		
		♂	♀	♂	♀	
1000	250	14 (0.028)	37 (0.074)	14 (0.028)	14 (0.028)	79 (0.0790)
2000	500	81 (0.081)	120 (0.120)	58 (0.058)	58 (0.058)	317 (0.1585)
4000	1000	197 (0.098)	283 (0.141)	202 (0.101)	198 (0.099)	880 (0.2200)
6000	1500	276 (0.092)	333 (0.111)	406 (0.135)	287 (0.096)	1302 (0.2170)
Mean		142 (0.07)	193.25(0.11)	170 (0.08)	139.25 (0.07)	615.25 (0.1686)

Table 2.5. Analysis of deviance table. The response variable is the incidence of *Aphthona lacertosa* on spurge patches at various distance from release sites on grass and shrub landscapes. The model is a Generalized Linear Model fit with Binomial errors and a logit link. Distance is treated as a factor with 2 levels – *near* to and *far* from release sites (see Methods).

Term	df	Deviance	$Pr(\chi^2)$	β	*t*-value
Null	59	81.50		0.50	1.65
DISTANCE	1	7.28	0.01	-1.05	-2.45
LANDSCAPE	1	0.43	0.51	-0.08	-0.27
DISTANCE x LANDSCAPE	1	4.62	0.03	-0.89	-2.08
Residual	56	69.17			

Table 2.6. Analysis of deviance table. The response variable is *Aphthona lacertosa* tibia length. The model is a Generalized Linear Model fit with Gaussian errors and an identity link. Statistics presented (except for df) are based on the mean of 1000 models fit to the resampled data.

Term	df	Deviance	F-value	Pr(F)	β	*t*-value
Null	279	352630.40			387.46	179.93
SEX	1	10419.43	8.60	0.004	-5.81	-2.69
DISTANCE	1	8504.01	6.97	0.009	5.89	2.73
LANDSCAPE	1	1530.16	1.26	0.263	-2.18	-1.02
SEX x DISTANCE	1	3442.95	2.85	0.092	3.10	1.44
SEX x LANDSCAPE	1	407.19	0.34	0.562	-1.29	-0.60
LANDSCAPE x DISTANCE	1	6557.29	5.41	0.021	-4.86	-2.27
Residual	273	321769.4				

Table 2.7. Analysis of deviance table. The response variable is *Aphthona lacertosa* wing length (leading-edge vein), corrected for body size. The model is a Generalized Linear Model fit with Gaussian errors and an identity link. Statistics presented (except for df) are based on the mean of 1000 models fit to the resampled data.

Term	df	Deviance	F-value	Pr(F)	β	*t*-value
Null	279	319970.5			-1.83	-1.05
SEX	1	35881.5	45.18	<0.001	-11.32	-6.47
DISTANCE	1	36015.9	45.33	<0.001	10.66	6.11
LANDSCAPE	1	169.0	0.21	0.64	-0.32	-0.18
SEX x DISTANCE	1	18070.6	22.73	<0.001	-8.86	-5.07
SEX x LANDSCAPE	1	721.1	0.91	0.34	0.54	0.31
LANDSCAPE x DISTANCE	1	20118.2	25.36	<0.001	-8.71	-5.02
Residual	273	208994.2				

Table 2.8. Analysis of deviance table. The response variable is *Aphthona lacertosa* wing width, corrected for body size. The model is a Generalized Linear Model fit with Gaussian errors and an identity link. Statistics presented (except for df) are based on the mean of 1000 models fit to the resampled data.

Term	df	Deviance	F-value	Pr(F)	β	*t*-value
Null	279	115867.03			-1.06	-1.01
SEX	1	12075.35	42.61	<0.001	-9.56	-6.48
DISTANCE	1	11204.81	39.52	<0.001	8.41	5.71
LANDSCAPE	1	512.44	1.80	0.18	-2.48	-1.69
SEX x DISTANCE	1	7725.59	27.24	<0.001	-11.57	-5.54
SEX x LANDSCAPE	1	1511.05	5.34	0.02	3.44	1.65
LANDSCAPE x DISTANCE	1	8278.01	29.21	<0.001	-11.19	-5.40
Residual	273	74559.78				

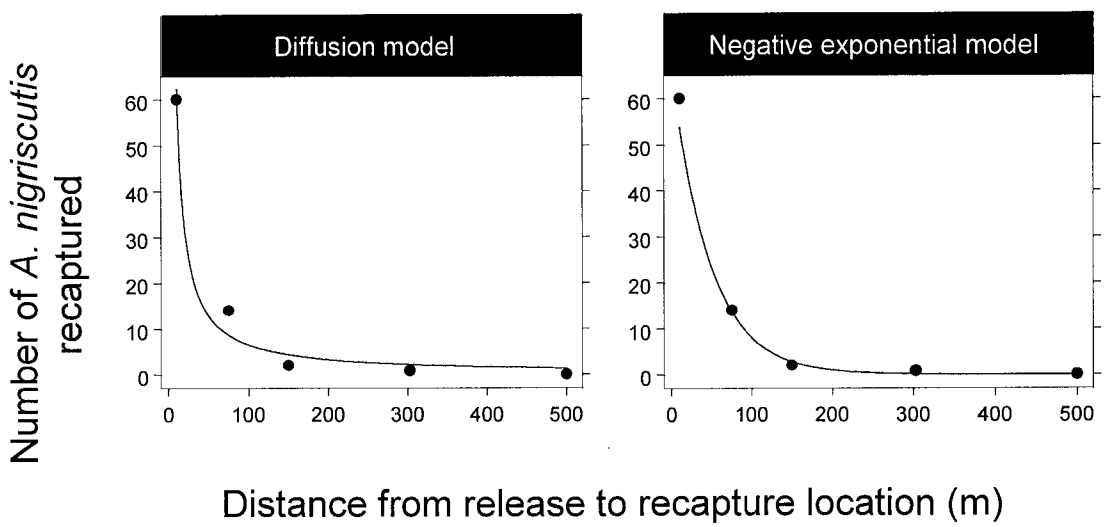

Figure 2.1. Results of diffusion (A) and negative exponential (B) models fit to mass-mark-recapture data for *Aphthona nigriscutis* released at 5 distances (10, 75, 150, 300, and 500 m) from a single spurge patch on a grass-dominated landscape in 1998. Parameter estimates and their precision are presented in Table 2.1.

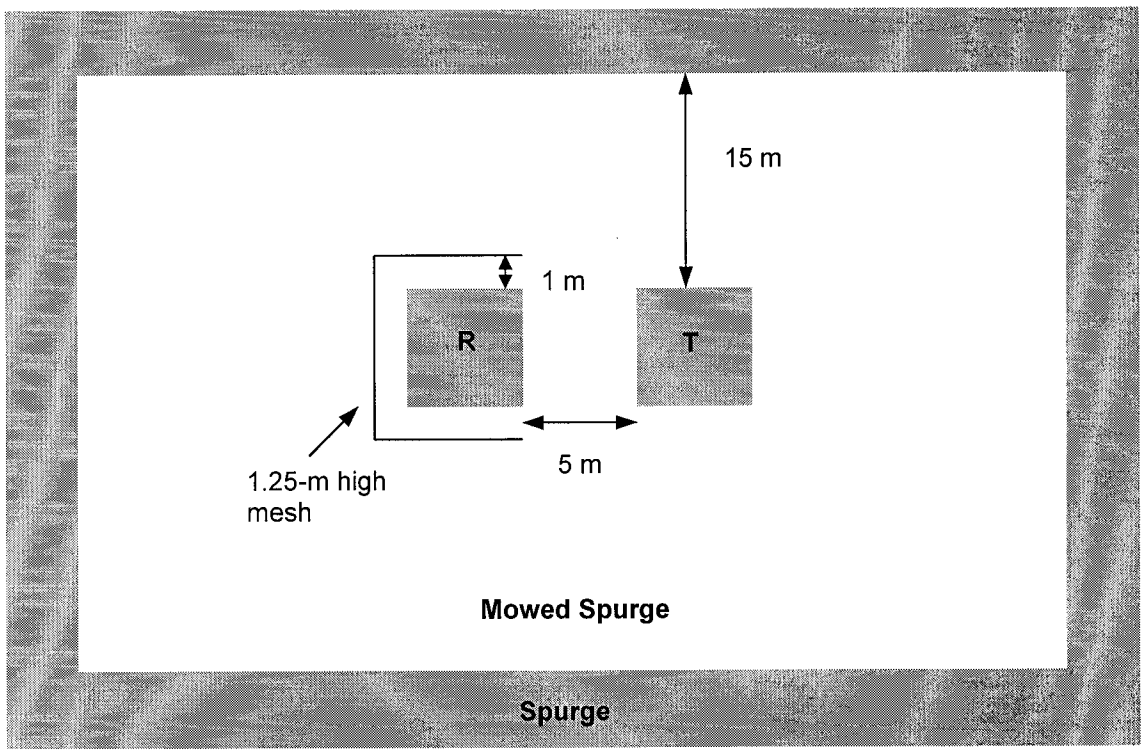

Figure 2.2. Schematic representation of the experimental arena for the first emigration experiment. The diagram illustrates the patch and fence configuration for a single release. Releases of different densities (7 in total) were conducted on each of 7 experimental arenas. Beetles were released in one patch (indicated by R) and emigrants were captured on the fence and in the target patch (indicated by T).

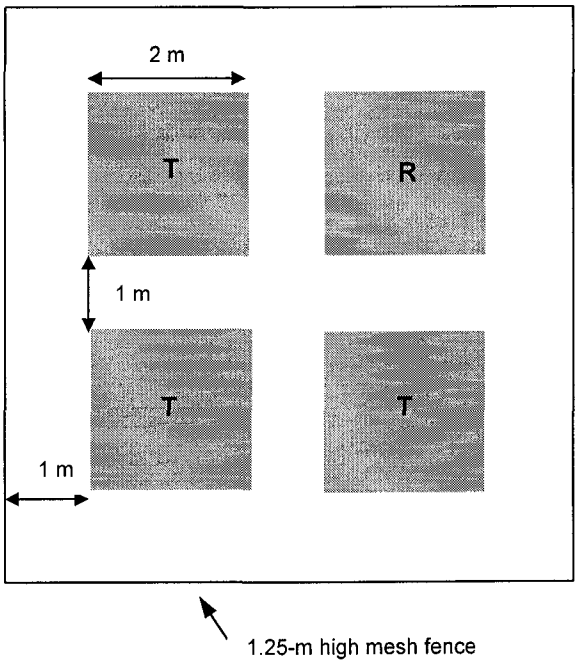

Figure 2.3. Schematic representation of the experimental arena for the second emigration experiment. A single release of *Aphthona lacertosa* was conducted in one patch (indicated by R) and emigrants were recaptured on the fence and in the 3 target patches (indicated by T). A total of 4 releases, each of different density, was conducted on 4 separate arenas.

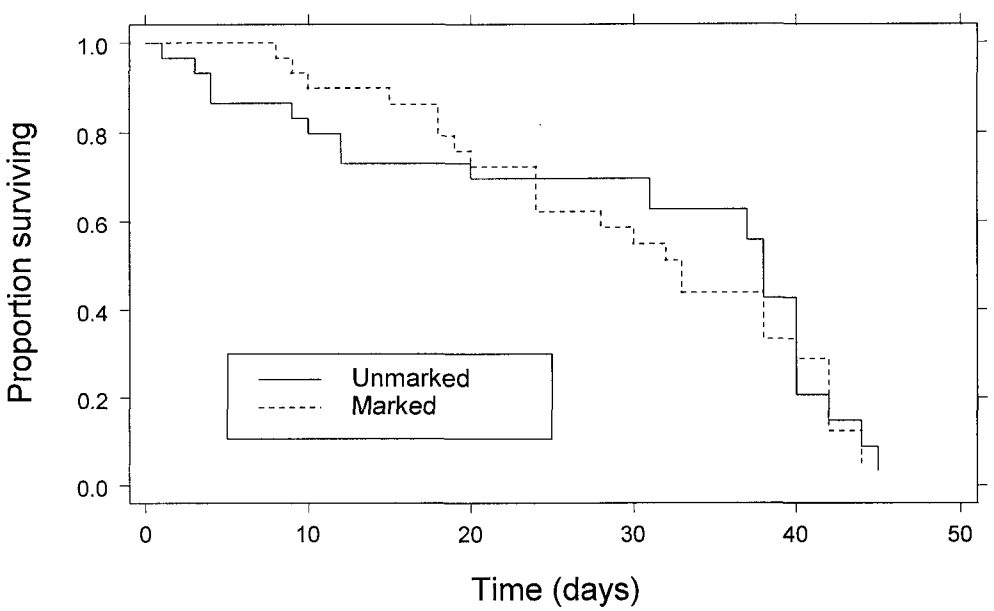

Figure 2.4. Survival curves for unmarked and marked *Aphthona lacertosa* observed in the lab.

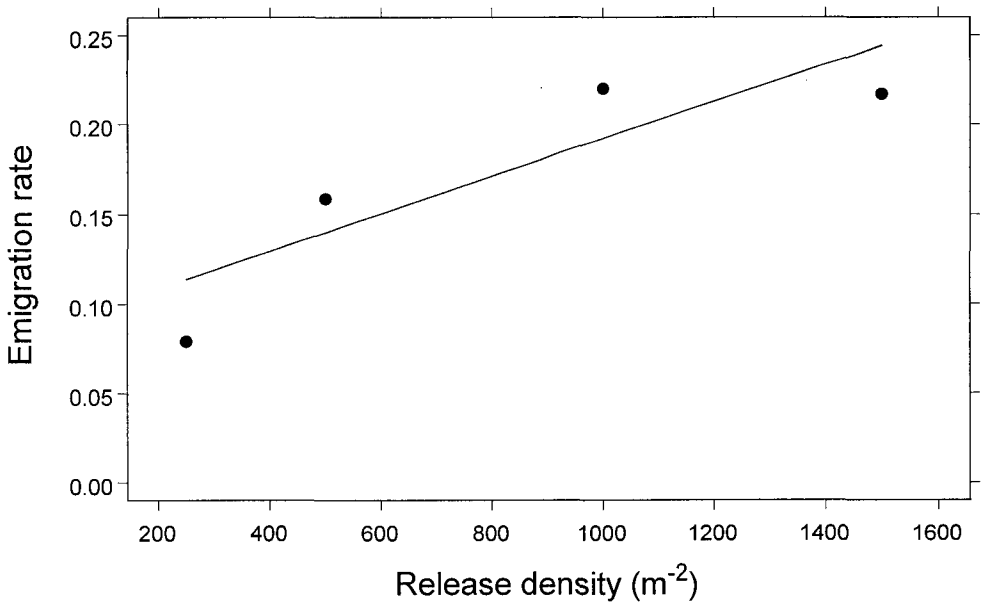

Figure 2.5. The proportion of *Aphthona lacertosa* emigrating from patches as a function of release density. The regression line is from a Generalized Linear Model fit with binomial errors and logit link.

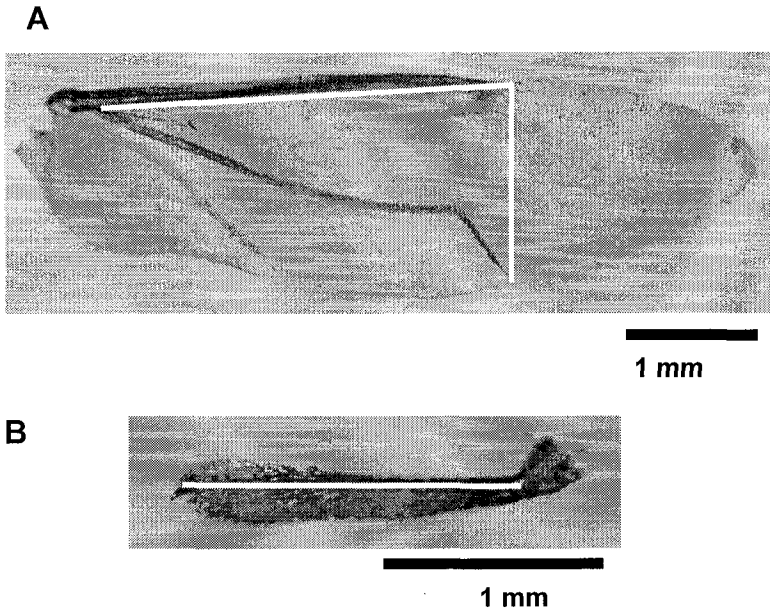

Figure 2.6. The proportion of *Aphthona lacertosa* emigrating from patches as a function of release density. The regression line is from a Generalized Linear Model fit with binomial errors and logit link.

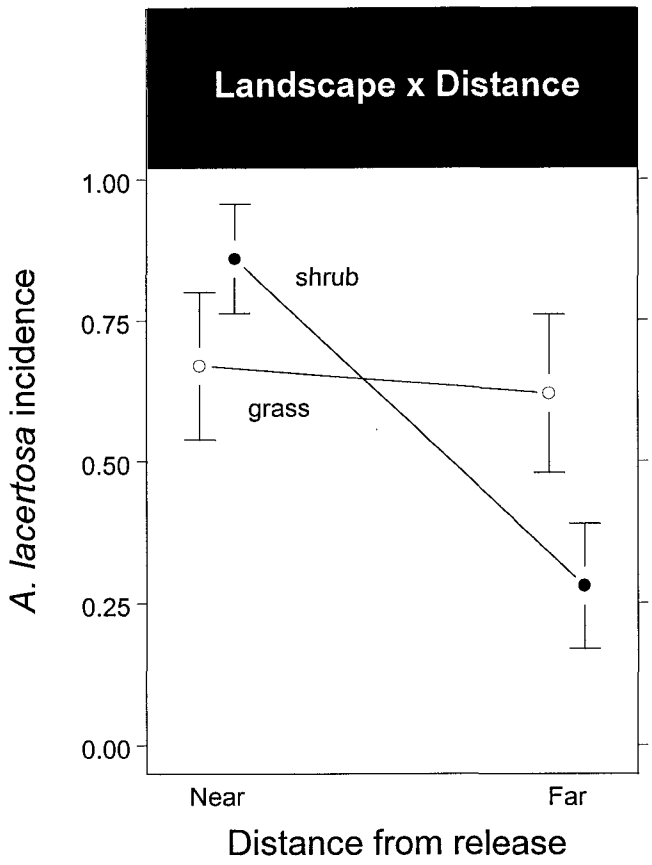

Figure 2.7. Interaction plot showing differences in *Aphthona lacertosa* incidence on spurge patches located near to and far from 1997 release sites, according to landscape type: grass- or shrub-dominated. Data points are means and error bars are ± 1 se.

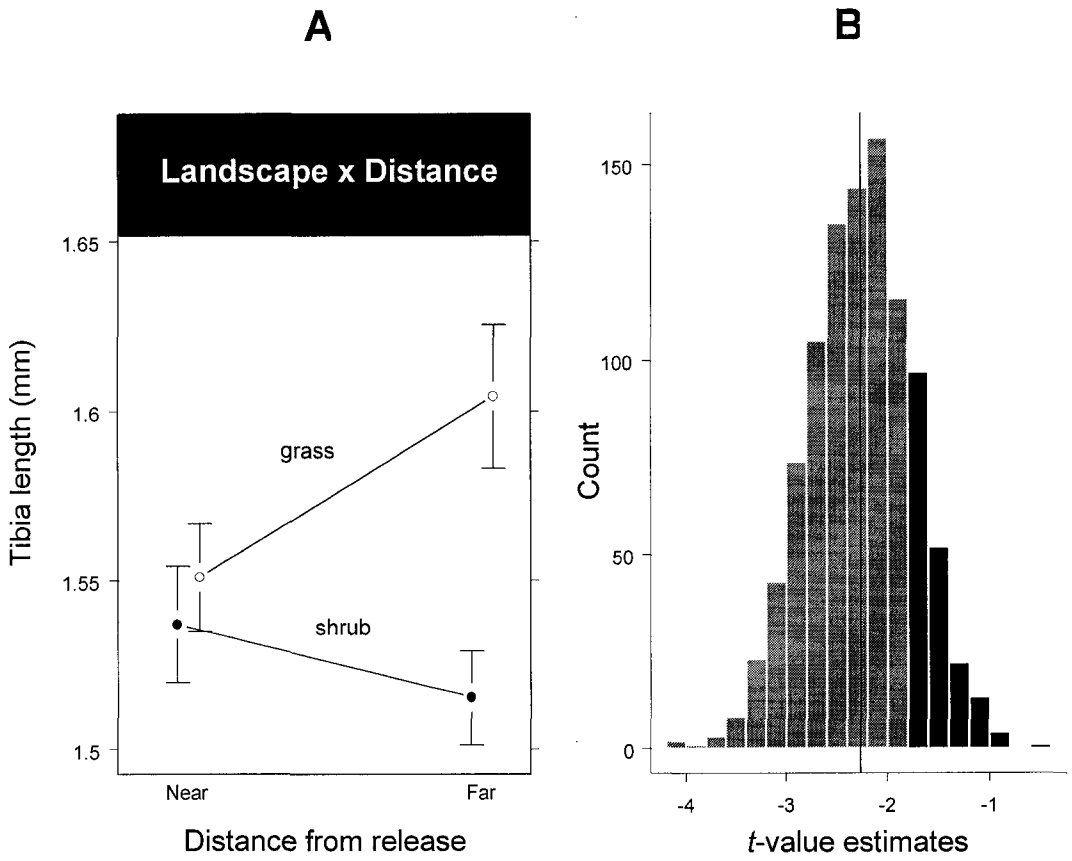

Figure 2.8. Interaction plot (A) showing differences in tibia lengths for *Aphthona lacertosa* individuals collected on spurge patches near to and far from 1997 release sites, according to landscape type: grass- or shrub-dominated. Data points are means and error bars are ± 1 se. The histogram (B) illustrates the distribution of *t*-values obtained for the interaction term in the 1000 bootstrapped glm models. The mean *t*-value is indicated by the vertical line. Non-significant (α = 0.05) *t*-values are shaded black.

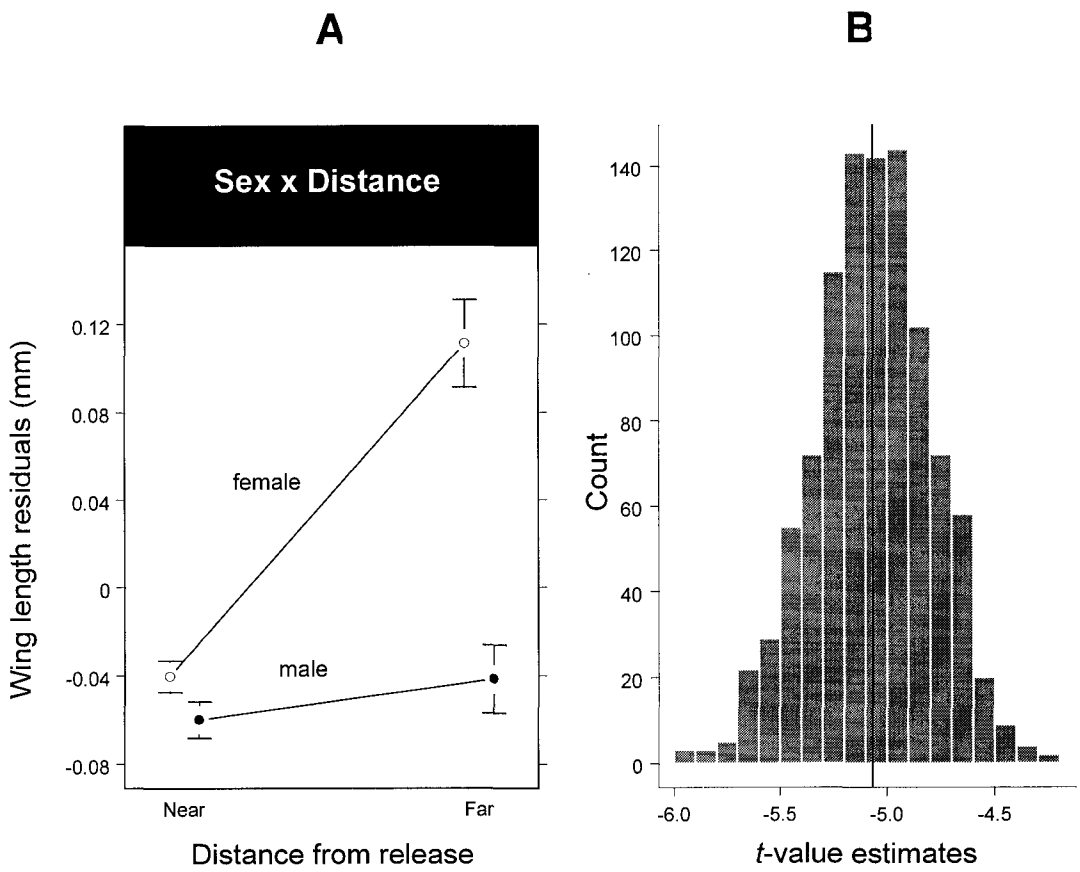

Figure 2.9. Interaction plot (A) showing differences in wing lengths, controlled for overall body size, for *Aphthona lacertosa* individuals collected on spurge patches near to and far from 1997 release sites, according to sex. Data points are means and error bars are ± 1 se. The histogram (B) illustrates the distribution of *t*-values obtained for the interaction term in the 1000 bootstrapped glm models. The mean *t*-value is indicated by the vertical line. No non-significant *t*-values were obtained.

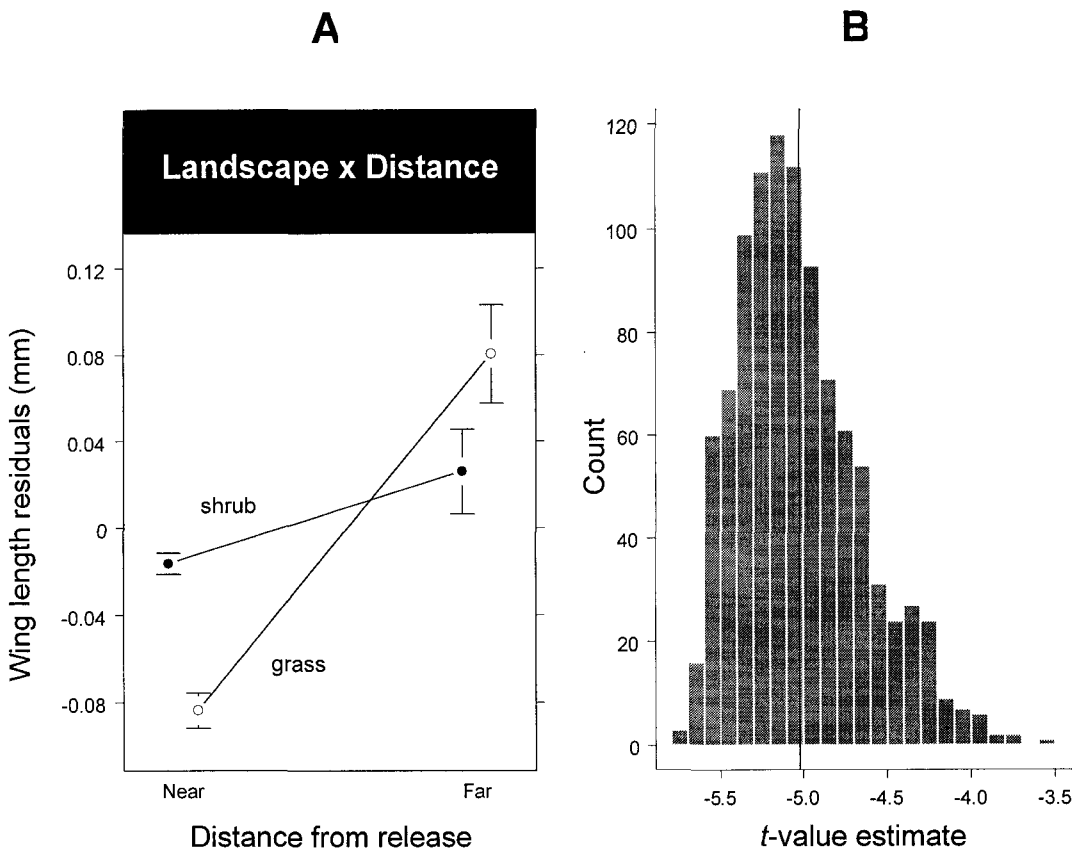

Figure 2.10. Interaction plot (A) showing differences in wing lengths, controlled for overall body size, for *Aphthona lacertosa* individuals collected on spurge patches near to and far from 1997 release sites, according to landscape type: grass- or shrub-dominated. Data points are means and error bars are ± 1 se. The histogram (B) illustrates the distribution of *t*-values obtained for the interaction term in the 1000 bootstrapped glm models. The mean *t*-value is indicated by the vertical line. No non-significant *t*-values were obtained.

Chapter 3

An exploration of the spatial dynamics and impact of *Aphthona* flea beetles on leafy spurge

3.1 Introduction

Organisms respond to their environment across a variety of spatial (and temporal) scales (Wiens 1989; Levin 1992) and interactions that are relevant to population dynamics and persistence may play out on much broader scales than are traditionally studied (May 1994; Roland and Taylor 1997). Studies of biocontrol agent impact on invasive weeds generally focus on interactions between the target weed, the biocontrol agent(s), and other features of the environment at local spatial scales (McEvoy *et al.* 1993; Kirby *et al.* 2000; Sheppard *et al.* 2001). While these studies are vital to understanding how weed biocontrol systems operate, additional insight into important processes can be gained by augmenting local-scale studies with data collected at broader scales that encompass whole release landscapes and/or regions containing multiple releases (Huffaker and Kennett 1959; McEvoy *et al.* 1991; Harrison *et al.* 1995).

In addition, the role that habitat features may play in the establishment of *Aphthona* flea beetle releases (McClay *et al.* 1995; Jacobs *et al.* 2001) and the influence these beetles have on leafy spurge populations (Kirby *et al.* 2000) has been evaluated at a local scale (*e.g.,* 10's of m), centred on initial release sites, but has not been explored at broader scales comprising entire release landscapes (*e.g.,* 100's to 1000's of m). Whole landscapes infested with spurge are often characterized by clusters of spurge patches of varying size and distance from one another and releases of *Aphthona* beetles are usually made in the largest patches (*e.g.,* 1000 – 100 000 m^2 in size). While initial signs of agent establishment and impact may appear near to release points, other processes, such as agent dispersal and habitat use, that may have longer-term implications for release success (see Chapter 4) occur over broader scales. Purposeful redistribution of agents on a landscape-by-landscape basis is obviously impractical, and so, understanding the extent to which agents disperse from initial release sites and show impact on distant weed patches should be an important goal of post-release monitoring programs.

In this chapter I present data from a single, intensive-study landscape comprised of numerous spurge patches of varying size and degree of isolation. Two *Aphthona* flea beetle species were present on the landscape; *A. lacertosa* originated from a single release conducted in 1997 and *A. nigriscutis* originated from releases made in the general area prior to 1997. The objectives of this study were: (1) to explore the importance of habitat attributes measured at both fine- (*i.e.,* attributes measured at scales of 1 m or less) and broader-scales (*i.e.,* attributes measured at scales of 10's to 100's of m) on densities of *A. lacertosa* and *A. nigriscutis* over two years and (2) to determine the extent to which *Aphthona* beetles influence spurge population densities on patches isolated from initial release locations.

3.2 Methods

3.2.1 Study landscape

All data were collected from a single, intensive-study landscape located on the Blood Indian Reserve, Southern Alberta (Fig. G.1). Further details of the landscape are presented in the General Methods. In 1997 two releases of 2000 individuals each were made on the landscape, one of *A. lacertosa* and one of *A. nigriscutis*. Preliminary samples collected in 1998 indicated that the *A. lacertosa* release had successfully established but that the *A. nigriscutis* release had not (possibly due to sheep grazing immediately following the release; RD Thomson, *personal*

communication), however, *A. nigriscutis* was present throughout much of the landscape at low densities (*personal observation*).

In 1998, 198 spurge patches were identified and mapped on the study landscape and 67 (34 %) of these were selected for yearly monitoring of habitat characteristics and beetle densities. Because it was unknown how rapidly *Aphthona* flea beetles spread from a point release and colonize distant patches, I split sampling effort into two distinct regions of the landscape. The first sampling region (Microgrid) was centered on the 1997 *A. lacertosa* release site and was comprised of 29 small spurge patches (range: 0.97 to 106.4 m^2, median ± 1 sd: 15.09 ± 23.32 m^2) located within a single, deep coulee (Fig. 3.1). The maximum distance from the 1997 *A. lacertosa* release point to any spurge patch on the Microgrid was 193 m. The second sampling region (Mesogrid) encompassed the remainder of the landscape and was comprised of 38 patches that range in size from 0.2 m^2 to 2641.9 m^2 (median ± 1 sd: 305.28 ± 560.73 m^2) (Fig. 3.1). The maximum distance from the 1997 *A. lacertosa* release point to any spurge patch on the Mesogrid was 1295 m.

3.2.2 Sampling methods

Permanent sample points were selected haphazardly within the central portion of each of the 67 patches. In an effort to balance sampling effort among patches of different size, I varied the number of sample locations (range: 1 to 5) approximately according to the square root of patch size. At each sample location adult beetle densities were sampled non-destructively using a modified leaf blower to vacuum beetles from the ground and off vegetation. To define the area to be vacuumed and to prevent beetles escaping, a garbage can with the bottom cut out (0.135 m^2 opening) was placed around the sample point and the interior was vacuumed for 45 s. The samples, collected in a fine mesh sock, were emptied into a clear plastic container and any beetles present were identified and counted and then returned to the original location within the patch.

Although adult *Aphthona* beetles can defoliate spurge stems, it is the root-feeding larvae that provide lasting damage to spurge plants (Harris 1984). Unfortunately, attempts to sample larvae using a combination of emergence traps and soil cores were both unfruitful and impractical given the broad extent of sampling involved. It was for these reasons that adult densities were sampled and used as an index of population density.

Fine-scale habitat data were collected using 0.0625 m^2 quadrats placed at each of the permanent sample locations. Spurge stems were counted in quadrats and separated according to flowering, and vegetative stems. Digital photographs were taken of each quadrat and the percent cover of forbs and grass, woody vegetation, bare ground, and litter were estimated from the photographs. Percentages of the cover classes were not restricted to sum to 100 % because several of the cover classes occupied different vertical strata within the quadrats. Because the cover classes were highly correlated with one another, I used Principal Components Analysis (PCA) to create uncorrelated variables derived from the original cover classes. The first three principal components, accounting for 94.7 % of the variation in the original cover classes, were used in the habitat models described below. Table 3.1 shows the composition of the 3 PCA-derived variables. Broader-scale habitat data were collected using a combination of GPS and GIS tools (see General Methods). A summary of the variables used as predictors in the statistical models described below is presented in Table 3.3.

3.2.3 Statistical analyses

3.2.3.1 Effects of habitat on beetle density

I used linear mixed-effects models (LME models - Pinhéiro and Bates 2000) to explore the relationships among various fine- and broader-scale habitat attributes and *Aphthona* densities on the study landscape. This approach allowed me to determine specifically whether broader-scale habitat variables, such as patch-size and patch isolation, explain additional variability in *Aphthona* densities after accounting for more commonly studied effects of fine-scale habitat variables, such as spurge density.

I used LME models instead of more common tools (*e.g.,* ANOVA, GLM) because of the hierarchical nature of the survey data – *e.g.,* multiple counts of beetles and assessments of fine-scale habitat were made within multiple spurge patches. Using a more conventional regression approach was not valid because the fine-scale data effectively were pseudo-replicated. LME models account for the hierarchical data structure by allowing the partitioning of error terms according to a grouping factor (Pinhéiro and Bates 2000), in this case individual spurge patches. Beetle densities were modeled separately for the two species and the two years (1999 & 2000) in which detailed habitat data were collected. As indicated earlier, sampling effort on the landscape was divided between two regions – Microgrid and Mesogrid (Fig. 3.1) – that were distinct both in their distance from the 1997 *A. lacertosa* release site and in the size and distribution of spurge

patches present (see Fig. 3.1). To determine whether *A. lacertosa* densities were different in these two regions, I tested whether the factor GRID had a significant relationship with *A. lacertosa* density, in addition to the other habitat variables.

The surveys were restricted to a single landscape on which single releases of both species were made, therefore, beetle densities may not be independent even among widely separated spurge patches. This potential lack of independence among sampled patches was accounted for by removing the effects of spatial location from beetle density estimates prior to assessing habitat relationships. To do this I fit loess surfaces using the spatial coordinates of the sample locations to the density data for each beetle species in each year using generalized additive models (GAMs – Hastie and Tibshirani 1990; Preisler *et al.* 1997). I then used the residuals from the GAMs, which were normally distributed (or approximately so), as the response variables for the LME models.

Because the goal of this exercise was to determine if broader-scale habitat attributes explain patterns of beetle density above and beyond that explained by fine-scale attributes, I adopted a conservative modelling approach. I fit significant fine-scale habitat variables before assessing the effects of the broader-scale habitat variables. Thus, models were specified in a two-stage, stepwise fashion, retaining the term at each iteration that contributed the maximum change in log-likelihood from the previous model and dropping subsequently non-significant terms. This procedure was followed until the model could not be significantly ($\alpha = 0.1$) improved by the addition of another term. Adequacy of the final models was assessed using residual diagnostics (McCullagh & Nelder 1989; Pinhéiro and Bates 2000). Quadratic terms for variables (excluding NNB1) were tested to determine whether significant relationships were monotonic or curvi-linear. Only significant terms are included in the final models presented.

There was potential for relationships between the habitat variables and beetle densities to change between years because separate LME's were fit for each year of survey data. It is of interest to know whether these differences were due to changes in the habitat variables themselves or to changes in habitat preference of the beetles, the latter possibly resulting from changes in other variables, such as precipitation, that were not measured. Therefore, as a follow-up analysis, I assessed whether there were significant changes between 1999 and 2000 for any of the fine-scale habitat variables. Wilcox rank-sum tests were used to determine whether the means of each fine-scale variable were significantly different between the two years. However, because the PCA-

derived variables fit in the LME models were derived from habitat data pooled between years there was little between-year difference in the means for each PC variable. Therefore, I present results of tests for between-year differences in the original percent cover variables.

Spatial variation in beetle density was removed prior to analysis with LME models (see above) and this potentially down-played the importance of the broader-scale variables. I, therefore, followed-up the LME model analyses by fitting tree-based regression models (also referred to as CART – classification and regression trees: Breiman *et al.* 1984; Venables and Ripley 1994; De'ath and Fabricius 2000) to the original beetle density data (*i.e.,* without spatial variation removed) to further explore the relationships between the broader-scale habitat variables and *Aphthona* beetle densities. Tree-based regression can reveal complex interactions among predictor variables without the level of replication or balanced design typically required by traditional regression methods and thus represents a powerful tool to augment analyses using more traditional approaches.

Variation in a response such as beetle density is explained by tree-based models via successive splitting of the response into increasingly homogeneous groups according to the predictor variables (or a subset of them) specified at the outset. Regression trees are 'grown' as a series of nodes where the data are split according to binary decisions based on the predictor variable that best minimizes the variability in the response at each node (here expressed as deviance – the sum of squares about the mean value of the response variable at that node; Clark and Pregibon 1992). Terminal nodes are groups of observations that can no longer be split in an optimal way according to the predictor variables supplied. In many cases trees become 'over-grown' (analogous to an over-specified linear regression model) and 'pruning' is used to arrive at a parsimonious model by removing nodes that do not contribute substantially to the model's predictive ability. Pruning is commonly achieved via a cross-validation approach that uses random subsets of the complete dataset to fit trees of all possible sizes and compare the predictions of these trees to a reserved subset of the data (Venables and Ripley 1994; De'ath 2002). The deviance (prediction error) for each tree plotted against tree size can reveal the smallest tree nearest the minimum deviance. Successive cross-validation runs can be used to determine if there is a consistent tree size (the most parsimonious tree) close to the minimum deviance (Andersen *et al.* 2000).

I fit separate regression trees to *A. nigriscutis* and *A. lacertosa* density data in each of the two years, 1999 and 2000. I used only the broad-scale predictor variables for these analyses: DIST2REL (or DIST2NREL), SHBAREA, NNB1, and PATCHSIZE (see Table 3.2 for a description). The results of the regression tree modelling exercise are presented graphically.

3.2.3.2 Effects of beetle density on spurge

I used geostatistics to visualize landscape-level trends in spurge and beetle densities over the three sample years. Semivariograms of log-transformed spurge and beetle densities were modeled using a weighted non-linear least-squares algorithm with a spherical covariance structure (Cressie 1993) and ordinary kriging (Rossi *et al.* 1992; Cressie 1993) was used to generate interpolated maps on a 10-m resolution grid defined by the convex hull drawn around the outer sample locations. Geostatistics are conventionally used to model spatial dependencies in continuously distributed variables, whereas the spurge and beetle density data are patchily distributed over the study landscape (see Fig. 3.1). For this reason, the interpolated maps are used as general guides to visualize broad-scale trends over the entire landscape rather than as tools to predict spurge or beetle densities at specific, unsampled locations.

Beetle impact on leafy spurge was assessed by regressing beetle density on the change in spurge stem density between consecutive years. I expected there to be a one-year lag between adult beetle density and a change in spurge stem density because root-feeding larvae cause the majority of impact on the plant (Harris 1984). Therefore, changes in spurge stem density between consecutive years (*i.e.*, t-1 and t) should be related best to adult beetle density in the first year of the sequence (*i.e.*, t-1). Linear regression models were fit to the patch-specific means of spurge stem and beetle densities and were weighted according to the number of observation made in each patch. Separate models were fit for each species and for the total densities of the two species combined, according to the sample grid (Microgrid or Mesogrid) to determine if the species exhibited differential impact on spurge stems and to determine how these differences might be manifested at two different scales of habitat patch distribution (Microgrid versus Mesogrid). In addition, stem densities were separated into flowering and vegetative stems and new regression models were fit for each and for the two sampling grids to determine whether beetle impact was focused on one or the other stem type and whether this differed between the two sampling grids. These models were fit using total beetle densities (see Results).

In addition to changes in spurge stem densities, spurge patch sizes may also change as a result of beetle activity. I, therefore, assessed the relationship between total beetle densities and changes in patch size between consecutive years as a second measure of beetle impact. For these analyses I fit weighted linear regressions to data from the Microgrid and Mesogrid separately and assessed the relationships between the log change in spurge patch size for years t-1 and t and total beetle densities at t-1.

Additional variation in spurge density changes not explained by adult beetle densities may be explained by habitat variables related either to larval densities or to spurge densities. As a check on this I augmented the Microgrid and Mesogrid models that fit total spurge stem density changes best (see previous paragraph) by testing for additional relationships with habitat variables (see Table 3.2) after accounting for the effect of adult beetle density.

Finally, to quantify the spatial extent of *A. lacertosa* impact on spurge density, I fit a cubic B-spline under the GAM framework (Hastie and Tibshirani 1990) to the patch-specific log change in spurge stem density between 1999 and 2000, using distance to the 1997 *A. lacertosa* release site as a predictor. The model was weighted for the number of observations made with in each spurge patch (as above). This non-parametric approach was adopted because a plot of the change in stem density as a function of distance from the *A. lacertosa* release suggested a non-linear relationship (see Fig. 3.6). The Microgrid and Mesogrid data were pooled for this analysis because I was interested in how beetle impact was distributed over the entire study landscape. I did not conduct a similar analysis for *A. nigriscutis* because this species appeared to have little impact on spurge density over most of the landscape (see Results).

3.3 Results

Of the 67 patches that were vacuum-sampled from 1999 to 2001, *A. lacertosa* was present in 46 (69%) patches in 1999, 27 (40%) patches in 2000, and 17 (25%) patches in 2001, whereas *A. nigriscutis* was present in 43 (64%) in 1999, 19 (28%) in 2000, and 18 (27%) in 2001. Twenty-three (34%) patches were occupied by both species in 1999, 7 (10%) in 2000, and 5 (7%) in 2001. The decrease in patch occupancy between 1999 and 2000 was in part due to the complete (or nearly so) disappearance of spurge stems on several patches in 2000, however, many of these patches re-appeared in 2001 but were not subsequently colonized by either species. Joint

occupancy by the two species was lower than expected in 1999 (observed = 34%, expected = 44%) but was the same as expected in the subsequent 2 years.

3.3.1 Habitat effects on beetle density

3.3.1.1 Fine- and broader-scale habitat variables combined (LME models)

The general goal of this model fitting exercise was to determine whether broader-scale habitat features could explain variation in beetle densities above and beyond that explained by fine-scale features. Results of the LME models (Tables 3.2 and 3.3) indicate that at least 1 broader-scale variable had a significant relationship with beetle density after accounting for fine-scale habitat effects in each of the 4 models fit.

There were varied relationships between the habitat attributes measured (see Table 3.2 for list) and beetle densities between years. No variable had a consistently significant relationship with density for both species and in both years, although spurge density – either total density (SPURGE) or vegetative density (VSPURGE) was significant in 3 of the 4 models. Furthermore, the factor GRID had no apparent relationship with *Aphthona* densities in either year, indicating that densities did not differ noticeably between the two sample grids (Tables 3.3 and 3.4).

For *A. lacertosa*, total spurge stem density (SPURGE) and PATCHSIZE had consistently significant relationships with beetle density between 1999 and 2000 but the nature of these relationships changed from monotonic, increasing for SPURGE and decreasing for PATCHSIZE, in 1999 to quadratic, initially increasing and then decreasing for both variables, in 2000 (Table 3.3). In addition, *A. lacertosa* densities in 1999 increased with increasing GRASSFORB cover but this relationship disappeared in 2000 (Table 3.3). The LME models explained a surprisingly small portion of the variation in *A. lacertosa* density; 0.08 in 1999 and 0.07 in 2000.

The fine-scale variables GROUND and GRASSFORB and the broader-scale variable PATCHSIZE all had quadratic relationships with *A. nigriscutis* density in 1999 (Table 3.4). *A. nigriscutis* densities initially decreased with increasing GROUND cover and then increased at higher values, whereas the opposite occurred for both GRASSFORB and PATCHSIZE (Table 3.4). None of these predictors were significant in 2000, instead *A. nigriscutis* densities increased with increasing VSPURGE and decreasing DIST2NIGREL (Table 3.4). As was the case for *A. lacertosa*, the LME models for *A.*

nigriscutis explained a surprisingly small portion of the variation in density; 0.18 in 1999 and 0.03 in 2000.

The between-year changes in relationships among fine-scale habitat variables and beetle density illuminated in Tables 3.3 and 3.4 suggest that the habitat variables themselves may have changed between years. Table 3.5 shows that most of the fine-scale habitat features did indeed change between years. However, the percent cover of grass and forbs, the dominant component of the PCA-derived variable GRASSFORB, did not change significantly, even though the relationships between this variable and both *A. lacertosa* and *A. nigriscutis* densities changed in significance between 1999 and 2000 (see Tables 3.3 & 3.4).

3.3.1.2 Broader-scale variables alone (tree-based models)

Results from the regression tree models are summarized graphically in Figs. 3.2 & 3.3. Using only the broader-scale habitat variables, the regression trees accounted for 52% (1999) and 58% (2000) of the total variation in *A. lacertosa* densities and 42% (1999 and 2000) of the total variation in *A. nigriscutis* densities; considerably more variation than the LME models that used both fine- and broader-scale variables. It should be noted that the relationships between the broader-scale variables and *Aphthona* density revealed by the tree-based models were generally consistent even when fine-scale variables were included (not presented). I chose to omit fine-scale variables from the analyses for ease of interpretation of the regression trees and because it was the relationships with broader-scale variables that were of most interest.

Comparison of the trees constructed for *A. lacertosa* densities observed in 1999 and 2000 indicates that DIST2REL was the single most important variable in both years (Fig. 3.2). In 1999, *A. lacertosa* densities generally were highest closer than 344 m to the 1997 release site but this was further modified by the proportion of shrub habitat surrounding spurge patches (SHBPROP), so that densities were higher on patches surrounded by at least some shrub habitat (Fig. 3.2). Beyond 344 m from the release site, densities were generally low, except for 6 small patches (PATCHSIZE) (Fig. 3.2). The pattern of relationships in 2000 was similar but slightly more complex than in 1999. Beetle densities were low to intermediate on patches within 143 m of the release site (this roughly corresponds to the Microgrid), were intermediate to high between 143 m and 561 m, and declined to 0 beyond 561 m. The former two situations, however, were complicated by interactions with SHBPROP and PATCHSIZE (Fig. 3.2).

Trees constructed for *A. nigriscutis* densities observed in 1999 and 2000 were somewhat different than those for *A. lacertosa* (Fig. 3.3). The variables PATCHSIZE and DIST2NREL (distance from 1997 *A. nigriscutis* release site) switched in importance from 1999 to 2000 (Fig. 3.3). In 1999 *A. nigriscutis* densities were lowest on patches less than 75 m^2 in size but this relationship was complicated by an interaction with patch isolation (NNB1), whereas, the higher densities found on patches greater than 75 m^2 in size also depended on DIST2NREL (Fig. 3.3). In 2000, however, *A. nigriscutis* densities were lowest on patches closer than 623 m from the release site and highest on patches that were not only greater than 15 m^2 in size but were also greater than 623 m from the *A. nigriscutis* release site (Fig. 3.3).

3.3.1.3 Comparison of LME and tree-based model results

Focusing strictly on the relationships between the broader-scale habitat variables and *Aphthona* density, it is of interest to compare the results from the LME and tree-based regression approaches. In general, the two methods revealed similar relationships between *Aphthona* density and the broader-scale habitat variables. The tree-based models, which were not constrained to use response variables with spatial variation removed, revealed the importance of spatial location relative to the 1997 release sites on beetle density (Figs. 3.2 and 3.3) and generally suggested that more complex relationships between density and broader-scale habitat exist than those revealed by the LME models (compare Table 3.3 with Fig. 3.2 and Table 3.4 with Fig. 3.3). A relationship between *A. nigriscutis* density and DIST2NREL was revealed by both methods but the nature of this relationship differed between the two methods; negative relationship for LME model (Table 3.4) and positive relationship for tree-based model (Fig. 3.3). The negative relationship likely arose as an artifact of the loess surface model fit to *A. nigriscutis* density prior to analysis with the LME method (see "Statistical analyses – effects of habitat on beetle density"). Maps of *A. nigriscutis* density over the study landscape show that higher densities were found in the NW of the study landscape (Fig. 3.4 G-I), thus supporting the tree-based model and conflicting with the LME model, with respect to the density – DIST2NREL relationship.

3.3.2 Beetle impact on leafy spurge

Interpolated maps of spurge and beetle densities (Fig. 3.4) illustrate the dynamic nature of the relationship between beetle and spurge density patterns over the entire study landscape. In 1999 spurge stem densities were lower around the 1997 *A. lacertosa* release location than elsewhere on the landscape (Fig 3.4 A). This area of low spurge density subsequently increased in size

dramatically in 2000 and generally corresponded to the area of highest *A. lacertosa* density in 1999 (compare Fig 3.4 B and D). On average spurge density decreased ($t_{169\ df} = -5.05$, $p < 0.001$) from 1999 to 2000, although there was some increase in other parts of the landscape (compare Fig. 3.4 A and B). In 2001 spurge density increased significantly ($t_{169\ df} = 5.69$, $p < 0.001$, Fig. 3.4 C) throughout much of the eastern portion of the landscape (Fig. 3.4 C), even though *A. lacertosa* density had increased slightly from 1999 to 2000 (Fig. 3.4 E – boxplot). Overall, there was no difference in spurge stem density between 1999 and 2001 ($t_{169} = 0.49$, $p = 0.62$), just their distribution changed.

Although no substantial differences in habitat – *Aphthona* density relationships were revealed between the Microgrid and Mesogrid sample areas, there were some clear differences with respect to impact on spurge populations (*personal observation*). I, therefore, proceed with graphical analyses of *Aphthona* impact on spurge populations separated according to sample area: Microgrid and Mesogrid.

Changes in total spurge stem density on the Microgrid between 1999 and 2000 were best correlated with either 1999 *A. lacertosa* densities alone, or with 1999 densities of both species (Fig. 3.5, left panels). The models for *A. lacertosa* densities alone and *Aphthona* densities (combined density of both species) are virtually identical, suggesting that *A. nigriscutis* played little role in declines in spurge density on the Microgrid. For the period 2000 to 2001, there was no relationship between change in spurge density and beetle density; spurge density increased during this period, regardless of 2000 beetle density (Fig. 3.5, right panels).

On the Mesogrid (Fig. 3.6), the regression model with *A. lacertosa* density alone accounted for slightly more variability in the change in spurge density from 1999-2000 but the model with *Aphthona* densities accounted for declines in spurge density where *A. lacertosa* was absent (Fig. 3.6, arrows on middle left & bottom left panels). The density of *A. nigriscutis* alone was not correlated with the change in spurge stem density (Fig. 3.6) and was, on average, lower than *A. lacertosa* throughout the entire landscape in 1999 and 2000 (1999: $t_{169\ df} = -4.37$, $p < 0.001$; 2000: $t_{169\ df} = -3.23$, $p = 0.001$) (Fig. 3.4 H-J). Boxplots of changes in *A. nigriscutis* densities between successive years (Fig. 3.4 H & I) and over the entire study period (Fig. 3.4 G) show that although there was considerable change in density at individual locations, the median change over the entire landscape was essentially zero. The increase in spurge density from 2000 to 2001 was poorly correlated with *Aphthona* density in 2000 (Fig. 3.6, right panels). Although *A. nigriscutis*

density was negatively correlated with the change in stem density between 2000 and 2001 on the Mesogrid (Fig. 3.6), the relationship was positive over much of the range of observed *A. nigriscutis* densities suggesting that the beetles merely limited increases in spurge density rather than reduced spurge density outright.

Flowering stem density on the Microgrid changed little with increasing beetle density (Fig. 3.7) but this was probably because the proportion of flowering stems on the Microgrid were very low at the outset of the study – 0.12 total stems present on the Microgrid versus 0.36 on the Mesogrid. In other words, beetle impact on flowering stems was low because the apparency (*sensu* Kareiva 1983) of these stems was low. Correspondingly, flowering stem density on the Mesogrid declined significantly with increasing beetle density (Fig. 3.7). That a linear regression model with initial flowering stem density fit as a covariate prior to fitting *Aphthona* density revealed a significant effect of initial stem density ($F_{1,36} = 16.6$, $p < 0.001$) but not *A. lacertosa* density ($F_{1,35} = 0.43$, $p > 0.5$), confirms this idea. Vegetative stem density declined significantly with increasing beetle density on both sample grids (Fig. 3.7).

Changes in spurge local populations were also assessed at a slightly broader scale than the preceding stem density analyses by measuring the change in spurge patch sizes between successive years. As with the changes in stem density, patch size decreased substantially on the Microgrid from 1999 to 2000 but this trend was reversed between 2000 and 2001 (Fig. 3.8). A total of 20 patches disappeared completely on the Microgrid in 2000 but 10 of these re-appeared in 2001. On the Mesogrid, patch size change was less variable overall and showed a slight decreasing trend between 1999 and 2000 and a slight increasing trend between 2000 and 2001 (Fig. 3.8). Three patches disappeared completely on the Mesogrid in 2000 and one of these re-appeared in 2001. Despite the apparent lack of a net decrease in patch size on either sample grid over the study period, there were some dramatic local decreases. For example, the large patch in which the 1997 *A. lacertosa* release was made (see Fig. 3.1, Microgrid) declined 38% (720.3 m^2) in area from 1999 to 2001 and 12 spurge patches disappeared between 1999 and 2001 (a total of 505.8 m^2).

Changes in patch size on the Microgrid, surprisingly, were not significantly related to beetle densities for either period (1999 – 2000 or 2000 – 2001) (Fig. 3.9). There was, however, some evidence that the largest increases in patch size between 2000 and 2001 occurred for unoccupied patches (Fig. 3.9, left panels), suggesting that at least patch occupancy by either (or both) species

influenced spurge dynamics at the patch scale. Changes in patch size on the Mesogrid were significantly and negatively related to *A. lacertosa* density alone and to *Aphthona* density but not for *A. nigriscutis* alone (Fig. 3.10). As for the stem density analyses (see Figs. 3.5 and 3.6) the regression model using *Aphthona* density appeared to be a better predictor of patch size change than was *A. lacertosa* density alone (Fig. 3.10, arrows on bottom and middle left panels). Also, in correspondence with the stem density analyses, there were no significant relationships between beetle density and changes in patch size between 2000 and 2001 (Fig. 3.10, right panels).

Focusing on the relationship between total beetle density and changes in spurge stem density, I fit multiple linear regression models to determine whether any habitat attributes (see Table 3.2) could further explain changes in spurge density. These 'enhanced' impact models, fit as separate regressions for the two sample grids, indicate that after accounting for *Aphthona* density no fine-scale habitat variables were related to changes in spurge stem density, on either sample grid, but that greater declines in spurge density were observed on the more isolated patches on the Mesogrid (Table 3.6).

The maps of spurge and *A. lacertosa* density (Fig. 3.4) indicate that the distribution of *A. lacertosa* over the study area was confined mainly to the eastern portion of the landscape and that this was where the majority of impact on spurge densities occurred between 1999 and 2000. A GAM fit to the data indicates that decreases in spurge density occurred up to approximately 500 m from the 1997 *A. lacertosa* release site but thereafter spurge density increased slightly (Fig. 3.11, bottom panel). There was, however, a large amount of residual variation in spurge density changes, suggesting that *Aphthona* impact on spurge density can not be predicted adequately based only on distance from release sites. As indicated in Fig. 3.4 B-C, spurge density increased from 2000 to 2001 throughout most of the landscape but especially closer to the release site (Fig. 3.11, top panel).

3.4 Discussion

3.4.1 Habitat effects on beetle density

Significant fine-scale habitat effects were generally consistent with the findings of previous studies on *Aphthona* beetles (Maw 1981; McClay *et al.* 1995). *A. lacertosa* densities were highest at locations with high grass-forb cover (GRASSFORB) while *A. nigriscutis* densities were lowest at

high levels of grass-forb cover but highest with low ground litter cover and high bare ground (GROUND). These patterns of fine-scale habitat effects are generally thought to reflect *A. lacertosa*'s preference for mesic sites and *A. nigriscutis*' preference for xeric sites with relatively low vegetation and litter cover (Maw 1981; McClay *et al.* 1995; Fellows and Newton 1999; Nowierski *et al.* 2002). The relationships between habitat characteristics and beetle densities, however, differed between 1999 and 2000 and further analysis indicated that the differences, with respect to the amount of grass and forbs, were not due solely to between-year changes in the habitat variables themselves. Other variables not considered here may have played a role in the inconsistency of this effect on beetle density, the most likely of which may be weather. In the region of southern Alberta encompassing my study landscape, average annual precipitation, which is positively correlated with *A. nigriscutis* density (Jacobs *et al.* 2001), was at 79 % of the 30-year mean (50.5 mm) in 1999 and dropped to 45 % in 2000 suggesting that changes in precipitation levels may be partly responsible for the between-year changes in habitat effects on *Aphthona* beetles. Habitat selection and population dynamics of insects can be constrained by direct effects of weather on the insects themselves (Solbreck 1991; Kindvall 1995; Solbreck 1995) or by interactions with host plant phenology or other habitat features (Dobkin *et al.* 1987).

The broader-scale habitat attribute, spurge patch size, had the most consistently significant relationship with beetle densities, in both the LME and tree-based models. Interestingly, for *A. lacertosa* the relationship between patch size and density was negative in1999 and switched to a peaked relationship in 2000 (Table 3.3). The negative relationships reflect the non-equilibrium state of the released population. In other words, not enough time had elapsed since the 1997 release for *A. lacertosa* to fully colonize larger patches, especially patches that are far from the 1997 release location (Fig. 3.2). This relationship is illustrated in Fig. 3.12, where differences in *A. lacertosa* density between small and large patches are plotted, according to distance (near vs. far) from the 1997 release site. Releases of *A. nigriscutis* were made prior to 1997 within the vicinity of my study area, so this species has had more time to reach an equilibrium density with respect to patch size and this is supported by the peaked relationship between *A. nigriscutis* density and patch size revealed by the LME models (Table 3.4) and the positive relationship revealed by the tree-based models (Fig. 3.3).

Based on observations of immigration and movement rates in shrub- versus grass-dominated landscapes (Chapters 1 and 2), I had expected a negative relationship between the amount of shrub habitat surrounding spurge patches and *Aphthona* density. The tree-based models, however,

suggested a positive relationship between *A. lacertosa* density and the proportion of surrounding shrub habitat, note however that the tree model distinguishes between locations with and without (or nearly so) shrub habitat (Fig. 3.2 – SHRBPROP < 0.0004). The relationship may indicate that the presence of shrub habitat in the vicinity of spurge patches is an indicator of slightly moister conditions which *A. lacertosa* prefers (Nowierski *et al.* 2002). The lack of a clear relationship between the proportion of shrub habitat and either species suggests that while differences in immigration rates between shrub- and grass-surrounded spurge patches may be real, they may only be short-term phenomena that are mitigated by subsequent within-patch population growth, or such differences are only observed when overall movement rates are low. These ideas are explored in more detail in Chapter 5. Alternative explanations for the lack of a relationship between beetle density and amount of surrounding shrub habitat are as follows. First, shrub habitat comprised a minor portion of the non-habitat on the study landscape (10 %) and may thus have little effect on immigration rates compared to landscapes with greater shrub habitat cover; Moilanen and Hanski (1998) reached a similar conclusion in their study of landscape effects on the metapopulation dynamics of butterflies. Second, in addition to a lack of an effect of shrub habitat there was also no strong effect of patch isolation, suggesting that few spurge patches were beyond the movement range of either species. Effects of patch isolation and non-habitat surrounding spurge patches may only be apparent at spatial scales broader than those considered here. Individual insect species respond to habitat spatial structure (*e.g.,* patch isolation) at a variety of scales, including very broad scales (100's m to 1000 m) that are beyond the typical movement range of individuals but may encompass interactions among different populations (Krawchuk and Taylor *in press*; Roland and Taylor 1997).

3.4.2 Beetle impact on leafy spurge

Results from the graphical analyses of *Aphthona* impact on leafy spurge indicate that *A. lacertosa* was responsible for the majority of observed reductions in spurge stem density occurring on patches within approximately 500 m of the initial release site. Although distance from the 1997 release site was an important predictor of *A. lacertosa* density (tree-based models), distance was a relatively poor predictor of impact on spurge density (Fig. 3.11 – large amount of residual variation about regression line). Reductions in spurge density occurred between 1999 and 2000 but were largely nullified by spurge re-growth in 2001 and a concomitant reduction in density and distribution of *A. lacertosa* on the release landscape. Despite the large fluctuations in spurge density and patch size observed over the duration of the study, there were some local extinctions of spurge populations (patches); 10 on the Microgrid and 2 on the Mesogrid. All of these were

small patches (< 50 m^2) based on measurements taken in 1999. The anticipated effects of *A. nigriscutis* on spurge densities in general were not realized. Although some decreases in spurge density appeared due to the presence of *A. nigriscutis*, these were negligible compared to those attributable to *A. lacertosa*. These results were likely due to relatively low densities of *A. nigriscutis* on the study landscape arising from failure of the 1997 *A. nigriscutis* release to establish (see Methods: *Study landscape*). *A. nigriscutis'* presence on the landscape was probably a result of colonizers arising from releases made in the area prior to 1997 (see McClay *et al.* 1995).

The large fluctuations in spurge and *A. lacertosa* densities on the study landscape were somewhat unexpected. Although few previous studies document yearly changes in spurge and beetle densities (Bourchier *et al.* 2002), I had expected that observations of beetle impact would be less transient given the broad consensus that *Aphthona* spp. are providing successful control of spurge populations in several areas of western North America (Julien and Griffiths 1998; Anderson *et al.* 1999; Bourchier *et al.* 2002). Although my study documents the dynamics of a single release, the 2001 decline in *A. lacertosa* densities was observed at release sites throughout the Blood Reserve (RS Bourchier *unpublished data*) and may be related to drought conditions experienced throughout much of Alberta in 2000 and 2001. The simultaneous decline in *A. lacertosa* density and increase in spurge density in 2001 suggests that either *A. lacertosa* larval over-wintering mortality was high or female fecundity/oviposition was abnormally low during summer 2000. The latter may have arisen from the widespread, early senescence of spurge plants (*personal observation*) that resulted from the drought conditions. Reductions in larval densities would reduce damage to spurge root systems and potentially contribute to the observed rapid increase in stem densities following the decline in the previous year. Alternatively, stem density increases could arise from a seed bank that remains viable for 5-8 years (Selleck *et al.* 1962; Bowes and Thomas 1978). Either explanation suggests that strong density-dependence at low densities allows spurge to recover rapidly from short-term control (*e.g.*, Maxwell *at al.* 1988) and that longer-term monitoring is vital to understanding the dynamics of the spurge – *Aphthona* interaction and the extent to which density-dependence and other factors (*i.e.*, weather, native plant competition) influence this interaction.

The linear regressions of *Aphthona* densities on changes in spurge stem density revealed significant relationships but these explained, at best, only 29 % of the variation in spurge stem density changes. I expected there to be considerable residual variation in these models because

adult densities were used as an index of population density (see Methods) and it is the root-feeding larvae that produce lasting damage to spurge plants (Harris 1984). A variety of factors such as spurge demography, adult movement and aggregation behaviours, high larval mortality, female oviposition behaviour (*e.g.,* Shea *et al.* 2000), and habitat effects may contribute 'noise' to the relationship between adult *Aphthona* densities and changes in spurge stem density. Some habitat variables may be important for larval survival but have little effect on adult densities and thus have an indirect effect on spurge density changes. The enhanced impact models suggest that none of the fine-scale habitat variables that I measured had an effect on spurge density changes except those that were related to adult *Aphthona* densities (see "Habitat effects on beetle density"). One broader-scale variable, patch isolation, was significantly related to spurge density changes on Mesogrid patches, indicating that spurge densities decreased more on patches that were further away from their neighbours. Patch isolation was positively related to *A. nigriscutis* density in 1999 (Fig. 3.3) but *A. nigriscutis* generally had little impact on spurge density, so the result is somewhat puzzling. I am uncertain of how patch isolation might interact with changes in spurge density, other than through direct effects on adult densities which can arise from decreased (although in this case increased – see Fig. 3.3) immigration to more isolated patches, an effect that should be accounted for by fitting *Aphthona* density prior to assessing the effect of patch isolation (Table 3.6). The regression tree model (Fig. 3.3), however, illustrates that the relationship between adult beetle density occurs at very small isolation distances (*i.e.,* ca. 10 m) and only on relatively small patches (*i.e.,* < 75 m^2), implying that an effect of patch isolation on beetle impact only occurs at very small scales (*i.e.,* ≤ 10 m). Nevertheless, the result, along with relationships between patch size, spatial location, and beetle density in the habitat models, implies that successful weed biocontrol is related not only to the commonly studied fine-scale habitat features between agents, their host plants, and other habitat features but also to the rarely studied broader-scale features such as host-plant patch structure.

3.5 Speculation

Results presented in this study are in some ways novel and unconventional compared to the majority of post-release weed biocontrol studies. Most post-release studies concentrate on relationships between habitat and agent density at or within the immediate vicinity of release sites (McClay *et al.* 1995; Fellows and Newton 1999; Kirby *et al.* 2000; Jacobs *et al.* 2001), whereas I focus on those relationships over a broader extent and on patches that are isolated from an initial

release site by intervening non-habitat. While initial signs of establishment and impact (or their absence) are likely to appear in close proximity to release locations, ignoring processes that occur over a broader extent (*e.g.,* agent dispersal) misses out on important information regarding the dynamics of weed biocontrol systems. For example, the extent over which agent dispersal and impact occurs within a given time period can suggest the appropriate spatial scale(s) at which redistribution efforts should be focused. My results suggest that *A. lacertosa* reduces spurge densities up to about 600 m away from release sites within 3 years of release. However, habitat patch structure – typical patch sizes and distances between patches – and types of intervening non-habitat may influence agent movement rates and population dynamics (Wiens 1997; Hanski and Moilanen 1998; Chapter 5) and thus influence the extent of impact observed over broad areas. Although I found no strong and consistent effects of shrub habitat or patch isolation on beetle densities there may be interactions that occur on more heterogeneous landscapes or at spatial scales even broader than was considered here, illustrating a need for further study over a range of release landscape types before comprehensive management recommendations can be made.

In addition to the potential influence of spatial effects, temporal effects may play an important role in the dynamics of biocontrol systems. For example, increased environmental variability, possibly through extreme weather events or a changing climate (*e.g.,* Easterling *et al.* 1997), can lead to a reduction in successful establishment of biocontrol releases (Grevstad 1999). In a less drastic scenario, increased environmental variability may lead to altered relationships between insects and their host plants such as changes in the temporal coincidence of insect and host plant phenology (Dobkin *et al.* 1987; Hassell *et al.* 1993) or altered habitat suitability (Kindvall 1995; Solbreck 1995). Here, I illustrate that relationships between fine-scale habitat features and *Aphthona* density changed between consecutive years but that the changes in density – habitat relationships were not entirely due to habitat changes, suggesting that the beetles changed their preference for particular habitat types between 1999 and 2000. The changes in habitat preference coincided with a sharp decline in annual precipitation between 1999 and 2000, suggesting that weather may constrain habitat use by *Aphthona* beetles. Such changes in biocontrol agent - habitat relationships are likely to pose problems for biocontrol practitioners if their decisions rely mainly on habitat-based studies that predict establishment rates from fine-scale, short-term data alone (*e.g.,* Jacobs *et al.* 2001; Nowierski *et al.* 2002).

In the interest of seeking conclusions that may be generalized to other weed biocontrol systems, it is instructive to compare some of the key results of my study to features thought to be responsible for successful weed biocontrol. Other researchers have suggested general similarities and dissimilarities between successful weed biocontrol and insect control systems (McEvoy *et al.* 1993; Sheppard *et al.* 2001). For example, successful insect biocontrol is characterized by local instability in the interaction between host and natural enemy and this instability may also be common in successful weed biocontrol systems (McEvoy *et al.* 1993). In my study, this kind of local instability was evident from the large decreases in spurge density and the complete disappearance of several spurge patches. Further, McEvoy *et al.* (1993) also point out that successful natural enemies should be able to locate and aggregate at incipient weed outbreaks and contain or eliminate them much the same way as do successful insect predators or parasitoids. This too is supported by the fact that most of the spurge patches that were eliminated were in relative proximity to the 1997 *A. lacertosa* release and relatively small and presumably younger (Selleck *et al.* 1962) than much larger patches. Unlike insect biocontrol systems however, successful weed biocontrol may also be characterized by resource limitation and competition from native plant species acting to maintain weeds at low density following biocontrol agent impact (McEvoy *et al.* 1993; Sheppard *et al.* 1993). That spurge densities generally rebounded in 2001 to near 1999 levels indicates that resource limitation and/or competition effects were not apparent in my study, at least over a temporal scale of 1-2 years, perhaps as a result of heavy grazing by cattle on the landscape over all 3 years of the study (*e.g.*, Grigulis *et al.* 2001).

3.6 Conclusions

The transient effects of *A. lacertosa* and apparent minor effect of *A. nigriscutis* on spurge populations coupled with the changing relationships between fine-scale habitat and *Aphthona* densities presented here emphasize the need for long-term, post release study of weed biocontrol systems (McFadyen 1998; McEvoy and Coombs 1999; Blossey and Skinner 2000). Continued long-term study will aid identification of the underlying processes that drive weed – natural enemy dynamics and aid our ability to predict outcomes of future weed biocontrol introductions. I add to the plea for more post-release studies by suggesting that important information regarding the function of weed biocontrol systems can be gained by studying weed – enemy interactions at multiple spatial scales. Fine-scale studies centered on agent release sites need to be augmented by studies conducted over much broader scales than is the current norm to gain a more complete

understanding of how weed biocontrol systems operate. Results presented here suggest that distance from release site is a relatively poor predictor of beetle impact on spurge density, and that other factors such as patch size and fine-scale habitat features appear to influence the relationship between biocontrol agent density and impact on weed populations. Studies that integrate information across multiple spatial scales and over multiple insect/weed generations will speed the transition of weed biocontrol from a reactive to a predictive science.

3.7 References

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Table 3.1. Contributions of original cover class variables to PCA-derived variables used in habitat models.

PCA-derived variables	Loadings by cover class				Proportion of original variance
	Grass & forbs	Shrubs	Bare ground	Litter	
GROUND	0.227		-0.820	0.526	0.557
GRASSFORB	0.765	-0.225	-0.155	-0.153	0.226
SHRUB	0.145	-0.831	0.334	0.321	0.164

Table 3.2. Predictor variables fit in Linear Mixed-Effects habitat models. For log-transformed variables, 0.5 was added to quantities prior to taking the natural logarithm.

Fine-scale variables	Description
SPURGE	log counts of all spurge stems in 0.0625 m^2 quadrats
VSPURGE	log counts of vegetative spurge stems in 0.0625 m^2 quadrats
FSPURGE	log counts of flowering spurge stems in 0.0625 m^2 quadrats
GROUND	PCA-derived variable: +vely correlated with ground litter cover
GRASSFORB	PCA-derived variable: +vely correlated with grass & forb cover
SHRUB	PCA-derived variable: -vely correlated with shrub cover
Broader-scale variables	
GRID*	Factor describing whether sample point was located on the Microgrid or the Mesogrid
PATCHSIZE	log area of patch
NNB1	log distance to nearest neighbouring spurge patch
DIST2REL*	distance from sampled patch to 1997 *A. lacertosa* release point
DIST2NREL†	distance from sampled patch to 1997 *A. lacertosa* release point
SHRUBAREA	Area of shrub habitat within 50-m (Mesogrid) or 10-m (Microgrid) radius circle centred on sample sites

* fit only for *A. lacertosa* models

† fit only for *A. nigriscutis* models

Table 3.3. Summary of Linear Mixed-Effects models (LME) fit to *Aphthona lacertosa* densities sampled on the study landscape in 1999 and 2000. LME models were fit to account for the hierarchical data structure (see Methods). The models were fit in a two-stage, stepwise procedure with significant fine-scale habitat effects fit prior to testing for broader-scale habitat effects.

1999					2000				
Term	df	-2LL	β	*t*-value	Term	df	-2LL	β	*t*-value
Null	169	244.5	-0.05	-0.31	Null	169	419.7	-0.14	-0.87
SPURGE	1	6.39	0.14	3.57†	SPURGE	1	13.58	0.44	3.77‡
GRASSFORB	1	6.15	0.02	3.41†	$SPURGE^2$	1	5.97	-0.13	-3.44†
PATCHSIZE	1	6.66	-0.10	-3.65‡	PATCHSIZE	1	3.40	0.14	1.56
R^2	0.08				$PATCHSIZE^2$	1	5.18	-0.03	-3.30†
					R^2	0.07			

* $p(t) \leq 0.10$, † $p(t) \leq 0.05$, ‡ $p(t) \leq 0.01$

-2LL = Deviance

R^2 = Residual deviance / Null deviance

Table 3.4. Summary of model coefficients and their precision for habitat effects on *A. nigriscutis* abundances on the study landscape in 1999 and 2000. Linear mixed-effects models were fit to account for the hierarchical data structure (see Methods). The models were fit in a two-stage, stepwise procedure with significant fine-scale effects fit prior to testing for broader-scale effects.

1999					2000				
Term	df	-2LL	β	*t*	Term	df	-2LL	β	*t*
Null	169	159.0	-0.258	-1.62	Null	169	294.7	-0.063	-1.21
GROUND	1	5.2	-0.0051	-3.25†	VSPURGE	1	6.28	0.1078	3.53†
$GROUND^2$	1	7.64	0.0003	3.73‡	DIST2NREL	1	3.12	-0.0002	-1.76*
GRASSFORB	1	3.68	0.0037	1.61	R^2	0.03			
$GRASSFORB^2$	1	4.26	-0.0002	-3.03†					
PATCHSIZE	1	5.00	0.156	3.22†					
$PATCHSIZE^2$	1	3.46	-0.016	-1.84*					
R^2	0.18								

* $p(t) \leq 0.10$, † $p(t) \leq 0.05$, ‡ $p(t) \leq 0.01$

-2LL = Deviance

R^2 = Residual deviance / Null deviance

Table 3.5. Comparisons of fine-scale habitat variables between 1999 and 2000. The original components of the PCA-derived variables are presented instead of the derived variables. Wilcox rank-sum tests were used throughout and p-values were drawn from *Z* distributions. For all variables n = 170 in both years. The data were pooled between Micro- and Mesogrids prior to testing for differences.

Habitat variable	1999 mean (sd)	2000 mean (sd)	Z	p-value
VSPURGE	71.76 (137.70)	44.25 (83.92)	3.52	0.0004
FSPURGE	25.74 (34.51)	23.95 (35.62)	0.57	0.5701
SPURGE	97.51 (143.26)	68.19 (99.20)	3.17	0.0015
% grass and forbs	17.30 (15.50)	18.77 (23.17)	-1.16	0.2474
% shrubby veg	13.85 (14.32)	11.27 (10.33)	3.05	0.0404
% bare ground	20.89 (24.59)	15.49 (17.53)	3.25	0.0244
% litter	48.67 (20.68)	43.81 (13.24)	3.87	0.0041

Table 3.6. Analysis of deviance tables. The response variable is the log change in total spurge stem densities between 1999 and 2000. Separate generalized linear models, using an identity link and Gaussian errors, were fit for the Microgrid and Mesogrid. The data are patch-specific means and so the models were weighted by the number samples take in each patch. Only significant terms are presented.

Microgrid					Mesogrid				
Term	df	-2LL	F	β	Term	df	-2LL	F	β
Null	28	37.48		-0.38**	Null	37	89.37		0.46
APHDENS	1	10.87	10.87	-0.72**	APHDENS	1	19.25	10.72	-0.44**
Residual	27	26.61			NNB1	1	7.30	4.07	-0.26*
					Residual	35	63.82		

* $p(F) < 0.05$, ** $p(F) < 0.01$

-2LL = Deviance

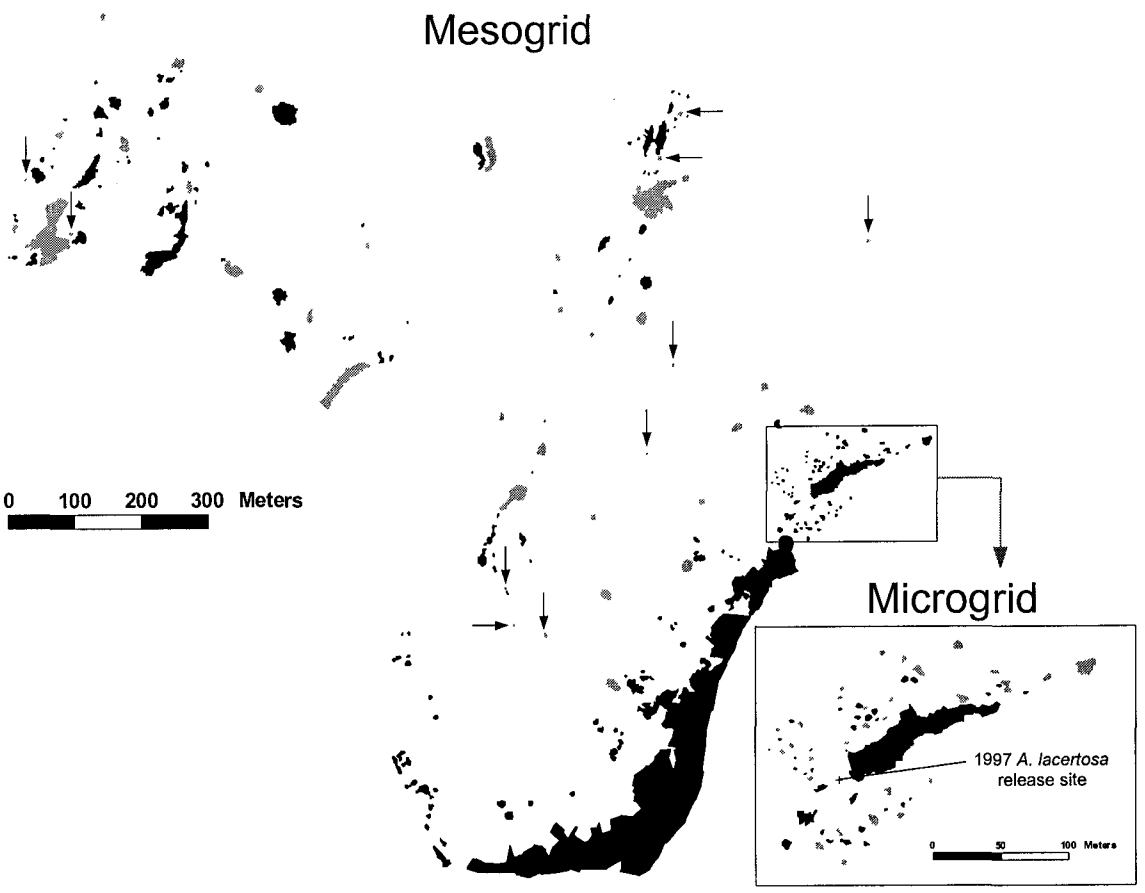

Figure 3.1. Map of spurge patches on the study landscape. Sampled patches are in light grey and arrows indicate location of small patches that were sampled. Microgrid patches are shown inset.

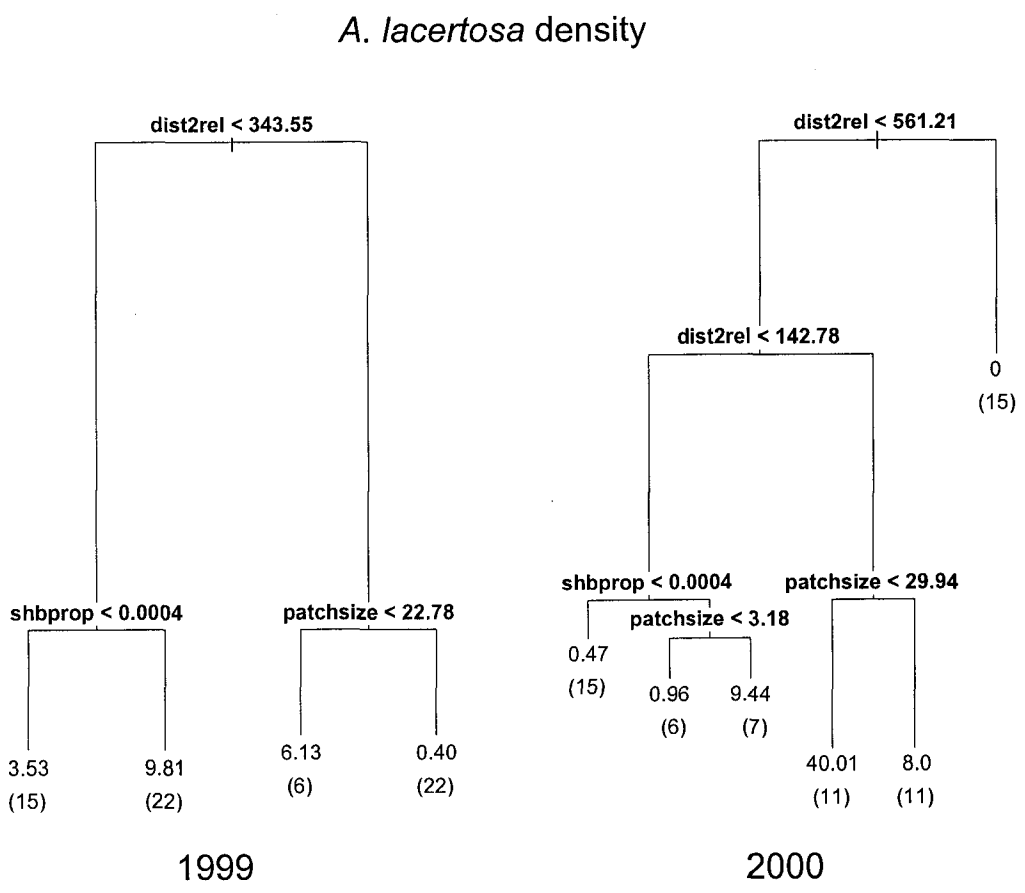

Figure 3.2. Regression trees fit to the *Aphthona lacertosa* density data using only the broader-scale habitat variables. Separate trees were fit for the 1999 and 2000 data. The distance between successive nodes is proportional to the variance in beetle density explained at the upper node. Model predictions are indicated at the terminal nodes as are the number of observations at those nodes (in parentheses).

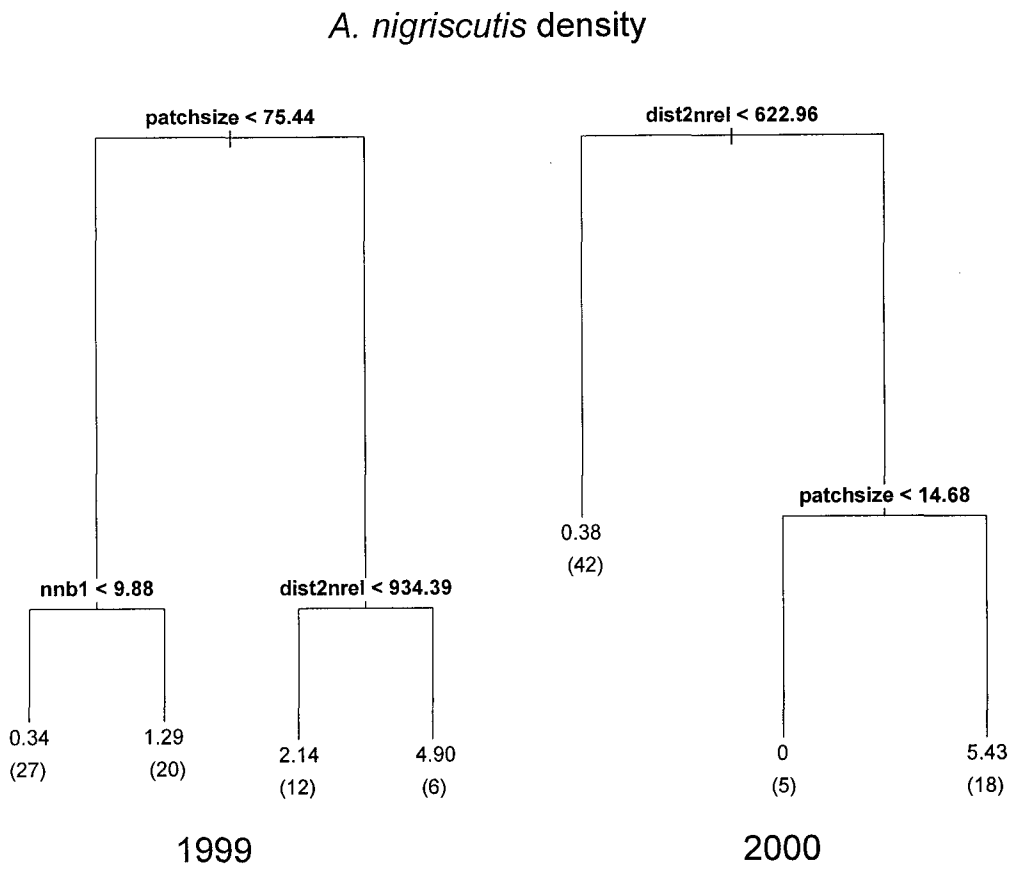

Figure 3.3. Regression trees fit to the *Aphthona nigriscutis* density data using only the broader-scale habitat variables. See Fig. 3.2 caption for further details.

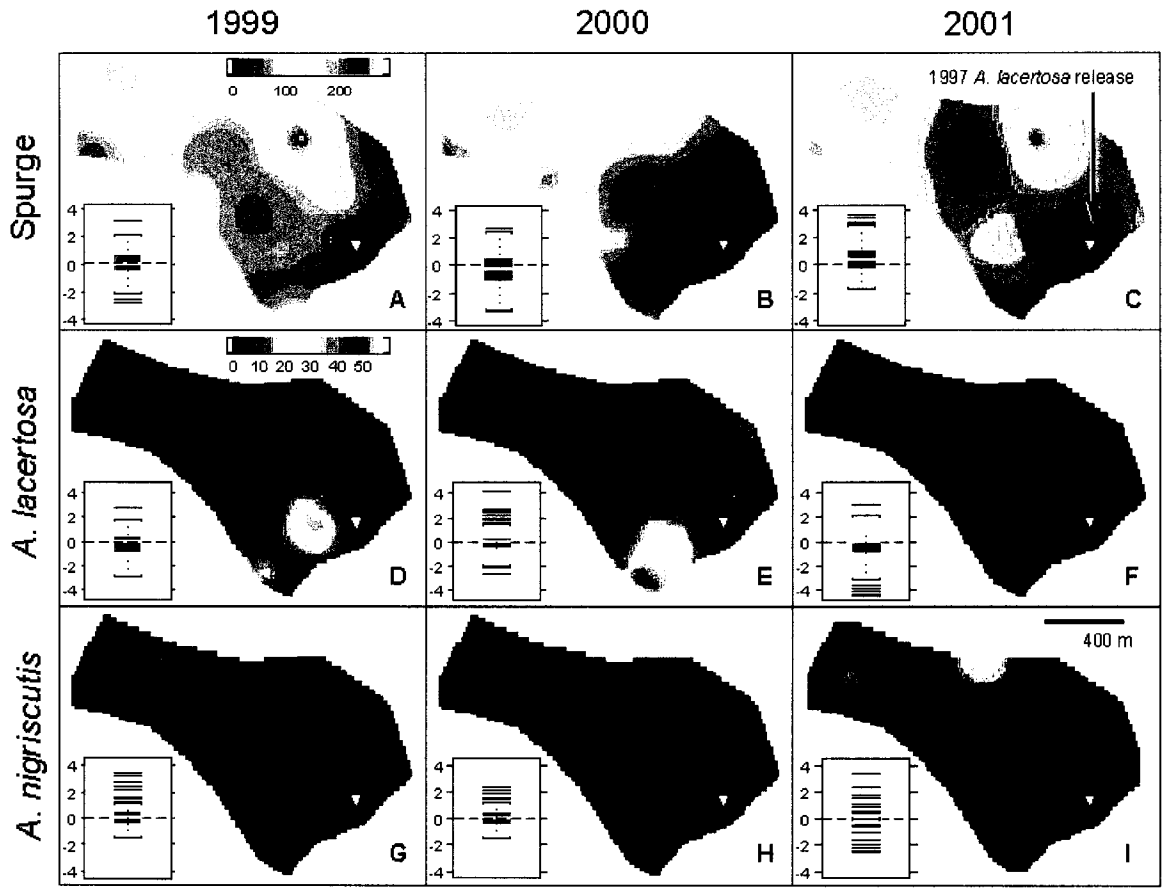

Figure 3.4. Interpolated maps illustrating spatial pattern of spurge and beetle densities in 1999, 2000 and 2001. Densities were interpolated by kriging point estimates from vacuum and quadrat data collected from a subset of 67 of the 198 extant patches (in 1999). The 1997 *Aphthona lacertosa* release is indicated by the inverted white triangles in each plot. Boxplots in the lower right corners of panels display the log change in spurge or beetle density between the years for all sampled patches. Boxplots in the 1999 panels display the net change from 1999 to 2001, boxplots in other panels display the change from the previous year to the current year (*i.e.* the boxplot for spurge in 2000 displays the log change in spurge density from 1999 to 2000). The boxplots illustrate the median value (white bar), inter-quartile range (box), 90th percentile (whiskers), and outliers (individual lines).

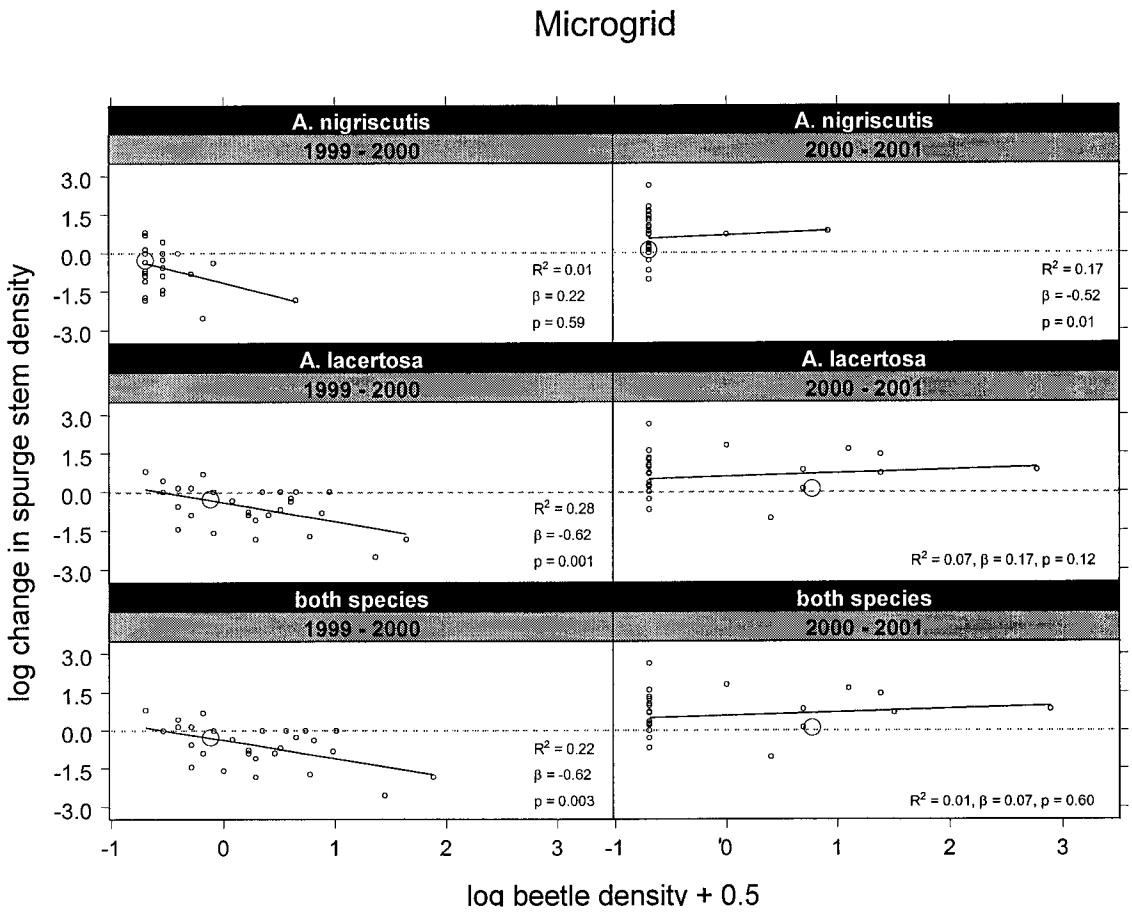

Figure 3.5. *Aphthona* flea beetle impact on leafy spurge on the Microgrid. The plots illustrate the relationship between beetle densities measured in 1999 and 2000 (both species, *A. lacertosa* alone, *A. nigriscutis* alone) and the change in leafy spurge stem density (flowering and vegetative) between 1999-2000 and 2000-2001. Negative values on the y-axis indicate a decrease in spurge stem density between the years indicated at the top of each panel. Data are patch-specific means of beetle and spurge stem densities and symbol sizes are proportional to the number of observations contributing to those means. Linear regressions were weighted according to the number of individual observation contributing to each data point.

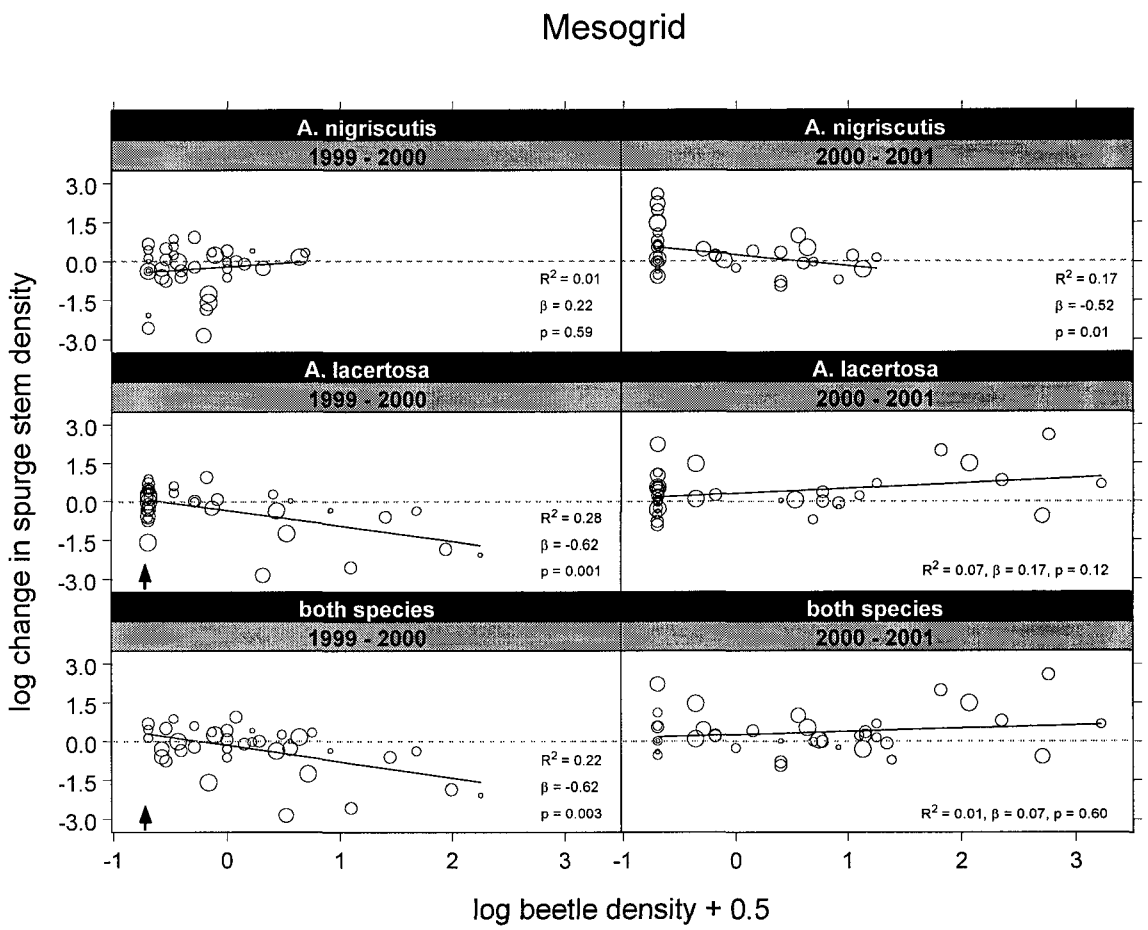

Figure 3.6. *Aphthona* flea beetle impact on leafy spurge on the Mesogrid. See Fig. 3.3 caption for details.

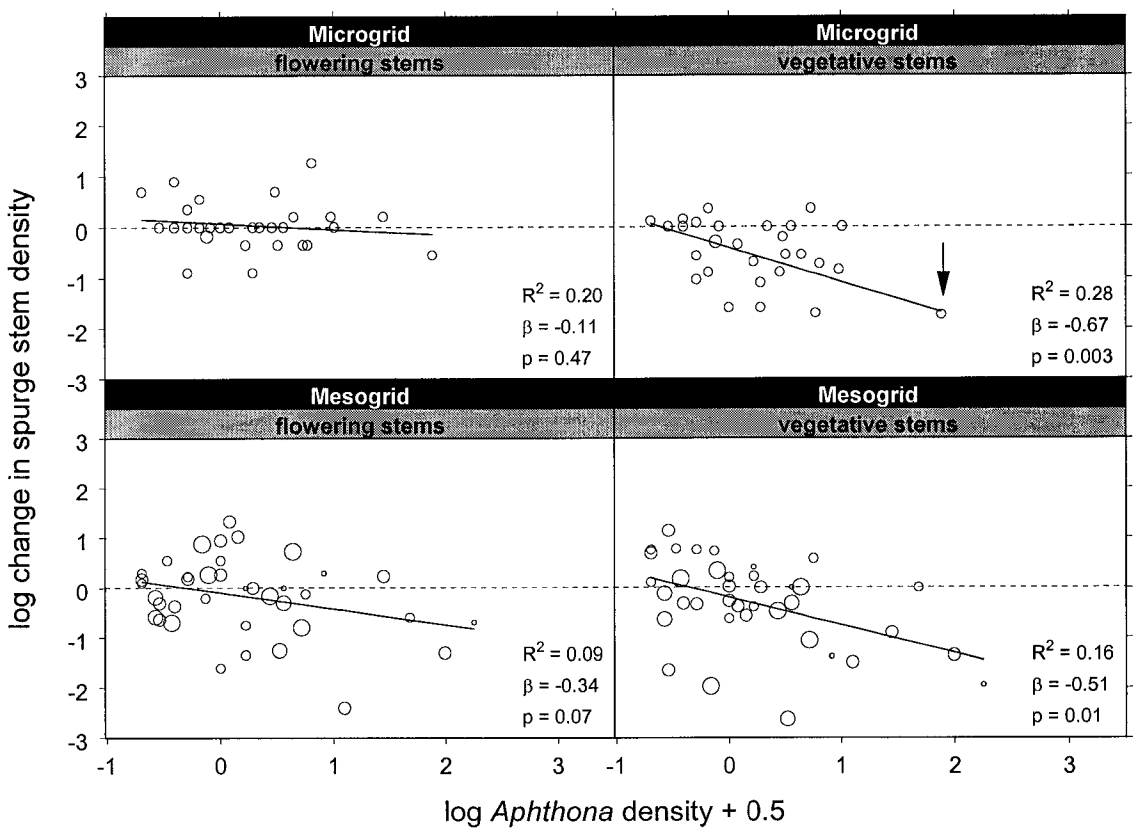

Figure 3.7. *Aphthona* flea beetle impact on flowering and vegetative leafy spurge stems. The plots illustrate the relationship between beetle densities measured in 1999 and 2000 (*A. lacertosa* and *A. nigriscutis* densities combined) and the change in flowering or vegetative leafy spurge stem density between 1999-2000 for the Microgrid and Mesogrid. Negative values on the y-axis indicate a decrease in spurge stem density between the years indicated at the top of each panel. Data are patch-specific means of beetle and spurge stem densities and symbol sizes are proportional to the number of observations contributing to those means. One high-leverage value (vegetative stems, Microgrid), indicated by arrow, had little effect on regression coefficient (included: $\beta = -0.67$, removed: $\beta = -0.66$).

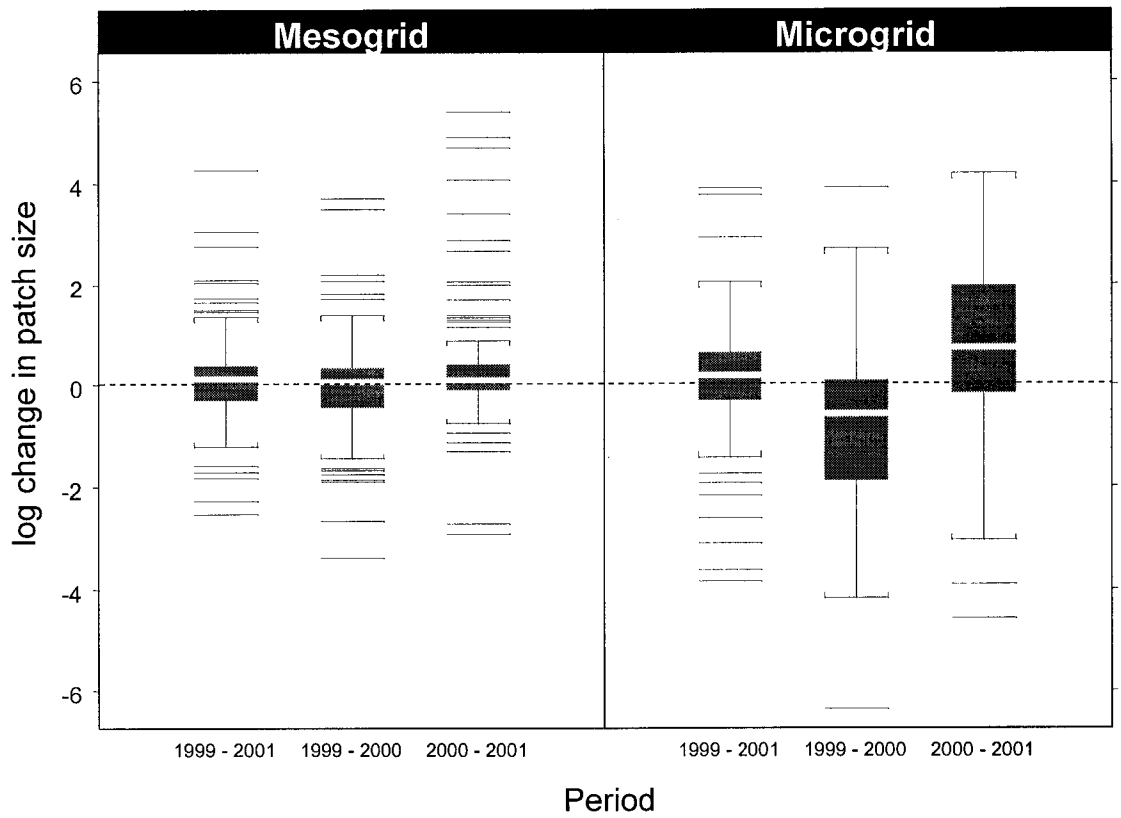

Figure 3.8. Boxplots illustrating the log change in leafy spurge patches sizes on the Mesogrid and the Microgrid between 1999 and 2000 and between 2000 and 2001. See Fig. 3.2 caption for boxplot details.

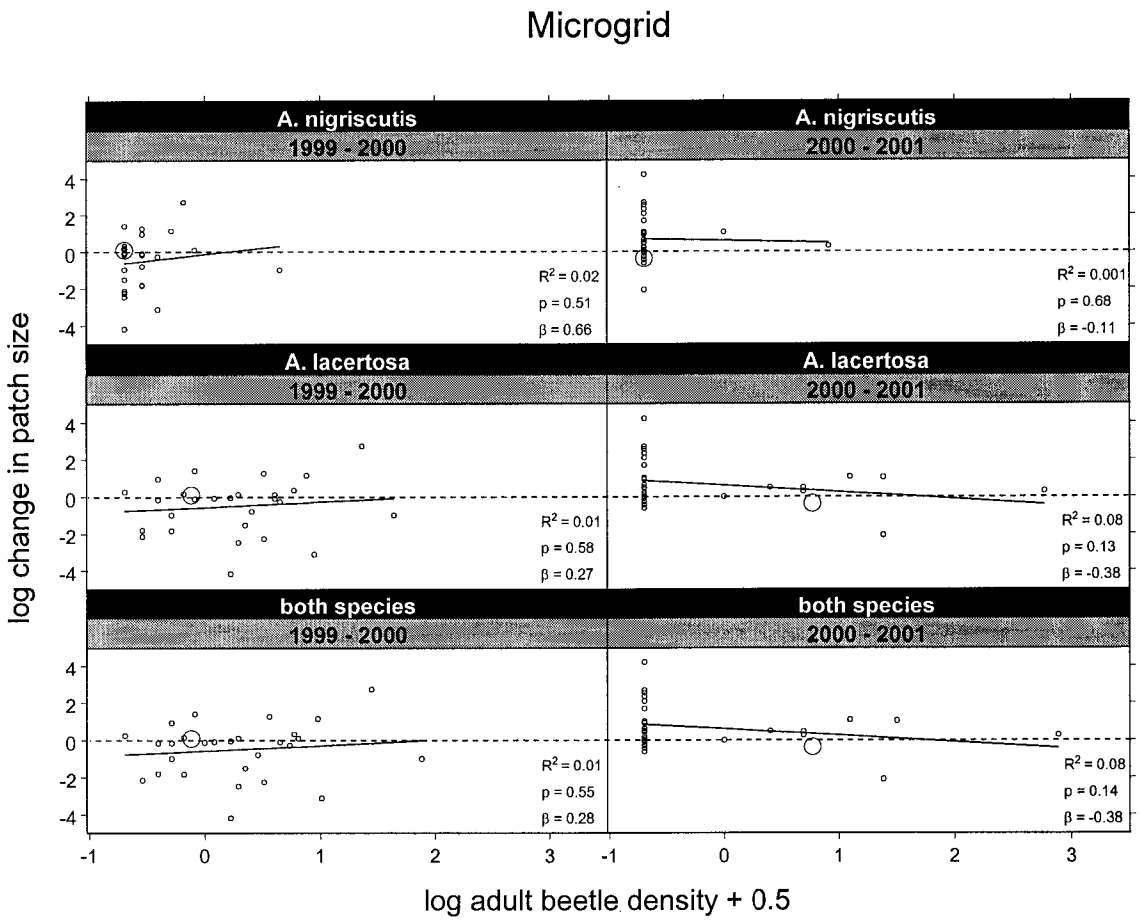

Figure 3.9. *Aphthona* flea beetle impact on leafy spurge at the patch scale, on the Microgrid. The plots illustrate the relationship between beetle densities measured in 1999 and 2000 (*A. lacertosa* alone, *A. nigriscutis* densities alone, and densities of both species combined) and the change in leafy spurge patch sizes between 1999-2000 and between 2000-2001. Negative values on the y-axis indicate a decrease in spurge patch size between the years indicated at the top of each panel. Density data are patch-specific means and symbol sizes are proportional to the number of observations contributing to those means.

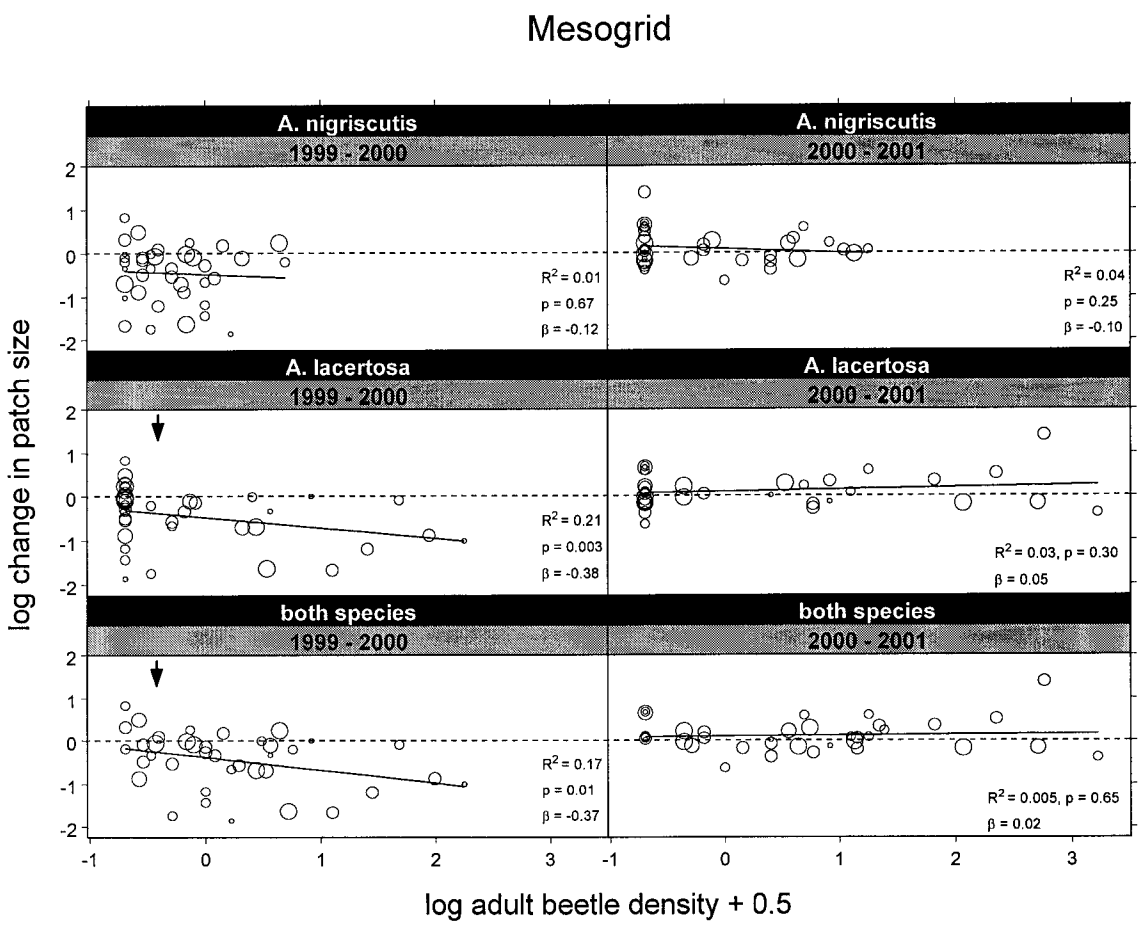

Figure 3.10. *Aphthona* flea beetle impact on leafy spurge at the patch scale, on the Mesogrid. The plots illustrate the relationship between beetle densities measured in 1999 and 2000 (*A. lacertosa* alone, *A. nigriscutis* densities alone, and densities of both species summed) and the change in leafy spurge patch sizes between 1999-2000 and between 2000-2001. See Fig. 3.9 caption for further details.

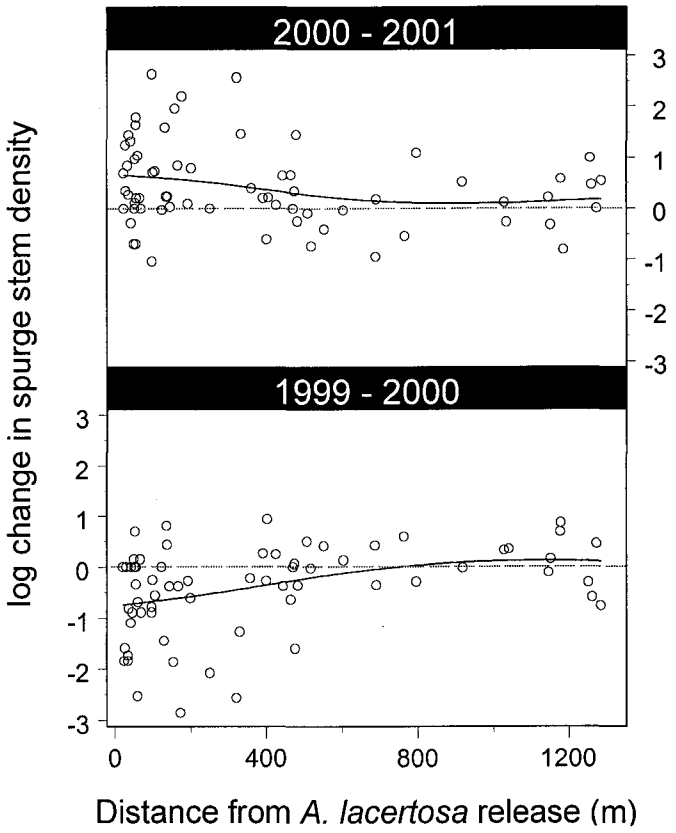

Figure 3.11. Relationships between spatial location relative to the 1997 *Aphthona lacertosa* release site and the log change in spurge stem density for the years 1999-2000 and 2000-2001. Regressions are cubic B-splines fit to the data using Generalized Additive Models (GAM). The regressions were weighted according to the number of observations contributing to patch-specific mean values.

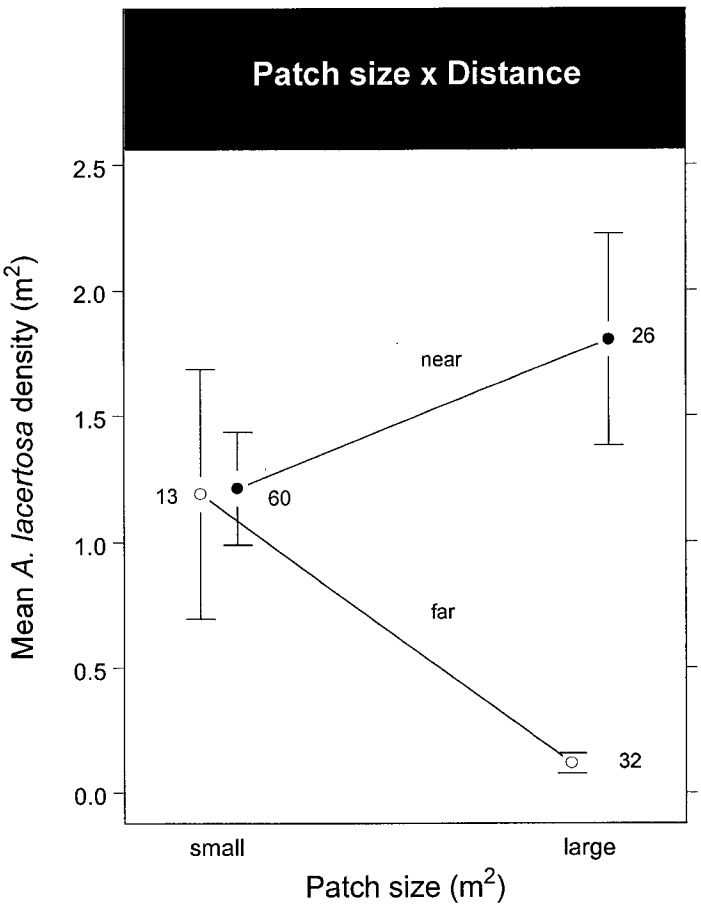

Figure 3.12. Interaction plot showing the difference in mean *Aphthona lacertosa* density on small and large patches, according to distance from the 1997 release site. Lines indicate direction of trend between means for each combination of patch size (small or large) and distance from release site (near or far). Error bars are ± 1 standard error. Pairs of data points are staggered for clarity. The variables patch size and distance were coerced from continuous variables into 2-level factors by splitting each according to its median value. Numbers next to data points indicate sample sizes for each mean.

Chapter 4

Influence of dispersal, stochasticity, and an Allee effect on the persistence of biocontrol agent introductions

4.1 Introduction

The practice of weed biocontrol often is criticized for great reliance on a 'trial-and-error' approach and little reliance on ecological theory (McEvoy and Coombs 2000). The trial-and-error approach has arisen in part because much of the potentially relevant theory is developed by studying insect biocontrol systems and direct applications of this theory to weed biocontrol issues are not always apparent or even possible. The field of weed biocontrol, therefore, needs more theoretical development in order for the practice to become more rigorous. Applications deriving from plant population dynamics theory (*e.g.,* Lonsdale *et al.* 1995; Lonsdale 1996; Rees and Paynter 1997) are well established but there remains little theory to guide researchers and practitioners in effective and efficient ways to conduct releases of biocontrol agents (Memmott *et al.* 1996; Memmott *et al.* 1998; Grevstad 1999*b*).

Recent studies (Grevstad 1999*a*; Shea and Possingham 2000) address the issue of optimal biocontrol agent release strategies under different regimes of demographic and environmental stochasticity and/or Allee effects. I am aware of few studies, however, that consider explicitly how weed biocontrol agent dispersal may affect release population persistence (see Hopper and Rousch 1993 for an insect biocontrol example). Dispersal may play two antagonistic roles during the early phase of population increase following an introduction. First, successful movement to unoccupied locations can establish new populations and spread the risk of overall extinction or failure of the release (den Boer 1968; Roff 1974). Second, emigration can act as a drain on local population size thus preventing substantial increase at the initial release location (Lewis and Kareiva 1993; Kean and Barlow 2000*a*). The extent to which one or the other of these scenarios dominates during biocontrol agent releases may play a role in determining the likelihood of successful establishment.

The goals of this study were to explore the interactions among the factors that may influence population persistence in the context of introductions of weed biocontrol agents and to determine the relative importance of those factors under a broad range of conditions. This kind of study is not intended to produce specific protocols for weed biocontrol releases but rather to highlight the potential interactions among key factors thought to limit release establishment and persistence. The results of such studies can be used as guides for the kind of data biocontrol researchers need to collect about candidate biocontrol agents and the environments into which they are to be released.

I use a spatially explicit, patch-based simulation model to explore the consequences of interactions between two components of dispersal – emigration rates and movement ability – in addition to those of environmental stochasticity and the Allee effect for the persistence of weed biocontrol releases of different sizes.

4.2 Methods

The simulations were run on a 12 x 12 lattice of uniform patches. Lattice boundaries were of the reflecting kind. At the start of a simulation, a specified number of individuals is released at a single patch, randomly chosen, near the centre of the lattice. I assume that releases are made sufficiently far apart that no two releases interact with one another and thus can be modeled as

independent simulation runs. This assumption often mirrors the way initial weed biocontrol releases are conducted (*e.g.,* McClay *et al.* 1995). In each generation, a constant proportion of individuals (ε) emigrates from each local population (N_j) and these individuals disperse equally in all directions. As a result of mortality during dispersal, the density of dispersers declines exponentially with distance from the source patch according to the parameter α. Strong dispersers have a relatively small α while weak dispersers have a larger α. Hereafter I refer to α as movement ability. This dispersal process is summarized by Eqns. 4.1 and 4.2, where S_i represents a measure of patch connectivity based on α, the pair-wise distance between the ith and jth patches (d_{ij}), and the number of dispersers emigrating from the jth patch (εN_j), summed over all patches where $i \neq j$,

$$S_i = \sum_{j=1}^{n} e^{-\alpha d_{ij}} \varepsilon N_j, i \neq j \tag{4.1}$$

Ignoring the summation, S_i represents connectivity as the number of individuals that could disperse from patch j to patch i as a negative exponential function of the distance between j and i. Of course, this equation ignores how emigrants from the jth patch are apportioned among the recipient patches (i). I, therefore, calculate a probability of colonization (or immigration), C_i, that is a function of S_i and the colonization (or immigration) ability of the dispersers, y',

$$C_i = \frac{1}{1 + \left[\frac{y'}{S_i}\right]^2} \tag{4.2}$$

Equation 4.2 is a sigmoid function, where y' determines how rapidly C_i approaches unity. These equations are similar to those used by Hanski in his incidence function model (Hanski 1994; Moilanen and Hanski 1998), except here I use εN_j to determine an actual number of dispersers emigrating from patch j rather than the surrogate A_j (patch area) used by Hanski (1994).

I convert C_i into an actual number of colonizers or immigrants that each patch receives in a single generation, M_i, using a Binomial random number generator. The number of immigrants (M_i) that each patch receives in a single generation represents the number of successful dispersal events out of the total pool of dispersers, where the probability of a successful event is specified

by the patch-specific immigration probability, C_i. The total pool of dispersers capable of colonizing or immigrating to the ith patch and from which M_i successful events are drawn is simply the sum of εN_j over all j patches ($j \neq i$) divided by the number of j patches for which S_i is $\geq$ 1.

Following dispersal, local population growth was modeled as a simple random walk (*e.g.,* Hanski *et al.* 1996; Kean and Barlow 2000*b*) with the following conditions,

$$N_t = N_{t-1}e^{r_t} \qquad \text{if } K \geq N_{t-1} > K_A \qquad (4.3a)$$

$$N_t = K^2/N_t \qquad \text{if } N_{t-1} > K \qquad (4.3b)$$

$$N_t = N_{t-1}e^{r_A} \qquad \text{if } N_{t-1} \leq K_A \qquad (4.3c)$$

The realized per capita reproductive rate (r_t – Eqn. 4.3a) varies in both space and time and can be treated as a normally distributed, random variable with mean r_d and variance v_r. For simplicity, I assume that r_t is uncorrelated both in space and time and thus environmental autocorrelation is negligible. Some other effects of spatial structure are considered in Chapter 5. The parameter v_r represents the level of demographic and environmental stochasticity experienced by an introduction. Demographic stochasticity, chance birth and death events, generally has its greatest influence at very small population sizes (Lande 1993; Grevstad 1999*a*). Because the smallest releases I consider here are of 100 individuals, I assume that demographic stochasticity has little influence on biocontrol release persistence (*e.g.,* Grevstad 1999*a*). Therefore, I consider the stochastic effects represented by v_r attributable to environmental conditions and focus on these hereafter.

Overcompensating density-dependence is incorporated into the model by imposing a reflecting ceiling on population size such that any population N_t that exceeds the carrying capacity (K) is instantaneously reduced to K^2/N_t (Eqn. 4.3b) thus providing dynamics comparable to the Ricker logistic model (Foley 1997) but without the pervasive effect of density-dependence on r_t. Although a discrete logistic model of the Ricker or Verhulst type is more conventional, the random walk model with a reflecting ceiling used here allows a straightforward exploration of the effects of variability about r_d on population persistence.

An Allee effect is included in the model by allowing populations above the threshold K_A to grow at the rate r_t, while populations at or below K_A decline at a constant rate, r_A (Eqn. 4.3c). The rate r_A can be considered as the intensity of the Allee effect (Grevstad 1999*a*). Clearly, K_A affects the persistence of releases in a straightforward way by causing releases to go extinct when $N_0 \leq K_A$. For this reason, I focus only on effects of r_A on release persistence and set K_A to a constant value ($K_A = 300$) for all simulations.

Others have used similar population models or scenarios to explore extinction dynamics. Using a non-spatial, discrete logistic model with emigration (or depletion), Sinha and Parthasarathy (1996) found that populations undergoing chaotic dynamics could persist if emigration (or depletion) rates were sufficiently high. Hanski *et al.* (1996) used the same random walk with reflecting ceiling model presented here but without Allee dynamics to illustrate that density-dependence was necessary for long-term persistence of single populations and metapopulations but that the frequency of density-dependence required for metapopulation persistence was much lower. Kean and Barlow (2000*b*) also used a random walk model but with a milder form of density-dependence (*i.e.,* no overcompensation) and no Allee effect to explore metapopulation persistence in a spatially explicit fashion that included local dispersal. Their results were similar to those of Hanski *et al.* (1996). None of these studies, however, combine overcompensation, an Allee effect, stochasticity, all in a spatially explicit context that incorporates emigration and immigration.

I conduct a factorial experiment to explore the interactions between environmental stochasticity (v_r), Allee effect intensity (r_A), emigration rate (ε), and movement ability (α) on population persistence for releases of different sizes. An introduction is deemed to have persisted if the initial release or any local populations arising from it are present after 20 generations. Typically, simulation experiments exploring factors that influence population persistence are run over long time periods (*e.g.,* 1000 generations), however, weed biocontrol programs have much shorter life spans and factors influencing introduction persistence over relatively short time scales are of greater interest to practitioners. Data presented are means of 500 replicate simulations for each combination of parameter values. I also conduct a sensitivity analysis to determine how changes in individual model parameter values affect release persistence. Lists of model parameter values used in the simulation experiment and those used in the sensitivity analysis are presented in Table 4.1.

4.3 Results

In the absence of dispersal ($\varepsilon = 0$), Allee effect intensity and environmental stochasticity both influence release population persistence. Larger initial populations are required as the intensity of the Allee effect increases (Fig. 4.1 A-C vs. D-F, $\varepsilon = 0$), while increasing environmental stochasticity reduces population persistence, regardless of initial release size (Fig. 4.1 A-C and D-F, $\varepsilon = 0$). Allee effect intensity, however, only influences release persistence for population sizes below the Allee threshold set by K_A ($K_A = 300$ throughout).

High emigration rates act as a drain on population growth, resulting in reduced persistence and only slight compensation is achieved by increasing the release population size (Fig. 4.1, $\varepsilon = 0.7$). Low to moderate emigration rates increase release persistence above that predicted in the absence of dispersal and this effect becomes more noticeable as v_r increases, although persistence probabilities decrease overall as v_r increases (Fig. 4.1, $\varepsilon = 0.1$ - 0.3, A-C). The effect of dispersal on release persistence is reduced noticeably when Allee effect intensity is high (Fig. 4.1, compare A-C to D-F). This interaction between Allee intensity and dispersal arises because the number of immigrants required to colonize successfully a previously unoccupied host-plant patch increases as Allee intensity increases.

Stronger movement ability ($\alpha = 0.02$) enhances release persistence (Fig. 4.2) by allowing more emigrants to survive dispersal and immigrate to patches farther away from the initial release, thus spreading extinction risk among more local populations.

Results of the sensitivity analysis on the model parameters illustrate that v_r and r_d have the greatest influence on release persistence probabilities, at least over the range of parameter values considered here (Table 4.1). Although sensitivity analysis reveals that the effects of α, ε, and r_A on release persistence are secondary (Table 4.1), the simulation experiment demonstrates that these parameters do influence release persistence. The size of initial release populations (N_0) has nearly as strong an effect on release persistence as v_r (Table 4.1) but this result is somewhat misleading. The Allee effect threshold (K_A) causes releases to go extinct in a deterministic fashion when $N_0 \leq K_A$ but once $N_0 > K_A$ there is little benefit to further increasing N_0 (Table 4.1, Fig. 4.1).

4.4 Discussion

Grevstad (1999*a*) illustrated the importance of both an Allee effect and environmental stochasticity on the persistence of biocontrol introductions, in the absence of dispersal. Similar results were obtained here but I show also that high emigration rates can reduce the probability of release persistence from what would be predicted in the absence of dispersal. Diffusion models illustrate that high emigration can lead to reduced population growth (Kean and Barlow 2000*a*) or failed introductions (Hopper and Rousch 1993) if the population growth rate can not compensate for loss through dispersal, even when release sizes are above an Allee threshold (Lewis and Kareiva 1993). My simulations are consistent with these findings and also suggest that there is only slight benefit to increasing release population size beyond the persistence threshold imposed by the Allee effect. Different results might be obtained if emigration rates were density-dependent. However, the prevalence of density-dependent emigration has rarely been explored in empirical systems (but see Denno and Peterson 1995 for a review) and results from Chapter 2 suggest that the biocontrol agent *Aphthona lacertosa* may not exhibit density-dependent emigration. The simplifying assumption of constant emigration rates, therefore, seems appropriate at least for some weed biocontrol systems.

The effects of dispersal on introduction persistence can be viewed as a trade-off whereby reductions in population growth through emigration are offset by spreading the risk of extinction over a number of local populations (den Boer 1968; Roff 1974). Increased movement ability further offsets the risk via increased colonization or increased immigration to established local populations (Brown and Kodric-Brown 1977). As the risk of extinction for all populations increases via increased environmental stochasticity, the relative benefit of dispersal to new local populations increases but this should only occur when there is spatial variability in population growth rates (Roff 1974; Kuno 1981). Variability was incorporated into the current model by allowing r_t to vary both in space and time but the effect of pattern in this variability was not examined.

Although I did not consider explicitly the effects of spatial pattern on introduction persistence, spatial heterogeneity in the quality and distribution of habitat patches or the types of unsuitable (matrix) habitat surrounding patches (*e.g.*, Chapter 1) may affect release persistence via an interaction with movement ability (Fahrig and Paloheimo 1987; Adler and Nuernberger 1994). For example, biocontrol agents can not colonize habitat patches if the degree of isolation among

patches exceeds the scale of agent dispersal. Conversely, introductions may fail if the majority of habitat patches within dispersal range of an initial release are of poor quality (Pulliam 1988), especially if Allee effects are strong (Keitt *et al.* 2001). In fact, my results indicate that the intensity of an Allee effect can reduce or eliminate the positive effect of movement on persistence even when habitat patches are within dispersal range. Scenarios such as these, coupled with the simulation results (Fig. 4.2), illustrate the potential importance of considering both the movement ability of the biocontrol agent and the structure of the landscapes (*sensu* Taylor *et al.* 1993) onto which biocontrol introductions are made.

In insect biocontrol systems, dispersal can play an important role in enemy aggregation and suppression of incipient insect pest outbreaks (Murdoch and Briggs 1996) and the influence of spatial structure on enemy dispersal can affect the level of pest suppression (Kareiva 1987; Walde and Nachman 1999). In addition, stability of the enemy-host interaction may occur at a metapopulation scale where individual local populations are prone to extinction but dispersal among local populations ensures overall persistence (Murdoch *et al.* 1985). Analogous ideas have not been pursued in weed biocontrol systems despite the fact that successful biocontrol may lead to deterministic local extinctions of weed and herbivore populations (McEvoy *et al.* 1993). In this case, long-term stability and biocontrol success may depend on the interaction between the spatial pattern of weed patches and the movement behaviour of the biocontrol agent. My results here suggest, at least for transient dynamics, that emigration rates and movement ability play a role in the establishment and persistence of biocontrol agent populations. The extent to which agent dispersal may influence weed biocontrol success (impact) is explored in Chapter 5.

The goal of this study was not to generate specific release protocols, however, some general conclusions regarding release strategies seem appropriate. First, the common practice of matching release site habitat conditions to the habitat preferences of the agent is well supported by the fact that population growth rates had a substantial effect on release persistence. Although this 'revelation' is self-evident, it is reassuring that the model supports common sense! Second, there is little extra benefit to making releases substantially greater than the minimum necessary to escape an Allee effect. Therefore, I advocate the use of trial releases where possible to ascertain potential thresholds in establishment induced by an Allee effect. In addition, further emphasis should be placed upon experiments to determine the prevalence of Allee effects for weed biocontrol agents, either during the agent selection process or prior to initiation of large-scale release programs. Third, efforts should be made to collect information regarding the movement

abilities of potential biocontrol agents. The relative insensitivity of the model to dispersal parameters suggests that even qualitative information regarding vagility and/or propensity to disperse (emigration) could improve release strategies.

The key result arising from this study is that emigration rates and movement ability, under the conditions explored here, can have straightforward but antagonistic effects on introduction persistence and failure to consider these effects, in addition to environmental stochasticity and Allee effects, may produce misleading predictions regarding biocontrol introduction persistence. The study illustrates that dispersal data of the kind modeled here can help determine biocontrol agent suitability and should aid the design of more efficient biocontrol agent release programs against target pests.

4.5 References

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Table 4.1. Parameter values used in the simulation experiment and results from the model sensitivity analysis. Each parameter was varied systematically across the range of values presented while holding all other parameters at a default value (in bold). Results are from means of 200 simulations for each combination of parameters. Values in parentheses next to parameter values in the first row indicate the percentage deviation from the default value.

Parameter & description	Simulation experiment	Sensitivity analysis	
	Value	Value	P(persist)
r_d (mean population growth rate)	1.0	0.25 (-75%)	0.18
		0.90 (-10%)	0.52
		1.0	**0.67**
		1.10 (+10%)	0.685
		1.75 (+75%)	0.855
v_r (environmental variability)	1.0, 1.5, 3.0	0.375	1.0
		1.35	0.745
		1.5	**0.67**
		1.65	0.55
		3.625	0.265
r_A (Allee growth rate)	-0.25, -1.0	-0.125	0.765
		-0.45	0.62
		-0.5	**0.67**
		-0.55	0.605
		-0.875	0.53
ε (emigration rate)	0, 0.1, 0.3, 0.7	0.075	0.565
		0.27	0.74
		0.3	**0.67**
		0.33	0.605
		0.525	0.53
α (distance-dependent movement rate – movement ability)	0.02, 0.03	0.00625	0.62
		0.0225	0.67
		0.025	**0.67**
		0.0275	0.61
		0.04375	0.415
y' (colonization ability)	0.5	0.125	0.65
		0.45	0.61
		0.5	**0.67**
		0.55	0.61
		0.875	0.645
N_0 (release size)	100, 300, 500, 700, 900, 1100	175	0
		630	0.565
		700	**0.67**
		770	0.65
		1225	0.705

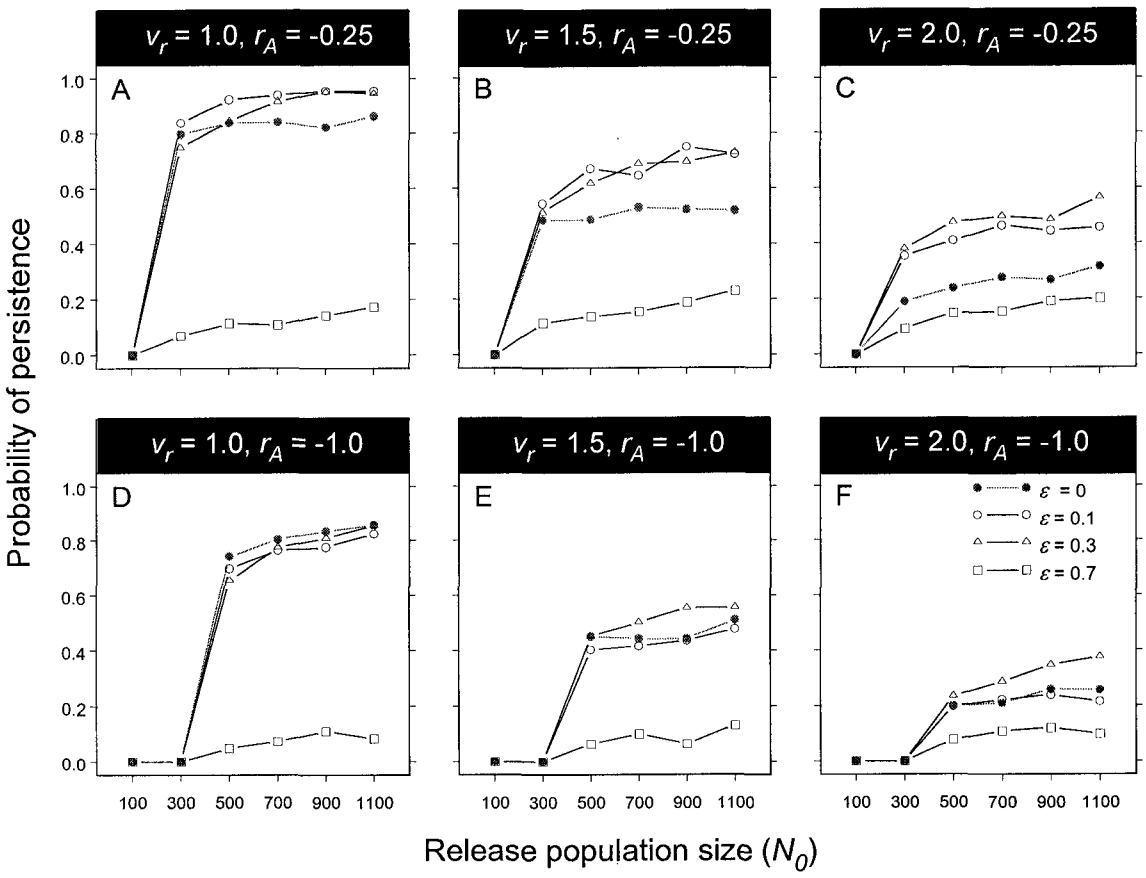

Figure 4.1. The influence of interactions between emigration rate (ε), environmental stochasticity (v_r), and Allee effect intensity (r_A) on the probability of introduction persistence, as a function of initial release population size. Panels A-C illustrate the effects of ε and v_r under a low intensity Allee effect (r_A = -0.25) and panels D-F illustrate the same effects under a high intensity Allee effect (r_A = -1.0). For all panels, movement ability (α) was held constant at α = 0.025. Note however, that no dispersal occurs when ε = 0. Data presented are based on means of 500 replicate simulations for each combination of parameter levels. An introduction was deemed to have persisted if the initial release or any local populations arising from it were present after 20 generations.

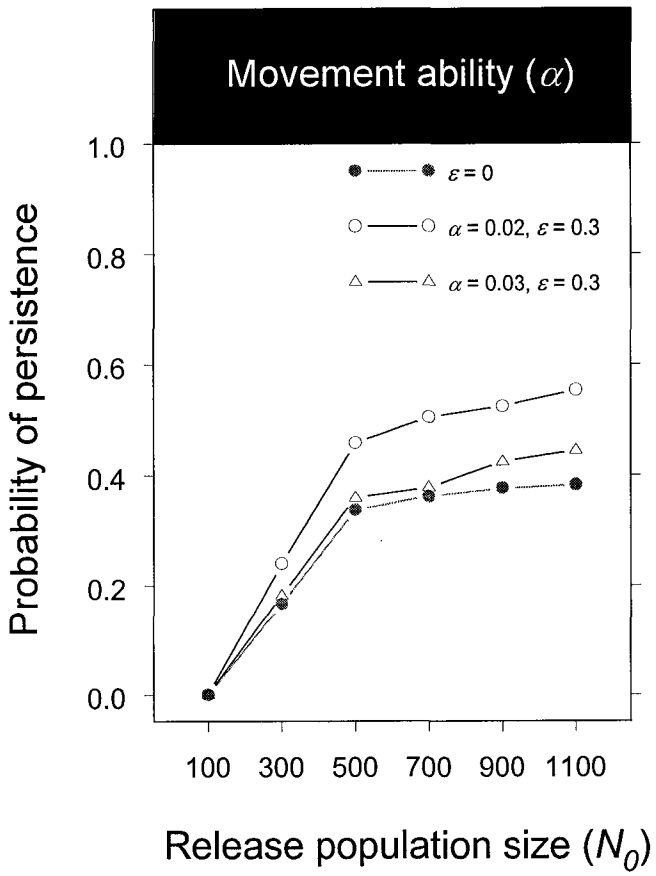

Figure 4.2. The influence of movement ability (α) on the probability of introduction persistence, as a function of initial release population size. Results presented are for a low intensity Allee effect (r_A = -0.25), moderate environmental stochasticity (v_r = 1.5), and moderate emigration rate (ε = 0.3), except for the no dispersal situation where ε = 0. See Figure 1 caption for further model details. The relationship presented here was representative of those for other values of the model parameters v_r, r_A, and ε.

Chapter 5

The role of matrix habitat in the spatial population dynamics and impact of *Aphthona lacertosa* on leafy spurge

5.1 Introduction

Understanding how biocontrol agent populations propagate over the landscapes on which they are released is an important component of being able to predict success of weed biocontrol release programs. Few studies, however, have been conducted to examine weed biocontrol agent rates of spread or patterns of host-patch colonization (but see Huffaker and Kennett 1959; Rudd and McEvoy 1996; Grevstad and Herzig 1997), let alone how these processes may influence biocontrol agent population dynamics (Shigesada and Kawasaki 1997).

One feature of release landscapes that has the potential to alter colonization patterns and rates of spread for biocontrol agents is the type(s) and amount of matrix habitat present. Numerous studies show that various aspects of landscape structure, such as the types of habitat present and their spatial arrangements, influence how organisms move between different resources (*e.g.*, foraging and breeding sites) and between different populations (Fahrig and Merriam 1985; Pither

and Taylor 1998; St. Clair *et al.* 1998; Jonsen and Taylor 2000*a*; With *et al.* 2002). In particular, the influence of matrix habitat on dispersal may be a key component of the spatial population dynamics of many species that occupy patchy habitat (Wiens 1997; Jonsen and Taylor 2000*b*; Roland *et al.* 2000; Chapter 1). Matrix habitat generally has little or no resource value, may confer higher mortality rates on animals that move through it versus suitable habitat (Zollner and Lima 1999), and in some cases may restrict animal movement rates relative to those through other habitats (Roland *et al.* 2000; Ricketts 2001; Chapter 2). The sum total of these effects may influence local population dynamics by reducing (or increasing) the potential 'rescue effect' of dispersal on local population size (Brown and Kodric-Brown 1977) or by reducing the potential for colonization of unoccupied habitat (Fahrig and Merriam 1985). The key point is that without a consideration of the structure of landscapes *vis-a-vis* matrix habitat and how particular species interact with that structure, reliable predictions of colonization patterns or overall population dynamics may not be possible.

In the context of weed biocontrol programmes, landscape effects may have important implications for impact on target weeds through their influence on host-patch colonization patterns and local population dynamics following point releases of biocontrol agents. These effects will be of particular importance in situations where purposeful redistribution of established biocontrol agent populations are logistically or economically difficult. In other words, most rangeland weeds. Thus exploration of situations under which landscape effects on biocontrol agent dispersal and population dynamics can occur should allow managers to make more informed decisions regarding release and redistribution strategies.

The purpose of this exercise was to explore how dispersal and population growth of a released biocontrol agent and its impact on a target weed may be influenced by the spatial structure of the landscape onto which it is released. I approached this problem by developing a simulation model that incorporates dispersal between biocontrol agent local populations, a local population growth function, and an empirically derived impact function that relates changes in host patch size to agent densities. The model was parameterized from empirical data collected from the leafy spurge – *Aphthona* flea beetle biocontrol system described in previous chapters and run on a digital representation (Fig. 5.1) of a release landscape (see Fig. G.1) comprised of a mosaic of spurge patches and two matrix habitats (grass and shrub). I ran two separate forms of the model, one with an effect of matrix habitat on movement rates and one without. Thus comparison of the predictive ability of the two models will yield an indication of the importance of matrix habitat –

dispersal interactions on *A. lacertosa* spatial dynamics and impact on leafy spurge. Model predictions regarding patch occupancy patterns and local population sizes were tested using field data collected from the release landscape in 2000 and 2001.

5.2 Methods

5.2.1 Simulation model

The simulation model presented here is a spatially explicit, patch-based model that uses the Virtual Migration (VM) model (Hanski *et al.* 2000) as a dispersal function coupled with a stochastic Gompertz population growth model and an empirically derived impact function that relates how beetle densities influence changes in spurge patch size. The model includes information on the location and size of individual patches as well as the proportion of grass and shrub matrix habitat lying along the direct paths between all pairs of patches. Differences in habitat quality among patches were not incorporated into the model because it was not possible to record habitat data for all the patches on the network.

5.2.2 The landscape

The simulation model was run on a digitized representation of the intensive study landscape described in the General Methods (see Fig. G-1). The shrub and grass layers from the GIS were converted into a raster image with a resolution of 5.58 m^2 / pixel (Fig. 5.1). Matrix habitat on the landscape was dominated by grassland with shrubs occupying only 8 % of the total area. Spurge patches, indicated by the black dots in Fig. 5.1, were mapped *in situ* and their centroids, calculated using the S-Plus for ArcView extension v1.1 (Insightful Corp.), were used to define the patch locations in the simulation model. Distances between patches, however, were measured from edge-to-edge between all pairs of patches using the Analysis Extension v1.3 for ArcView (SWEGIS).

5.2.3 Dispersal

The model presented here uses different dispersal and population growth functions from those used in the model presented in Chapter 4. Here, dispersal is modeled using a modified version of the VM model (Hanski *et al.* 2000) which allows a more biologically realistic representation of the dispersal process than the dispersal function presented in Chapter 4. The dispersal function

used here calculates patch connectivity in a similar manner to that used in Chapter 4 but here connectivity is determined from each patch acting as a source of dispersers to all potential receiving patches. This is the conceptual opposite of the connectivity measure used in Chapter 4. The basic assumptions, however, are similar to those in Chapter 4 (see Eqn. 4.1), here patch connectivity (S_j) is calculated from the following formula,

$$S_j = \sum_{k,j\neq k} \exp(-\alpha d_{jk}) A_k^{\zeta_{im}} . \qquad (5.1)$$

The measure assumes that dispersers move out equally in all directions and the number of dispersers declines exponentially (α) with increasing distance between source and recipient patches (d_{jk}). However, since S_j is measured from the source to potential recipient patches, there is little sense in modifying it by the population sizes of the recipient patches (*cf.* Eqn. 4.1). Instead, connectivity is modified by the sizes (area) of the recipient patches (A_k) and the additional parameter ζ_{im} determines the degree to which immigration is affected by the size of the recipient patches (*i.e.*, $\zeta_{im} = 0$, immigration is independent of patch size; $\zeta_{im} = 1$, immigration is directly proportional to patch size).

In Chapters 1 and 1.2 I illustrated that habitat elements in the matrix can influence dispersal to different degrees. This effect can be incorporated into the model by using different α's for each habitat component of the matrix and summing their contributions to S_j (Moilanen and Hanski 1998),

$$S_j = \sum_{k,j\neq k} \exp(\sum_{h} -\alpha_h d_{hjk}) A_k^{\zeta_{im}} . \qquad (5.2)$$

The parameter α_h is the movement rate in matrix habitat component h and d_{hjk} is the Euclidean distance between patches j and k passing through habitat h. In the study I present here, there are two matrix habitats and thus two α's; α_{gr} – the movement rate through grassland and α_{sh} - the movement rate through shrub habitat.

Another key assumption of the model is that the survival of dispersers decreases with decreasing connectivity, measured by S_j. Dispersal survivorship (ϕ_{mj}) is modeled by the following formula,

$$\phi_{mj} = \frac{S_j^2}{\lambda + S_j^2}. \tag{5.3}$$

The parameter λ determines how rapidly ϕ_{mj} approaches 1 for a given level of connectivity thus a higher λ means higher dispersal mortality. Individuals that survive dispersal are assumed to be distributed among the recipient patches in proportion to the patches' contribution to the connectivity of the source patch. Hanski *et al.* (2000) combine Equations 5.2 and 5.3 to determine the probability ($\psi_{j,k}$) of an individual leaving patch j and successfully arriving at patch k which forms the basis for analyses of mark-recapture data in patch networks. Here, I multiply $\psi_{j,k}$ by the number of emigrants ($N_j\varepsilon_j$) leaving patch j and sum over all j to determine the number of immigrants (M_k) arriving at patch k,

$$M_k = \sum_{j \neq k} \psi_{j,k} N_j \varepsilon_j = \sum_{j \neq k} \frac{\exp(-\alpha_h d_{hjk}) A_k^{\zeta_{im}}}{\frac{\lambda}{S_j} + S_j} N_j \varepsilon_j . \tag{5.4}$$

Where ε_j specifies the patch-specific emigration rate which is a function of a base emigration rate (η) that is scaled to patch size (A_j) raised to the power $-\zeta_{em}$,

$$\varepsilon_j = \eta A_j^{-\zeta_{em}}. \tag{5.5}$$

Thus emigration rates decrease with increasing patch size when $-\zeta_{em} > 0$ and are constant across patch size when $-\zeta_{em} = 0$.

Hanski *et al.* (2000) point out that $\psi_{j,k}$ (and by extension M_k) not only depends on the distance between patches and the size of a given receiving patch but also on the number and sizes of other patches in the vicinity of the source patch and on the size of the source patch. The larger the value of ζ_{im} the more 'attractive' are large patches to dispersers, whereas, the larger the value of ζ_{em} the lower the rate of emigration from larger patches. Although these assumed relationships are justified by empirical evidence (Turchin 1986; Grevstad and Herzig 1998), the generality and importance of patch area-scaled immigration and emigration for insect population dynamics have

yet to be determined. Therefore, to keep the simulations as simple as possible, I set $\zeta_{im} = \zeta_{em} = 0$ for the simulations presented here.

The dispersal function presented here can be parameterized using individual mark-recapture data taken from a network of patches (Hanski *et al.* 2000). Given the small size of *Aphthona* beetles (ca. 3-4 mm long), however, it was impractical to carry out an individual mark-recapture experiment. In light of this I used experimental data presented in Chapters 1 and 2 to estimate the parameters α_{gr}, α_{sh}, and ε for the simulation model's dispersal function. Estimation of dispersal mortality, λ, was not possible from my field data and so I conducted a series of model calibration runs (not presented) to determine an appropriate value for λ. Dispersal parameter estimates and details of the methods used to obtain them are presented in Chapter 3.

5.2.5 Population growth

In Chapter 4, I modeled growth within patches using a random walk function with a reflecting ceiling (Eqns. 4.3 a-c) that allowed a simple and direct exploration of the effect of stochasticity in population growth rates on biocontrol release persistence. Although the model has been used elsewhere for theoretical purposes (Hanski *et al.*1996; Kean and Barlow 2000) it is less commonly used for comparisons with empirical population data. Field data collected at *A. lacertosa* release sites throughout the Blood Reserve in 1999 and 2000 (RS Bourchier, *unpublished data*) suggest that a Gompertz model (Royama 1981; Dennis and Taper 1994) may be a suitable descriptor of *A. lacertosa* population growth (Fig. 5.2 A). The model has the form:

$$N_t = N_{t-1} \exp[a + b \log(N_{t-1}) + Z_{t-1}], \qquad (5.6)$$

where a corresponds to the intrinsic growth rate, b determines the strength of density-dependence, and Z_{t-1} is environmental stochasticity represented as a Normally distributed random variable with mean 0 and variance v_r. Typically, growth models such as the Gompertz and Ricker-logistic are fit using a suitably long time series but this is not available for *A. lacertosa* (*i.e.,* the first releases in Alberta were in 1997), so I used spatially replicated data collected over 2 years as a surrogate. Population growth estimates are likely biased because the Gompertz and Ricker models do not account for dispersal or spatial correlations in the environment, which undoubtedly exist in the field data. Techniques exist to estimate population growth rates from spatial datasets, taking into account dispersal and environmental correlations (Lele *et al.* 1998) but these are beyond the

scope of the current study. I, therefore, acknowledge that *A. lacertosa* growth estimates (below) likely underestimate actual growth rates because emigration from release sites was not taken into account.

A linear regression of $\log(N_{t-1})$ on the per capita rate of increase $[\log(N_t) - \log(N_{t-1})]$ suggests a = 3.1740 and b = -0.5073 ($F_{1, 16}$ = 9.238, p = 0.008, R^2 = 0.366) (Fig. 5.2 A). In comparison, a regression of N_{t-1} on the per capita rate of increase (implying Ricker-type dynamics) yielded a poorer fit to the Blood Reserve data ($F_{1, 16}$ = 6.059, p = 0.03, R^2 = 0.27) (Fig. 5.2 B). Field data were not available to estimate v_r and so I explore the influence of different levels of environmental stochasticity on model predictions (see Results: *Sensitivity analysis*).

5.2.6 Impact

Successful biocontrol systems are characterized by decreases in pest density or some other appropriate population measure. I assume patch size is an appropriate indicator of spurge population size and focus on factors that may influence rates of change in patch size. This assumption is supported by empirical evidence that spurge stem density is positively correlated with spurge patch size (Pearson's r = 0.55, n = 134, p < 0.001) (Fig. 5.3). I modeled beetle impact on spurge patches by using the empirically observed relationship between *A. lacertosa* density and change in spurge patch size. This relationship was presented in Chapter 3 (Fig. 3.9) and here I modify the regression model to account for *A. nigriscutis* density prior to determining the effect of *A. lacertosa* density on changes in spurge patch size between 1999 and 2000. After accounting for a non-significant effect of *A. nigriscutis* on changes in spurge patch size, adult *A. lacertosa* densities in the previous year were significantly correlated with spurge patch decreases in the current year (Table 5.1). Thus beetle impact on spurge patch size takes the form of a linear relationship in the simulation model:

$$\delta_I = P_E - P_I \log(N_{t-1}), \qquad (5.7)$$

where the change in patch size (δ_I) is a linear function of the rate of patch expansion in the absence of beetles (P_E) and the impact (P_I) per unit log beetle density (N_{t-1}) in the preceding year. This equation implies a linear transition from increasing patch-size at low agent densities to decreasing patch-size at higher agent densities. Estimates and their precision for the parameters P_E and P_I are presented in Table 5.1. Clearly, other factors such as competition from native plants

(Sheppard *et al.* 2001) influence the growth rate of spurge patches but to incorporate these factors into the model, without prior assessment of their importance relative to that of biocontrol agent impact, would add undue complexity to the analyses.

5.2.7 Field data

Beetle incidence and density estimates for each patch were used to evaluate the simulation model. Sampling for beetle densities was conducted on the intensive-study landscape (described in Chapter 3) and on an adjacent landscape to the East (Fig. 5.1). Over the duration of the study a total of 379 patches was sampled, 326 in 2000 and 358 in 2001. The different sample sizes reflects the loss of previously extant spurge patches and establishment of new patches between the two sample years.

All spurge patches were sampled during two 1-week periods in mid-June and mid-July in each of the years 2000 and 2001. These sample periods roughly corresponded to shortly before and shortly after expected peak adult densities in 2000 and 2001. Transects were walked along the long axis of each patch and beetle densities were estimated using a sweep net. Beetles in the sweep net were removed into a large, clear plastic container after every 20 sweeps and counts were estimated to the nearest 5 beetles for low densities (< 50 beetles) and to the nearest 50 beetles for higher densities (> 50 beetles). This procedure was continued until the sampler reached the far side of the patch.

5.2.8 Model analysis

5.2.8.1 Model evaluation

The lack of a long-term (*e.g.,* 20-year) time series precludes fully validating the model. Nonetheless, some important model predictions can be evaluated with the present field dataset. Default model runs were conducted using the parameter values presented in Table 5.3. Model predictions regarding beetle population densities and patch occupancy were compared to field observations taken in 2000 and 2001. In addition, model predictions regarding changes in overall spurge cover and individual patch sizes were compared to field data. The model was initialized with two releases of 2000 *A. lacertosa* each in the two patches where actual releases were made in 1997 (Fig. 5.1, indicated by the 2 filled triangles) and the model was iterated for 5 years to correspond with the field data collected in 2000 and 2001 (*ie.,* in years 4 and 5 following the releases in 1997). A total of 200 replicate runs was used and the model's predictions regarding *A.*

lacertosa occupancy and local population size for individual spurge patches were compared to field data collected in 2000 and 2001. This procedure was conducted twice, once for model runs without a matrix effect on dispersal and once for models incorporating a matrix effect on dispersal.

5.2.8.2 Sensitivity analysis

A sensitivity analysis was carried out by varying the values of individual parameters by ± 50 %, ± 20 %, and ± 10 % of the default values (see Table 5.2). The mean of the logarithm of local beetle populations 5 and 20 years after introduction and the proportion change in overall spurge cover were viewed relative to those generated by the default parameter set. These comparisons were used to determine which parameters had the largest effects on model predictions and how those effects might change over time.

5.2.9 Putting the model to work

In order to understand more generally how matrix habitat might affect weed biocontrol releases, I altered the structure of the release landscape by increasing the cover of shrub habitat. Three new landscapes were created, each identical to the original landscape presented in Fig. 5.1 but with increased shrub habitat cover. Each of the existing shrub patches was enlarged by adding a buffer of 1 m, 5 m, or 25 m which corresponded to an increase in shrub matrix cover over the original landscape of 2 %, 7 %, or 22 %, respectively. I ran the simulation model, using separate estimates for movement rate through grass and shrub habitats, on each of these new landscapes and compared model predictions for the mean local population size to the predictions generated on the original landscape. In addition, I compared model predictions for runs using the movement rate parameters for grass (α_{gr}) and shrub (α_{sh}) habitat estimated for *A. lacertosa* and for *A. nigriscutis* (presented in Chapter 2). I do not have estimates of other model parameters for *A. nigriscutis*, so I used *A. lacertosa* parameter estimates in combination with *A. nigriscutis* movement rate parameters. The goals of these simulation experiments were: (1) to determine how an increase in cover of a matrix habitat that is restrictive to movement might influence biocontrol agent population dynamics and (2) to determine how biocontrol agent species with different movement characteristics would perform when introduced onto landscapes with different matrix habitat characteristics.

5.3 Results

5.3.1 Model evaluation

5.3.1.1 Patch occupancy

The release populations spread from the two origins and colonized approximately two-thirds of the patches on the landscape within 5 years. The rate of spread predicted by the model was comparable but slightly lower than that observed based on patch occupancy in 2000 (Fig. 5.4) and the proportion concordance between observed and predicted patch occupancies was 0.76 (for the simulated data, patches were considered occupied if the predicted mean occupancies > 0.5). There was, however, greater discrepancy between the model and field data in 2001 which arose from substantial turnover in observed patch occupancy (Fig. 5.4); the proportion concordance for 2001 patch occupancies was 0.56. These concordance values were both significantly greater than those expected based on a random pattern of patch occupancy (2000: $\chi^2 = 45.37$, df = 1, p = 0; 2001: $\chi^2 = 3.71$, df = 1, p = 0.05). Field observations of patches that were occupied in 2000 but were unoccupied in 2001 were possibly due to drought conditions experienced throughout 2001 (see Chapter 3). Although environmental stochasticity was incorporated into the model via the parameter v_r, the default level of stochasticity ($v_r = 0.1$) was insufficient to model the large fluctuation in patch occupancy observed.

Simulations run with an effect of matrix habitat on movement rates produced marginally better occupancy predictions. The proportion concordance between observed and predicted occupancies for 2000 and 2001 were 0.71 and 0.58, respectively. Both of these values were significantly greater than that expected based on a random pattern of patch occupancy (2000: $\chi^2 = 31.34$, df = 1, p = 0; 2001: $\chi^2 = 3.38$, df = 1, p = 0.06), however, neither were significantly different from concordance values for the model run without a matrix effect (2000: $\chi^2 = 1.86$, df = 1, p = 0.17; 2001: $\chi^2 = 0.732$, df = 1, p = 0.39).

5.3.1.2 Local population density

Comparisons of observed and predicted local population densities for 2000 and 2001 indicate substantial variability in model fit (Fig. 5.5). The model predictions match the field data qualitatively but predicted local densities were generally higher than was observed throughout much of the range of population density. Even so, linear regressions fit to the data had slopes that were not significantly different from 1 (Fig. 5.5) although the y-intercept for the 2001 data was

significantly less than 0 (Table 5.3, a), suggesting a systematic departure in model fit. Again, this discrepancy in fit was most likely due to the drought conditions experienced in 2001. Enhancing the model by using separate estimates of α for grass (α_{gr}) and shrub (α_{sh}) matrix habitats yielded only slight improvement in model fit as judged by the regression models fit to these data (Table 5.3, b). I explore this result in more detail later on.

5.3.1.3 Beetle impact

Plots of log patch size illustrate increasing discrepancy between model predictions and field data with increasing time since release (Fig. 5.6). The model tends to over-predict the effect of beetle density on subsequent spurge patch size but correctly predicts that smaller patches, closer to the release location tend to be eliminated by the beetles (Fig. 5.6). Despite the discrepancy in model fit for individual patches, the model did a reasonable job at predicting the mean change in spurge patch size between consecutive years, although variability about the mean was substantially greater for the field data (Fig. 5.7). These impact results illustrate that the model does not predict well the specific patches that are eliminated or reduced in size by *A. lacertosa* but does predict well the overall reduction in spurge cover during a given time period and the general locality (distance from release) in which impact should occur.

5.3.2 Sensitivity analysis

Initial sensitivity analyses were conducted for results after 5 beetle generations (years) following release to better understand model behaviour during the time-frame in which the model was evaluated. The results for this short-term analysis are summarized along the top row in Fig. 5.8. A second set of sensitivity analyses were run for 20 beetle generations to determine how the model behaved over a longer temporal scale. The results for this longer-term analysis are presented along the bottom row in Fig. 5.8. Most interestingly, the importance of the dispersal parameters, especially the distance-dependent movement rate through grass (α_{gr}), was reduced substantially as the number of generations since release increased from 5 to 20 (Fig. 5.8, compare top and bottom main panels).

Simulation results after 5 generations were most sensitive to the population growth parameter, a, the distance-dependent movement rate through grass matrix, α_{gr}, and the impact parameter, P_I (Fig. 5.8). Both the mean local population size and the proportion reduction in spurge area increased with increasing a and decreasing α_{gr} (*i.e.*, an increase in the average movement

distance) but only the proportion reduction in spurge increased with increasing P_I (Fig. 5.8). The rest of the model parameters had small or no discernable influence on either of the model predictions.

When simulations were run for 20 generations, the population growth parameters a and b clearly had the strongest influence on mean local population size and, in addition to P_I, also strongly influenced the proportion reduction in overall spurge area (Fig. 5.8). The density-dependence parameter, b, however, had less of an effect on beetle impact on spurge than it did on beetle population size (Fig. 5.8, compare b among panels). Model predictions were relatively insensitive to the values of the other parameters (Fig. 5.8). A reassuring feature of the analyses is that the model was insensitive or only slightly sensitive to the two parameters for which empirical data were not available, environmental stochasticity, v_r, and dispersal mortality, λ, and the parameter that was estimated with the least precision, P_E, (see Table 5.1).

5.3.3 Putting the model to work

Earlier, I illustrated that the simulation model with separate parameters for movement rates through grass and shrub matrix habitats was only a marginal improvement over a model with a single movement rate parameter (Table 5.3). Results from the sensitivity analysis, however, suggest that the movement rate through grass matrix can influence mean local population size and the overall reduction in spurge cover (Fig. 5.8) during the early stages of a biocontrol release but that the effect disappears over time as the release spreads over the landscape. Furthermore, movement rates through shrub habitat had little effect on population size or impact on spurge and this was most likely due a combination of the low percentage of shrub habitat (8 %) on the study landscape and the relatively small difference in *A. lacertosa* movement rates through the two matrix habitats (see Chapters 1 & 2).

An important question to address is, do the observed movement rates through grass and shrub habitats have a stronger influence on local population size when releases are conducted on landscapes with different proportions of the two matrix habitats? The answer to that question is no and yes. Simulations run with the movement rates estimated for *A. lacertosa* (see Table 5.2 for values) on the original landscape and 3 new landscapes with increasing amounts of shrub habitat yielded only slight decreases in the mean local population size (Fig. 5.9). These decreases were greatest but by no means large on the 25-m buffer landscape (30 % shrub habitat) after 5

generations but were only barely perceptible after 20 generations. On the other hand, simulations using the movement rates estimated for *A. nigriscutis* (α_{gr} = 0.0101, α_{sh} = 0.0371), a species for which shrub habitat was more restrictive to movement than for *A. lacertosa*, yielded substantially larger decreases in the mean local population size (Fig. 5.9). Even after 20 generations, the mean local population size for *A. nigriscutis* was noticeably lower on the landscape with highest shrub cover in comparison to the original landscape (Fig. 5.9). These results indicate that effects of matrix habitat on biocontrol release dynamics are dependent not only on the proportions of the matrix habitats but also on the degree to which a given matrix habitat(s) restricts movement and that these effects can differ among closely related species.

5.4 Discussion

The simulations presented here illustrate that weed biocontrol release dynamics can be predicted, at least qualitatively and in the short term, using information regarding agent dispersal, population growth, impact rate, and the spatial configuration of habitat. Furthermore, a comparison of models with and without an effect of matrix habitat on movement rates suggests that shrub habitat in the matrix exerts only minor influence on the colonization and local population dynamics of *A. lacertosa* on the study landscape. This is perhaps not a surprise given that the difference in *A. lacertosa* colonization (Chapter 1, Fig. 1.1) and movement rates (Chapter 2) through grass and shrub matrix habitats was relatively small and that surveys of beetle densities on the study landscape revealed no effects of the amount of shrub habitat within a given distance from sample points (Chapter 3). Using a similar modelling approach, Moilanen and Hanski (1998) found a similarly weak effect of matrix habitat on occupancy patterns of the butterfly *Melitea cinxia*. They attributed the result to inadequacies in satellite data used to classify the landscape, the technical difficulties of modelling dispersal in a realistic fashion, and the generally homogeneous structure of their study landscape. The latter two explanations may apply here as well.

I modeled dispersal using a modification of the Virtual Migration (VM) model of Hanski *et al.* (2000). The model assumes that dispersers follow the most direct route between any two spurge patches and ignores the potential influence of behavioural responses to features such as boundaries between different habitats (cf. Jonsen and Taylor 2000*b*) or, under the current implementation, different mortality rates among the habitats (Zollner and Lima 1999). Failure to

incorporate important components of the dispersal process such as habitat boundary responses or habitat-specific mortality rates into the model may have reduced the likelihood of producing substantially better predictions when landscape effects were considered. For example, Roland *et al.* (2000) illustrated that movement between alpine meadows by the butterfly *Parnassius smintheus* was impeded both by the presence and size of forest patches between meadows, suggesting that boundary responses as well as reduced movement rates through a restrictive habitat influence the movement of individuals between local populations.

In addition, the landscape used here, as in Moilanen and Hanski's (1998) study, was quite homogeneous with low shrub habitat coverage (8 %) and this likely reduced the importance of restricted movement through shrub habitat. This conclusion is supported by the fact that mean local population sizes decreased when the amount of shrub habitat was increased in the simulation model and that the effect was intensified when *A. nigriscutis* – a species for which shrub matrix was even more restrictive to movement – movement rates were substituted into the model (Fig. 5.9, compare *A. lacertosa* to *A. nigriscutis*). Thus it would seem that the influence of landscape – dispersal interactions on release dynamics depends upon the amounts of different matrix habitats on the landscape and also upon the degree to which a particular habitat restricts movement for a given biocontrol agent.

However, the effects of matrix habitat on movement for biocontrol agents with high population growth rates may be of relatively little consequence for local population dynamics. This point is illustrated in Figure 5.10, where two sets of simulations were run on the default landscape and on the 30 % shrub cover landscape, both with *A. nigriscutis* dispersal parameters but with intrinsic growth rates set either at the default value of 3.174 or at 0.5 (with equivalent density-dependence). Examination of the mean local population sizes at 5 and 20 years following release indicates that the influence of greater amounts of shrub habitat is transient when the intrinsic growth rate is high but the effect is much longer lasting at a lower growth rate. Furthermore, results from the sensitivity analysis suggest that any effect of differential movement rates through matrix habitats on local population sizes or on reduction in local weed populations are transient, at best. The sensitivity analysis also revealed that the mean local population size was most sensitive to the population growth rate and the strength of density-dependence experienced by populations. Combined, these results suggest that population growth rates and the prevalence of density-dependence play more important roles in determining local population sizes and impact on weed populations than do landscape – dispersal interactions.

If population growth rates and density-dependence are the primary factors influencing *A. lacertosa* local population sizes and impact on spurge patches then what role might fine-scale habitat features within spurge patches play? Results presented in Chapter 3 illustrate that densities of both *A. lacertosa* and *A. nigriscutis* are influenced in different ways by spurge stem densities and the amount of bare ground or grass within spurge patches. *Aphthona nigriscutis* prefers xeric spurge patches with moderate to low spurge cover and moderate to high amounts of bare ground (Jacobs *et al.* 2001; Maw 1981), whereas *A. lacertosa*, in its native range, is found more commonly in mesic sites with generally higher spurge cover and less bare ground (Bourchier *et al.* 2002; Nowierski *et al.* 2002). These responses to fine-scale habitat may translate into among-patch differences in population growth rates and/or carrying capacities that could explain much of the discrepancies between observed and predicted local population sizes and impact on local spurge populations. However, my simulations illustrate that fine-scale habitat data, which are difficult to collect over entire release landscapes, are not necessary to make predictions regarding average agent population sizes or impact on spurge at a landscape level.

Clearly, other factors such as the specifics of a given weed species' population dynamics and competition from other plant species are involved in determining the outcome of weed biocontrol introductions. For example, elevated recruitment from a soil seed-bank may increase the time to local extinction of weed populations even in the presence of high biocontrol agent densities (Lonsdale *et al.* 1995). Furthermore, competition from other plant species may reduce weed vigour (Sheppard *et al.* 2001) or reduce weed survivorship outright (McEvoy *et al.* 1993). The combination of herbivory and plant competition in some cases may be of little additional benefit (Sheppard *et al.* 2001) and in other cases may further reduce weed survivorship (McEvoy *et al.* 1993); the outcome of this combination may depend upon the intensity of both the competition among plant species present and the herbivory on the weed (Harper 1977; McEvoy *et al.* 1993). These, and/or other effects on local weed population change, were in part incorporated into the impact function by modelling the empirically observed relationship between beetle density and weed patch-size change (Eqn. 5.7) rather than using a more mechanistic function. In addition, much of the study landscape was subjected to high levels of cattle grazing and this likely reduced the importance of plant competition effects (Grigulis *et al.* 2001). Nevertheless, study of weed population dynamics and/or plant competition interactions with herbivory in a spatially explicit way has received little if any attention in the weed biocontrol literature but may reveal new insight into how weed biocontrol systems function.

Although fine-scale habitat data may not be necessary to predict average biocontrol agent population sizes or impact over entire release landscapes, substantial variation in quality among spurge patches may have important implications for biocontrol agent population structure. For example, under the scenario presented in this chapter the high movement and intrinsic growth rates of *A. lacertosa* suggest a patchy population structure (Harrison and Taylor 1997), at least at the scale of the study landscape, where there is little evidence of local population turnover for the biocontrol agent. A gradient in spurge patch quality arising, for example, from differences in spurge density or bare ground cover over the landscape may result in source-sink dynamics (Pulliam 1988) where marginal (sink) habitat remains occupied via dispersal from local populations in higher quality (source) habitat. This type of population structure implies that reproduction in low quality spurge patches may be quite low, or, not occur at all. Thus even though adult *Aphthona* beetles may occupy most spurge patches on a release landscape, impact on spurge in low-quality patches is not likely to occur because only the larvae exert lasting damage to spurge plants (Harris 1984). The use of stage-structured population models (*e.g.*, McEvoy and Combs 1999), augmented with the kind of spatial data presented here, may tease apart some of these ideas and improve understanding of the conditions under which introduced insects are and are not likely to be effective weed biocontrol agents.

Earlier I suggested that landscape – dispersal interactions may not strongly influence biocontrol agent population dynamics if intrinsic growth rates are high and/or the prevalence of density-dependence is low. However, for species with low intrinsic growth rates landscape – dispersal interactions may exert much more influence on biocontrol agent population dynamics. Stronger effects of landscape structure in these situations would suggest that different matrix habitats, or other features of the landscape such as the spatial arrangement or amount of habitat (weed patches), may be important factors for releases that fail to establish or to propagate over release landscapes (cf. Chapter 4). This illustrates the importance of quantifying biocontrol agent population growth and movement rates through typical landscapes that will be encountered following release in order to make more reliable predictions about how likely releases are to establish and propagate.

5.5 Conclusions

Evaluation of the simulation model used in this study suggests that movement through different matrix habitats has little influence on the patterns of *A. lacertosa* patch occupancy, local population size, and impact on leafy spurge. However, these results are specific to the landscape used in the simulation model and further analyses suggest that releases on similar landscapes but with greater cover of shrub habitat – a matrix element that impedes *Aphthona* movement – will be characterized by lower local population sizes, especially for biocontrol species with comparable movement rates but with lower intrinsic growth rates. This is a result that could not otherwise be predicted for actual field releases without prior assessment of movement and population growth rates of the biocontrol agent and without knowledge of the kinds of landscape onto which releases are made.

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Table 5.1. Regression coefficients and their precision for *Aphthona* beetle impact on spurge patch size. The response is the log change in spurge patch area between 1999 and 2000. The model is a linear regression with 32 observations and an R^2 of 0.43.

Term	Coefficient (se)	*t*-value	P(*t*)
Intercept (P_E)	0.1488 (0.1570)	0.9472	0.3514
log *A. nigriscutis* density	-0.1364 (0.1098)	-1.2420	0.2242
log *A. lacertosa* density (P_I)	-0.2784 (0.0597)	-4.6654	0.0001

Table 5.2. Default parameter values used in the sensitivity analysis. The default values, in all but two cases (see footnote) were obtained from empirical data. For the sensitivity analysis all values were varied individually by ± 10 %, 20 %, and 50 % of their default values.

Model component	Parameter	Description	Default value
Dispersal	ε	Emigration rate – constant among patches	0.1686
	α_{gr}	Distance-dependent movement rate through grass matrix habitat	0.0169
	α_{sh}	Distance-dependent movement rate through shrub matrix habitat	0.0234
	λ	Dispersal mortality	1*
Population growth	a	Intrinsic growth rate – constant among patches	3.1740
	b	Density-dependence parameter – constant among patches	-0.5073
	v_r	Environmental stochasticity – constant among patches	0.1*
Impact	P_E	Patch expansion rate – in absence of *A. lacertosa*	0.1488
	P_I	Impact rate – rate of log patch area decrease per unit log *A. lacertosa* density	-0.2784

* Not estimated from empirical data

Table 5.3. Summary of linear regression models fit to plots of predicted and observed local population densities in 2000 and 2001, for simulation models without (a) and with (b) an effect of matrix habitat on movement.

a) Without matrix effect

Year	Term	Coefficient (1 se)	*t*-value	P(*t*)	Model df	Model F	P(F)	R^2
2000	Intercept	-0.20 (0.37)	-0.53	0.60	1, 103	68.35	0	0.40
	Predicted local density	0.93 (0.11)	-0.63*	0.73*				
2001	Intercept	-1.27 (0.40)	-3.14	0.002	1, 78	95.94	0	0.55
	Predicted local density	1.11 (0.11)	0.95*	0.83*				

b) With matrix effect

Year	Term	Coefficient (1 se)	*t*-value	P(*t*)	Model df	Model F	P(F)	R^2
2000	Intercept	-0.30 (0.38)	-0.81	0.42	1, 95	73.57	0	0.43
	Predicted local density	0.96 (0.11)	-0.37*	0.64*				
2001	Intercept	-1.16 (0.40)	-3.93	0.004	1, 82	89.0	0	0.52
	Predicted local density	1.08 (0.11)	0.73*	0.76*				

* *t*-tests determine whether regression slopes are significantly different from 1

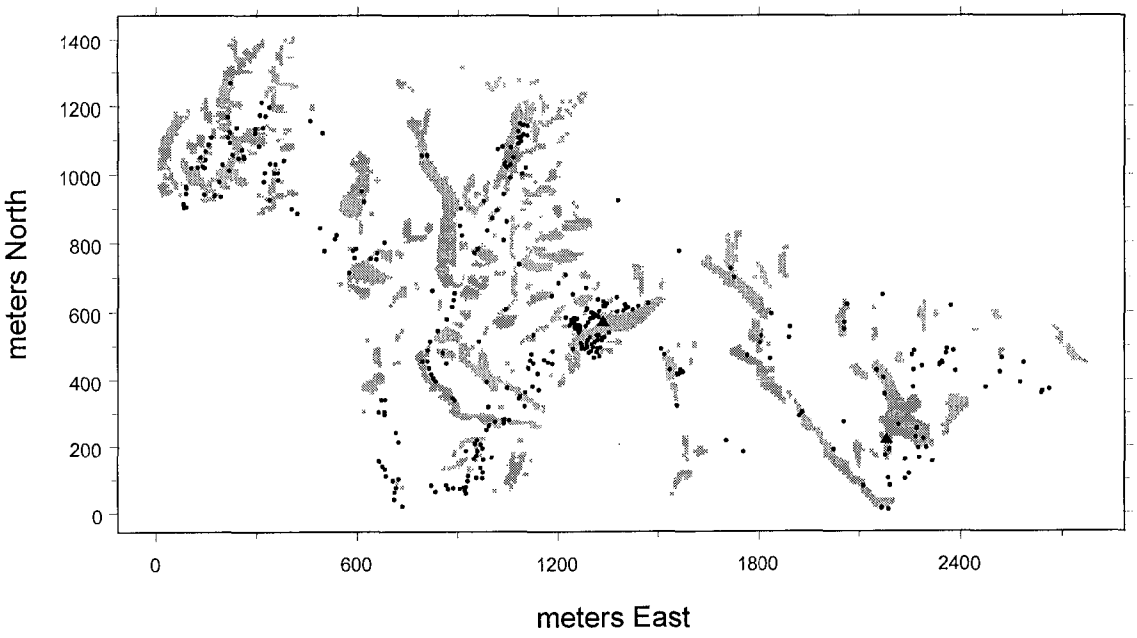


Figure 5.1. Raster image of study landscape with shrub matrix habitat shown as grey patches and spurge patch locations indicated by filled circles. Two releases of *A. lacertosa* were conducted both on the actual landscape and in all the simulations presented, these release locations are indicated by the ▲ symbols.

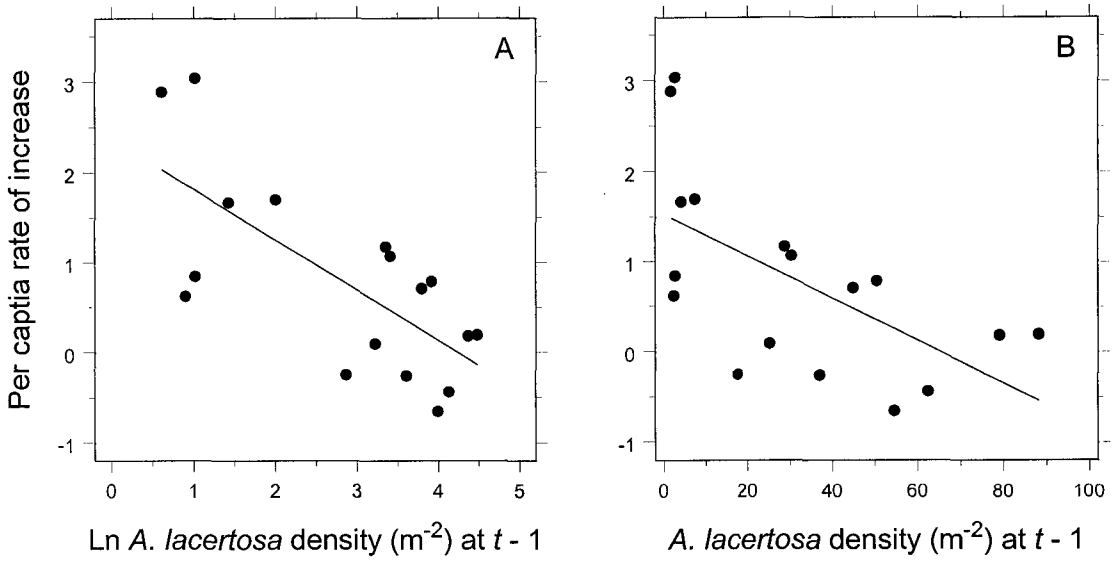


Figure 5.2. Plots of the per capita rate of increase of *A. lacertosa* (log density in 2000 – log density in 1999) as a function of (A) log density of beetles and (B) unlogged density of beetles measured in 1999 at 17 release sites on the Blood Indian Reserve in Southwest Alberta.

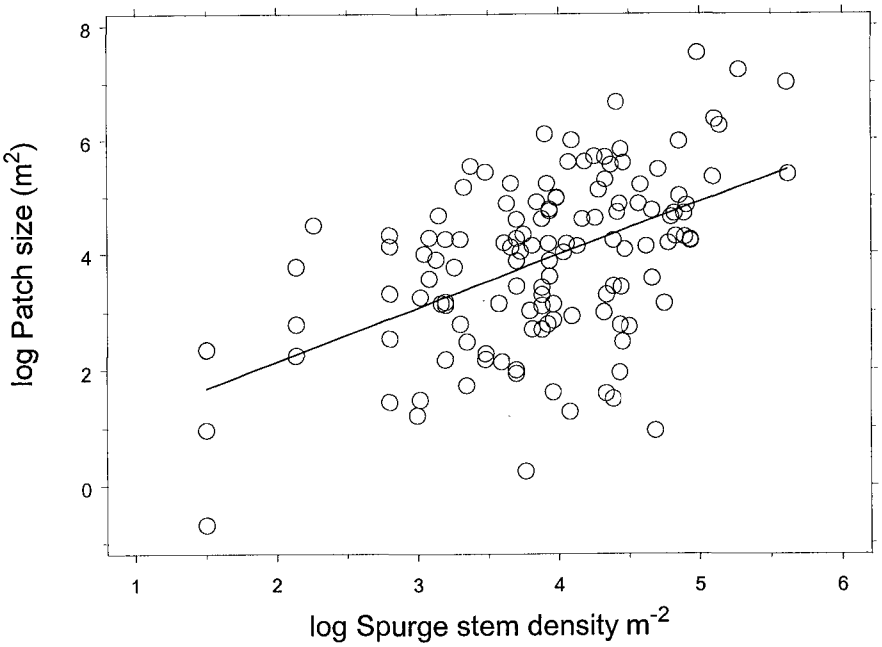


Figure 5.3. Correlation between leafy spurge log patch size and leafy spurge log stem density.

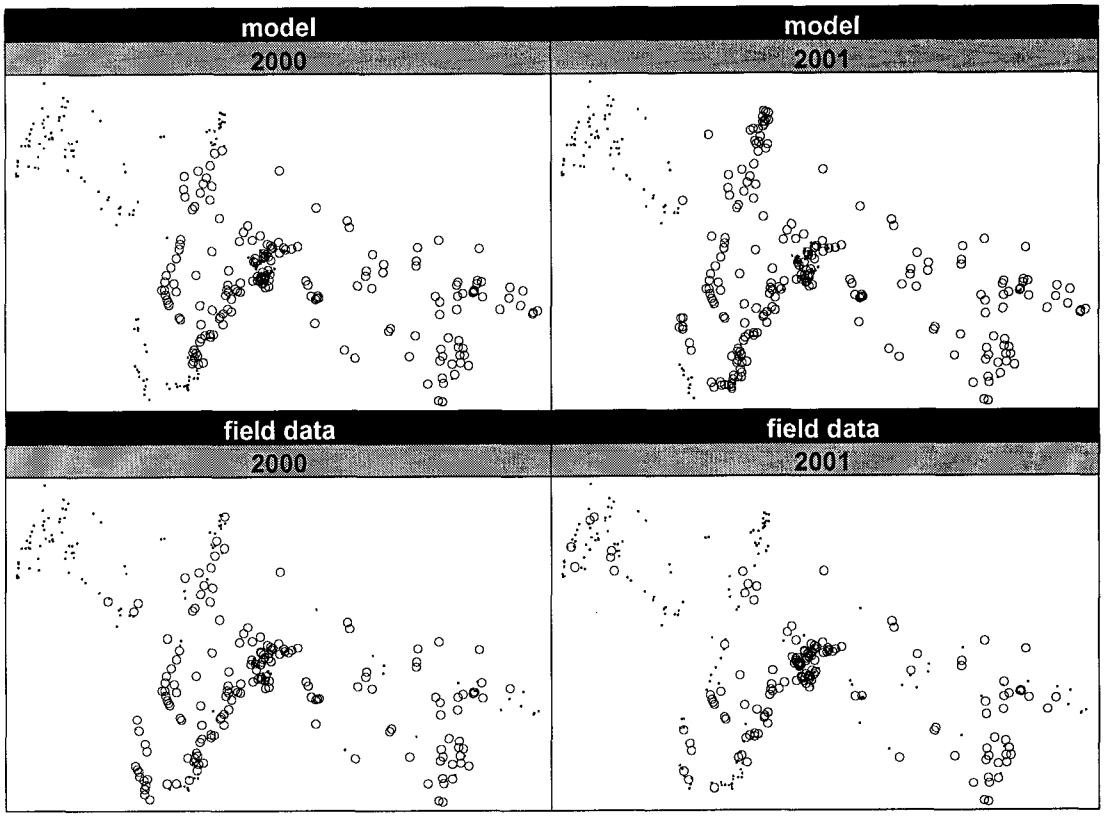


Figure 5.4. Comparison of patch occupancies observed in the field and predicted by the simulation model in 2000 and 2001. Occupied patches are indicated by large, empty circles, unoccupied patches are indicated by small, filled circles.

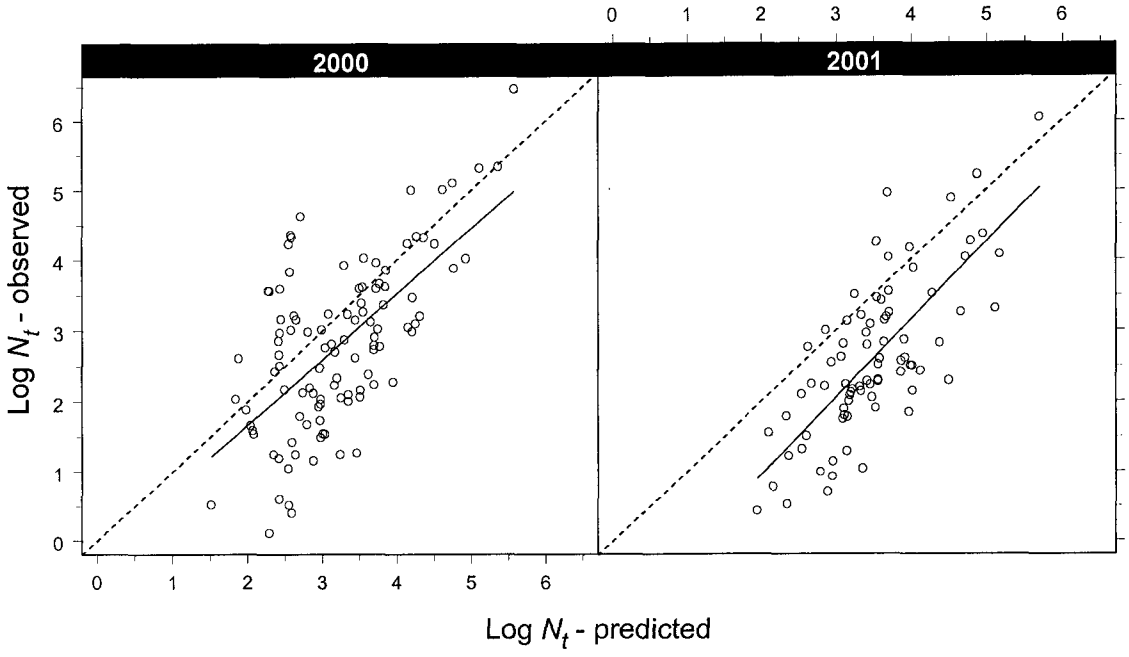


Figure 5.5. Comparison of log local population densities observed in the field and predicted by the simulation model. The dotted line indicates perfect agreement between observed and predicted data. The solid line is a linear regression of predicted values on observed values. The degree to which the regression line deviates from the dotted line is an indication of general discrepancy in simulation model fit to observed data. Regression statistics are presented in Table 5.3.

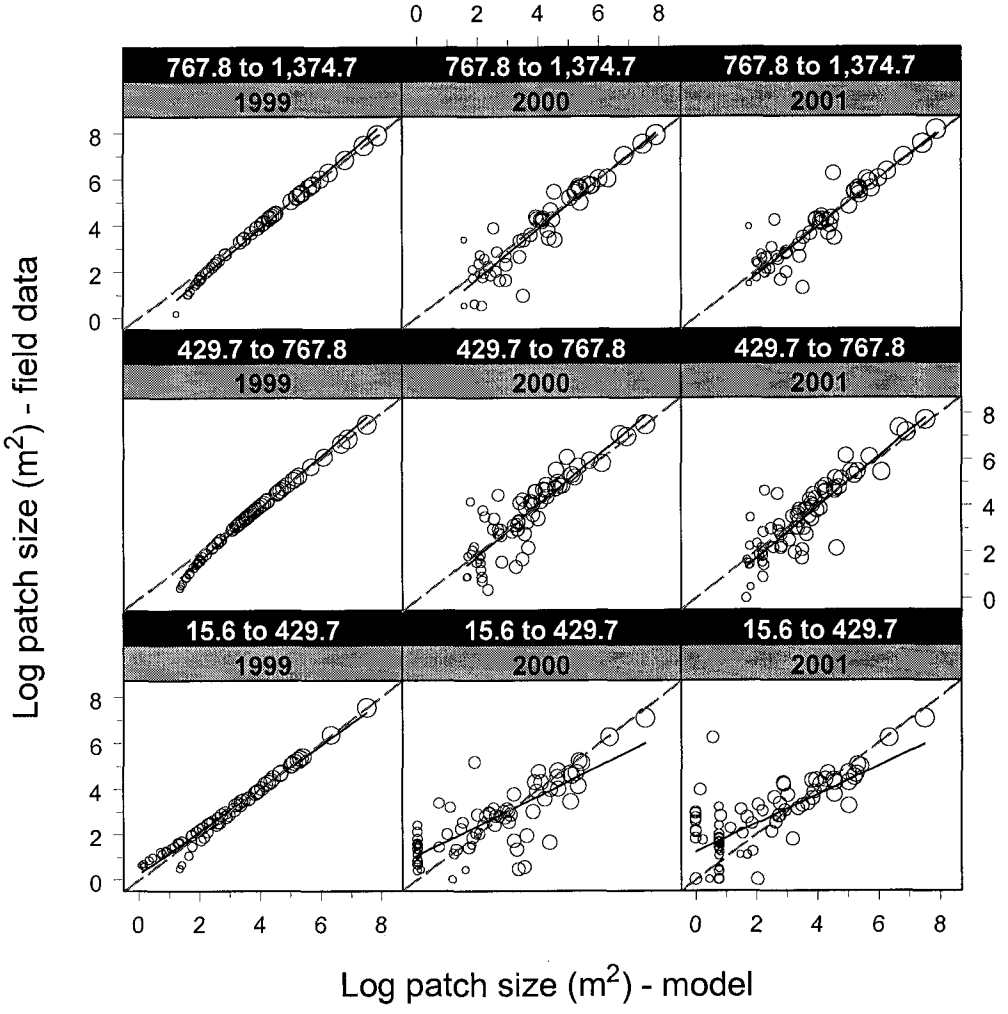


Figure 5.6. Comparison of leafy spurge log patch size observed in the field and predicted by the simulation model for each of the three years in which patch size field data were available and according to 3 classes of distance (m) from 1997 *Aphthona lacertosa* release site. As in the previous figure, the dotted lines in each panel indicate perfect agreement between observed and predicted data. The solid regression lines indicate general discrepancies in simulation model fit to observed data. The symbol size is proportional to the initial patch size (1999).

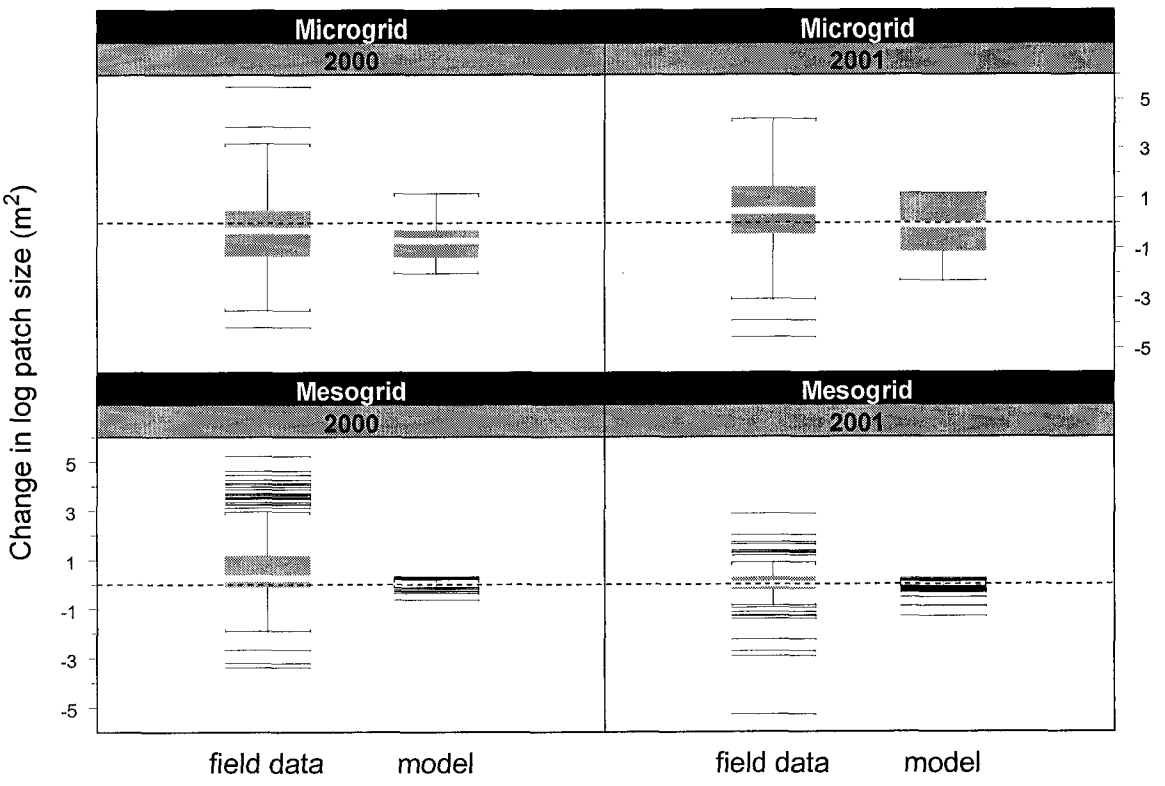
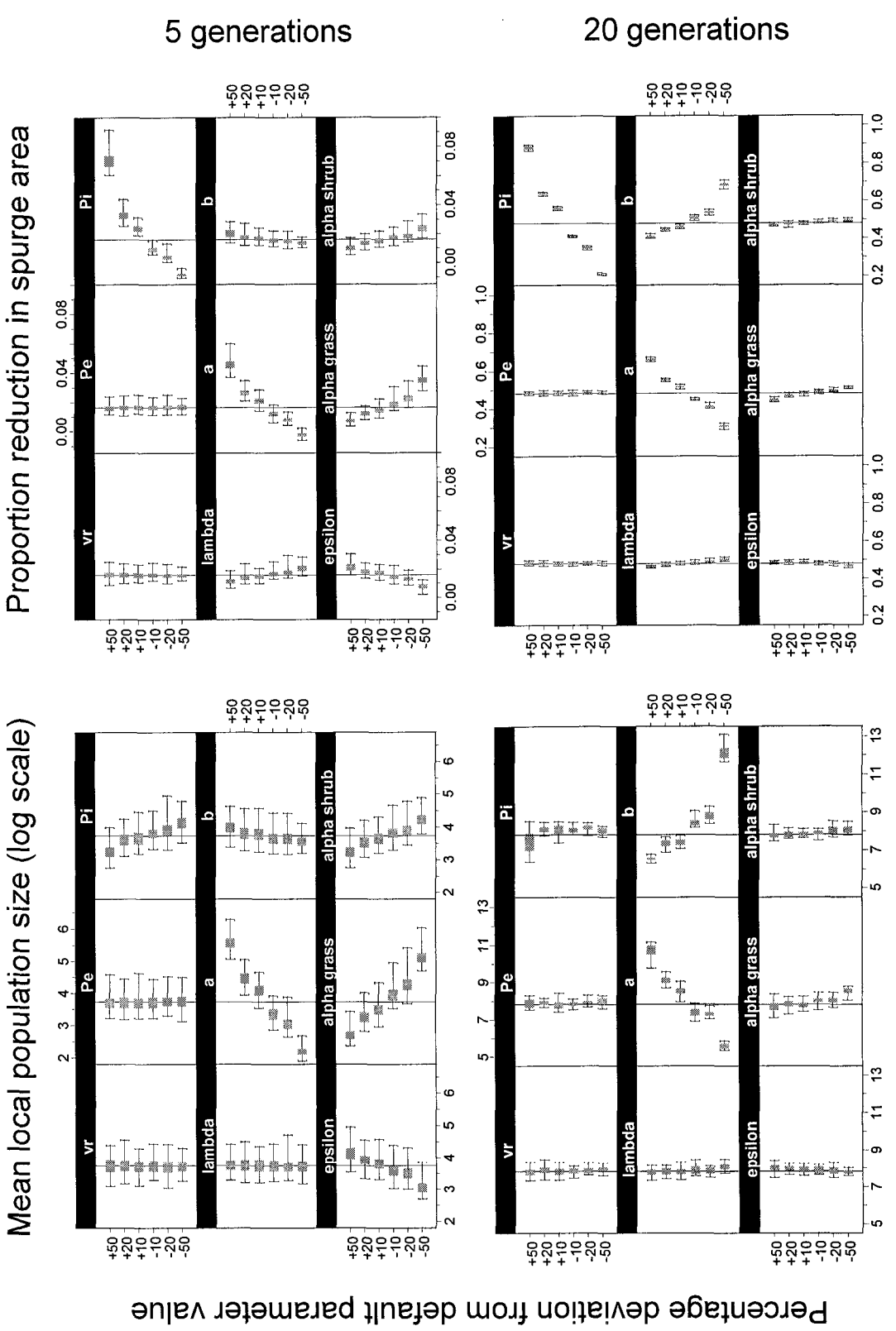


Figure 5.7. Boxplots of the overall log change in leafy spurge patch size between 1999 and 2000 (2000 heading) and between 2000 and 2001 (2001 heading), according to 2 different sample regions: Microgrid (within 200 m from the initial release location) and Mesogrid (250 – 1300 m from the initial release location).

Figure 5.8 (next page). Results of the sensitivity analysis performed on the simulation model. Each parameter was varied ± 10, 20, or 50 % from default values (see Table 5.2) while holding all other parameters at their default value. A total of 200 replicate runs was conducted for each of 6 values for each parameter plus 200 runs with all parameters at their default value, for a total of 11 000 runs. Individual box and whiskers represent the total variation among the 200 replicate runs for each parameter value. The spread among the 6 box and whiskers for a given parameter provides an indication of model sensitivity to that parameter. The mean response for runs with all parameters at their default value is indicated by the vertical lines in each panel. The results are presented for the two response variables for which model sensitivity was assessed – mean local population size (log-scale) and the proportion reduction in total spurge area. The response variables were measured at 5 generations (years) and 20 generations following initial biocontrol agent releases to determine whether model sensitivity changed with increasing time since release.



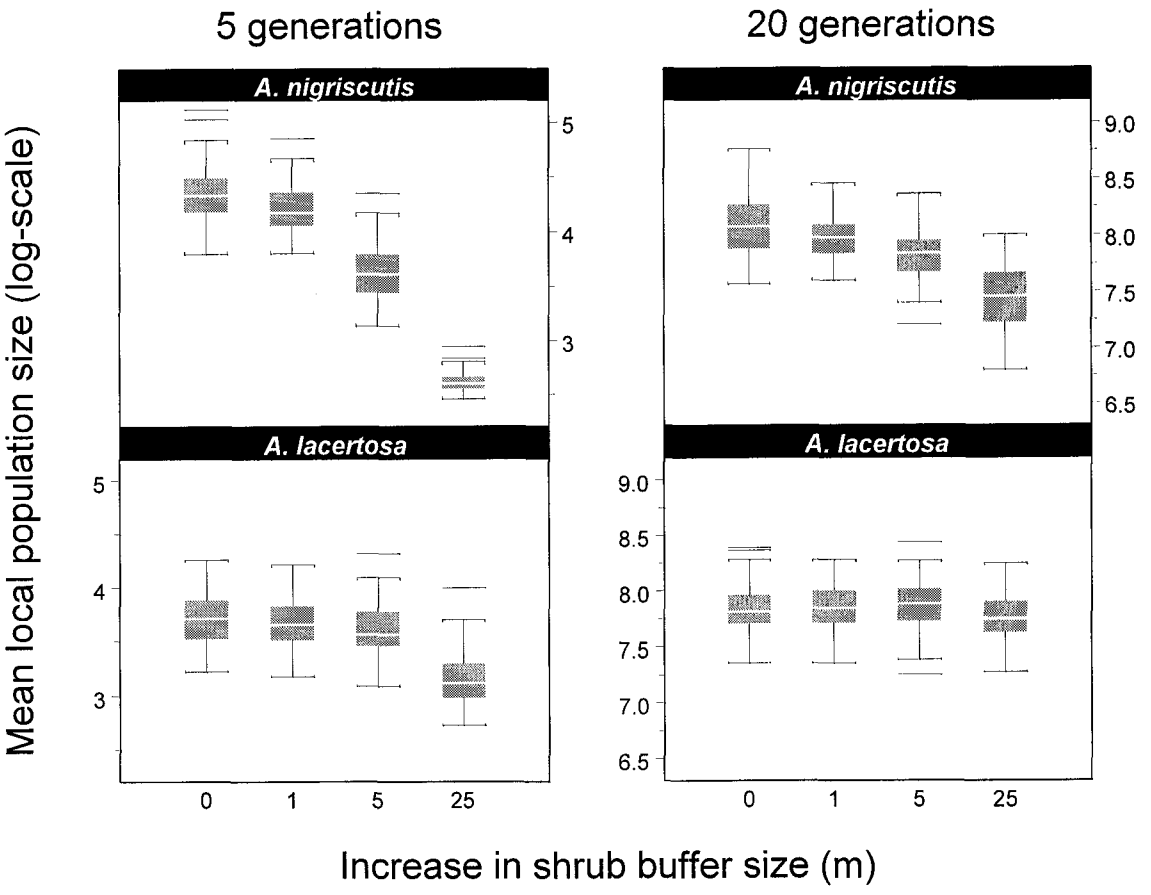


Figure 5.9. Boxplots illustrating the effect of different levels of shrub cover on mean local population sizes, according to time since release and for *A. lacertosa* and *A. nigriscutis* movement rates. All other parameters were set at the default levels for *A. lacertosa* (see Table 5.2).

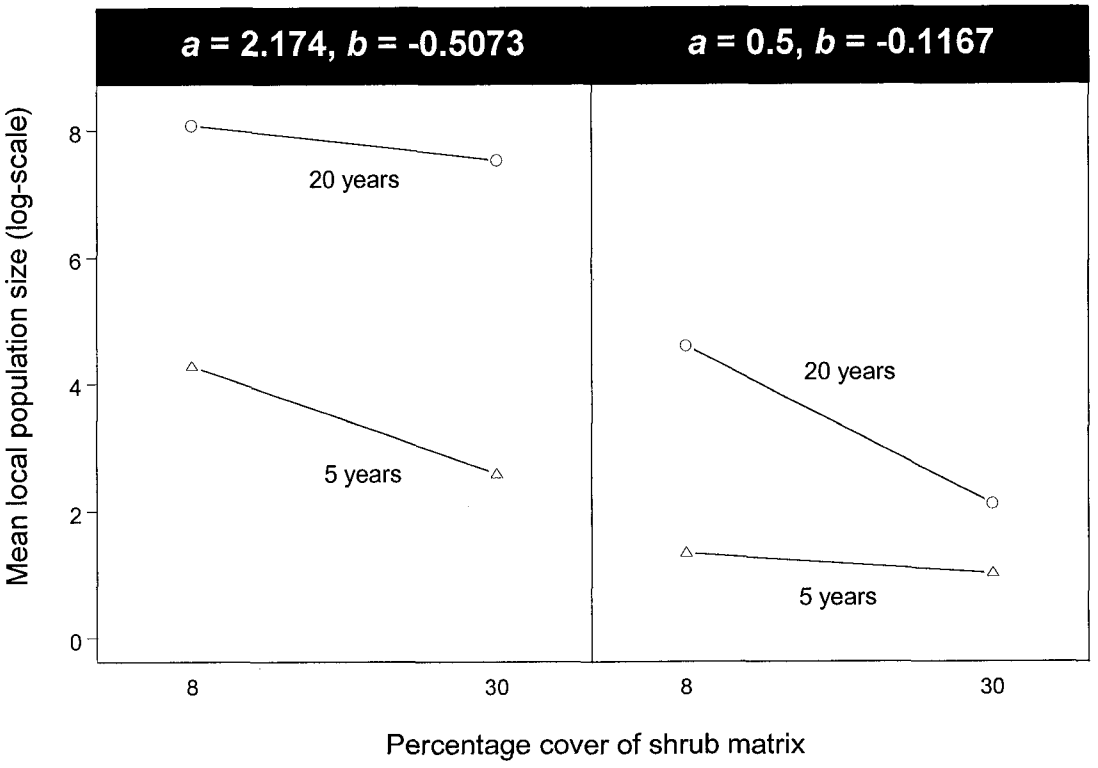


Figure 5.10. Interaction plots of the mean local population size (log-scale) on landscapes with 8 % shrub cover (study landscape) and 30 % shrub cover, according to time since release (5 and 20 years) and intrinsic growth rate (a = 3.174 and a = 0.5). The density-dependence parameter b was set so that local carrying capacities were equal (73.6 beetles m^{-2}) despite the different growth rates.

General Discussion

Current ecological theory acknowledges that local-scale phenomena alone rarely account for the patterns we observe in nature (Holling 1992; Levin 1992). Despite this, most weed biocontrol studies are conducted at local spatial scales, are not spatially explicit, and potential influences of phenomena occurring at broader scales are rarely assessed. Dispersal is one process that links local- and broader-scale phenomena to spatial population dynamics (Kareiva and Wennergren 1995). Theoretical (Kareiva 1990; Hanski 1991; Hanski 1994) and empirical studies acknowledge that movement is a fundamental component of population dynamics (Fahrig and Merriam 1985; Kareiva 1987), yet few studies directly examine the relationship between movement through landscapes and spatial population dynamics (*e.g.,* metapopulations) (but see Moilanen & Hanski 1998 for an example). From an ecological perspective, more studies are needed that link observed movement responses on heterogeneous landscapes directly to population dynamics (Wiens 1997) in order to determine the kinds of situation where movement and landscape structure are important to population processes. From an applied perspective, such studies not only will

provide a novel approach to studying weed biocontrol systems but may also improve our predictions about the circumstances under which a given biocontrol agent is likely or not likely to be effective.

The importance of agent dispersal

In this thesis, I have focused on quantifying dispersal and exploring how it may influence the population dynamics of weed biocontrol agents. The idea implicit throughout my thesis is that without detailed understanding of dispersal, we can not predict how and to what extent biocontrol populations will propagate from initial releases. This idea is critical not only to determine how effective particular agents are likely to be in locating their host-plants but also to determine how much risk is associated with introductions of particular agents. For example, Ewel *et al.* (1999) point out the need for research into the scales of agent dispersal to determine the risks associated with population expansions beyond focal areas. In part, the issue is one of political jurisdiction and how regulations and approvals for release should be governed when biocontrol agents can move beyond both political and ecological boundaries. Although my thesis does not focus on risk assessment *per se*, results of the kind of research I have presented will improve knowledge of key processes that influence biological invasions, whether they are deliberate or not.

In Chapter 1, I showed that *A. nigriscutis* had a much higher immigration probability when moving through a grass-dominated matrix than through a shrub-dominated matrix, whereas immigration probabilities for *A. lacertosa* were similar in both matrix habitats but significantly lower overall than for *A. nigriscutis*. My results suggest that the metapopulation dynamics of *A. nigriscutis* may be strongly affected by the type(s) of matrix habitat present on a landscape, whereas the dynamics of *A. lacertosa* may be much less influenced by matrix habitat. These effects also suggest that release strategies for weed biocontrol agents should be tailored according to the structure of the landscape onto which releases are planned and that no single strategy may be effective for all agents.

The key points to consider for any biocontrol agent is what are the habitat features that are likely to facilitate and to impede dispersal and how can the release strategy for that agent accommodate these differences. For example, releases made in landscapes (or regions) dominated by matrix habitats that are restrictive to dispersal may have to be spaced closer together than those made in areas dominated by less restrictive habitats. Such a strategy may be necessary to ensure that biocontrol agents are able to colonize sufficient amounts of habitat to ensure release persistence

and to aid establishment over entire regions. These ideas are, in part, supported by results presented in Chapter 2, where I showed that *A. lacertosa* incidence was noticeably lower on spurge patches located at least 200 m away from release sites on shrub-dominated landscapes than on grass-dominated landscapes. Results for *A. nigriscutis* could not be obtained because the study design hinged on the fact that *A. lacertosa* were first introduced in the study area only 2 years prior to the survey. In contrast, introductions of *A. nigriscutis* in the study area were conducted up to 20 years prior to the study (see section 2.4.1, p. 45). The result for *A. lacertosa* is noteworthy because it suggests that even small and statistically non-significant differences in *A. lacertosa* immigration at a local scale (i.e., <200 m; Chapter 1) can produce significant differences in patch occupancies at somewhat broader scales (≥ 200 m). Thus the same release strategy for *A. lacertosa* used on both landscape types appears to produce two different results, at least in terms of patch occupancy patterns and over a 2-year period following initial releases.

Additional efforts to tease apart some of the underlying mechanisms responsible for observed differences in immigration and patch occupancy between landscape types suggest that body size and wing morphology may play a role. In Chapter 2, I showed that *A. lacertosa* body and wing sizes differed as a function of distance from original release location and landscape type. Although the survey design elicited an unclear cause-and-effect relationship between morphology and patch occupancy patterns on the different landscapes, it seems that landscape structure, or related factors such as physiological stress imposed by different microclimatic conditions among the landscape types, was the more likely mechanism underlying the observed morphological differences. Therefore, assuming that dispersal through landscapes of different kinds is associated with a selection pressure for individuals with correspondingly different wing sizes, the issue then becomes a question of whether selection for these particular phenotypes is adaptive with respect to the goals of weed biocontrol.

In the case where selection favours large-winged individuals, the obvious trade-off, at least for females, is between larger wings for enhanced dispersal at the cost of reduced fecundity (Denno 1994 and references therein). Typically in these situations, more energy is diverted to the development of flight-related tissues (wings and muscle) than to egg production and this can influence intrinsic growth rates. Thus a trade-off between enhanced dispersal ability and intrinsic growth rates may be beneficial in early years following agent releases by ensuring that many new local populations are founded and that the release propagates over a broad area. If the large-winged phenotype is maintained in similar proportions in later years, however, populations may

not increase rapidly enough to provide the desired level of impact on weed populations. In naturally established and regulated populations, these kinds of relationships tend toward evolutionarily stable equilibria but for species introductions this is not always the case and maladapted phenotypes can often arise, be maintained, and spread throughout the introduced population (Simberloff and Stiling 1996; Tufto 2001; Hufbauer 2002). Scenarios where evolutionary processes alter life history parameters (*e.g.*, host-specificity, dispersal, and reproductive rates) of biocontrol agents need to be carefully considered and, where possible, studied *in situ* to ensure that future introductions are as effective and safe as possible. These ideas have been pointed out previously (Simberloff and Stiling 1996; McEvoy 1996) but, to date, little research has been conducted even to assess the extent to which evolutionary change may occur in weed biocontrol agents.

A spatial approach to weed biocontrol research

As mentioned earlier, dispersal is a process that links together various local- and broader-scale phenomena that influence population dynamics. Traditional weed biocontrol studies have focused on local-scale processes such as intra- and inter-specific competition (McEvoy *et al.* 1993; Notzold *et al.* 1998; Sheppard *et al.* 2001) and insect – host plant interactions (Crawley 1989 and references therein). Studies such as these are necessary and indeed have been vital to our basic understanding of both plant and insect population regulatory processes. However, the integration of metapopulation theory and a landscape (or spatial) perspective into the mainstream of ecology has led researchers to ask questions about how spatial heterogeneity of the environment influences population and community dynamics. These issues are being addressed in such diverse, applied fields as fisheries biology (Myers *et al.* 1997; Frank and Brickman 2000; Worm and Myers *in press*), conservation biology (St. Clair *et al.* 1998; Hanski and Thomas 1994; Roland *et al.* 2000), and insect biocontrol (Walde and Nachmann 1999; Kean and Barlow 2001). Although issues of spatial scale and dispersal of biocontrol agents have been acknowledged as potentially important factors in weed biocontrol success (McEvoy *et al.* 1993; McEvoy and Coombs 1999), surprisingly little research has focused explicitly on these issues.

In Chapter 3 I provided an example of how a spatial perspective can be used to study weed biocontrol processes in the context of a monitoring program. The study focused on quantifying: (1) the pattern of host-patch colonization from an initial biocontrol agent release location; (2) the role of habitat preferences on patterns of agent abundance; (3) linking distribution and abundance of agents to patterns of impact on the target weed. To accomplish these objectives I sacrificed

replication of observations at very fine scales (*i.e.*, < 1 m) in order to extend observations over a relatively broad area (ca. 3 km^2), encompassing much of the habitat surrounding a release site. The focus of the study was not on what was occurring solely within the locality of the initial release (*i.e.*, the release patch) but on what was occurring over the broader landscape that contained a release patch and many initially unoccupied habitat patches for the released agent.

Key results of this broader-scale observational study were that *A. lacertosa* was: (1) capable of colonizing isolated spurge patches up to approximately 600 m from the initial release location; and (2) associated with temporary reductions in spurge density up to approximately 500 m from the initial release location; and (3) *A. lacertosa* densities are related to both fine (within-patch) and broader-scale habitat features. Very few weed biocontrol studies have explicitly quantified the spatial extent over which agent colonization and impact occurs within a given period of time since an initial release (3 years in this case) (see Huffaker and Kennett 1959 for another example). This is surprising given that these data are relatively simple, albeit time-consuming, to collect. The advantage of investing the extra effort and time into collecting such spatially explicit data is that they: (1) provide important information regarding the scale(s) at which more detailed (but spatially less intensive) monitoring of releases should be made; (2) suggest appropriate scales at which future releases need to be made; (3) provide insight into how biocontrol agent populations spread from initial releases.

Integrating dispersal with other key processes

In the first three chapters of this thesis, I used empirical studies to quantify biocontrol agent dispersal, habitat preference, and impact on a target weed. In the last two chapters, I used simulation models to integrate information obtained from my empirical work in order to: (1) make general predictions regarding weed biocontrol success under different scenarios (Chapter 4) and (2) determine whether habitat – dispersal interactions can influence *Aphthona* flea beetle spatial population dynamics and impact on leafy spurge (Chapter 5).

In Chapter 4, I explored how dispersal may interact with other processes that are thought to be important in biocontrol release establishment; the Allee effect and environmental stochasticity (Grevstad 1998). As it turns out, understanding emigration rates and movement ability of biocontrol agents may improve predictions regarding the persistence of biocontrol releases. At the very least, qualitative knowledge of the propensity and ability to disperse should allow more informed decisions to be made regarding the optimal size of releases of a given biocontrol agent.

Such theoretical, 'data-free' explorations are useful for illustrating the kind of information that need to be collected for potential biocontrol agents, before release programmes are initiated but they can not provide detailed understanding of how specific biocontrol systems operate.

In Chapter 5, I integrated information regarding *A. lacertosa* dispersal, population growth, and impact rates to explore how matrix habitat could influence colonization of, and impact on a mosaic of leafy spurge patches. Overall, the model did a reasonable job of predicting local population densities of *A. lacertosa* and the average reduction in spurge patch size but it did a relatively poor job of predicting the specific patches that were eliminated or strongly reduced in size. This latter result may have occurred because of the implicit assumption that agent populations, all else being equal, will reach similar densities on all spurge patches. In other words, fine-scale habitat effects were excluded and these may partially explain the lack of concurrence between observed and predicted impact.

The inclusion of matrix habitat structure and its effect on dispersal in the model did little to improve model predictions. In part, this may be due to the relatively homogeneous structure of the landscape. Indeed, further simulation on landscapes with greater amounts of shrub habitat, but otherwise identical, produced noticeable reductions in the average size of agent local populations. It would, therefore, be instructive to attempt a future test of the model on other release landscapes that have different matrix habitat compositions and for which appropriate field data exist.

The empirical and simulation studies presented here represent a miniscule portion of the questions that could and need to be asked regarding weed biocontrol processes. Clearly, other approaches are needed that ask different questions and require different data. For example, my research has focused on agent dispersal and spatial population patterns and, for the most part, has ignored the population dynamics of the weed. Detailed understanding of the population dynamics of target weeds may expose life history stages that are particularly vulnerable to attack (*e.g.,* Rees and Paynter 1997). These kinds of studies are vital for making correct decisions about the kind of biocontrol agents needed for effective control of invasive weeds (McEvoy and Coombs 1999).

In fact, there are exciting possibilities for extending the spatially explicit approach I have taken in my research. McEvoy and Coombs (1999) suggest that structured population models for weed biocontrol could be used to improve the efficiency and safety of weed biocontrol programmes. These models can be used to identify vulnerable life history stages of target weeds and guide

efforts for the selection of the most appropriate biocontrol agents, rather than resorting to trial-and-error. These kinds of models have been employed to model weed population dynamics and to predict impact (Lonsdale *et al.* 1995; Rees and Paynter 1997; Shea and Kelly 1998) but effects of various biocontrol agents are typically incorporated as a generic, extra source of mortality. A logical extension would be to combine these approaches to model the stage-structured population dynamics of agents and target weeds jointly and in a spatially explicit fashion. This idea is not new to biocontrol research, it underlies much of the insect biocontrol modeling literature (Murdoch and Briggs 1996; McCauley *et al.* 2000; Kean and Barlow 2001). Under this framework a variety of hypotheses could be tested regarding the influence of spatial heterogeneity on both weed and agent populations and how different age/stage structure distributions influence the interactions between the two. Most importantly, joint spatial modelling of weed and agent stage-structured dynamics would provide insight into the mechanisms that are responsible for bringing agents and weeds together at periods during their life cycles when the weeds are most vulnerable and the agents are most potent.

A further elaboration of the joint spatial, stage-structured approach would be to incorporate abiotic effects (*e.g.,* disturbance, nutrient dynamics) and community interactions (*e.g.,* competition from native plants). The bottom-up effects of resource limitation and horizontal effects of plant competition appear to be important features that, when combined with herbivory, promote rapid and sustained extinction of weed local populations (McEvoy *et al.* 1993). To date, these interactions have been studied at fine scales, using detailed field experiments (McEvoy *et al.* 1993; Sheppard *et al.* 2001) but further study at regional scales, where other abiotic factors such as climatic and soil gradients and biotic factors such as agent dispersal also come into play, will likely require a modeling approach. A key benefit to a 'scaled-up' approach is that regional differences in biocontrol system function can be accounted for, thus allowing for more generally applicable predictions.

Conclusion

Recent calls and agenda for increased rigour in the design, implementation, and monitoring of weed biocontrol programmes (Kareiva 1996; Simberloff and Stiling 1996; McEvoy and Coombs 1999; Blossey and Skinner 2000) should have the effect of stimulating theoretical and applied research on the dynamics of weed biocontrol systems. I add to the call for increased rigour by stressing the importance of: (1) a spatially explicit approach to monitoring weed biocontrol

releases and (2) considering biocontrol agent dispersal abilities, how these interact with release landscapes, and how these interactions may influence the dynamics of released populations.

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