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Meadow suitability and quality for the alpine butterfly, *Parnassius smintheus*, in the east slopes of the Canadian Rockies.

by

Sherri L. Fownes ©

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

in

Environmental Biology and Ecology

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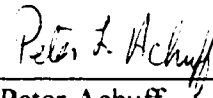
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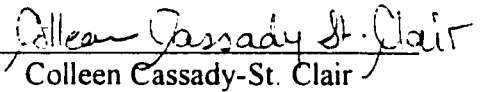
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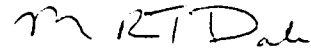
The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Me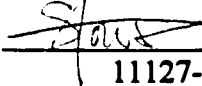adow suitability and quality for the alpine butterfly, *Parnassius smintheus*, in the east slopes of the Canadian Rockies** submitted by Sherri L. Fownes in partial fulfilment of the requirements for the degree of Master of Science in Environmental Biology and Ecology.
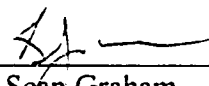
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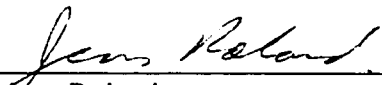
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"...During our first observation of these 'blood-creatures,' as we have termed them— after the colourful red liquid which is to be found in their bodies, and which appears to be of great significance to them in their poems, wars, and religious rituals—we supposed them incapable of speech, as those we were able to examine entirely lacked the organs for it. They had no wing-casings with which to stribulate—indeed they had no wings; they had no mandibles to click; and the chemical method was unknown to them, since they were devoid of antennae. 'Smell,' for them, is a perfunctory affair, confined to a flattened and numbed appendage on the front of the head. But after a time, we discovered that the incoherent squeakings and gruntings that emerged from them, especially when pinched, were in fact a form of language, and after that we made rapid progress..."

excerpt from the short-story "Cold-blooded," by Margaret Atwood
published by Coach House Press, Toronto, 1992.

for my family
thank you for teaching me to learn

Abstract

Behaviour of the alpine butterfly *Parnassius smintheus* and characteristics of its meadow habitat were studied. Female *P. smintheus*, despite frequent ovipositions off of the host plant (*Sedum lanceolatum*), more often oviposited in its presence and recognised suitable habitat patches as such. Monophagous larvae of *P. smintheus* were highly mobile in their first-instar (moving at least 1.2 metres/hour) and fifth-instars were capable of orientation to *S. lanceolatum*. On Jumpingpound Ridge the abundance of host plants in meadows was related to the abundance of larvae and adults, however, host plant spatial pattern was not. Slope, its correlate (soil texture), and the abundance of *S. lanceolatum* account for 56% of the variation in *P. smintheus* abundance among meadows. Larger-scale patterns of *P. smintheus* distribution beyond Jumpingpound Ridge, were explained, in part, by slope, soil texture and plant community. Findings from this study will improve population models of *P. smintheus* which are concurrently being developed.

Acknowledgements

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Chapter 1

General Introduction

"Butterflies, dragonflies, and others enhance the earth's beauty incontestably, and their symbolism has figured prominently in the art and literature of all cultures," (Pyle *et al.* 1981).

Butterfly Populations

Studies of butterfly populations have proliferated in the scientific literature over the past

two decades. One reason for the growth of interest in butterfly population ecology is their

use in testing metapopulation theory, and its application to issues of conservation biology.

A metapopulation is a group of local populations whose long-term persistence depends on

connectivity by occasional dispersal between groups (Hanski and Gilpin 1991, Harrison

1991). Butterflies have proven to be particularly amenable to applications of

metapopulation theory and population modelling because of the fragmented nature of their

habitat, their habitat specificity, and their relatively short life-span – adults seldom survive

for more than a few weeks. This facilitates development of large amd relevant data sets

over a relatively short period of time.

Most butterflies have phytophagous larvae which feed on one or a few closely related

species of plant (Ehrlich and Raven 1964, Chew 1975, Singer 1984). Although

somewhat less specialized than their larvae, adult butterflies also have strict habitat

requirements. Adults need suitable microclimates for thermoregulation (Weiss *et al.*

1988) and are often restricted to areas that receive abundant sunlight, such as grasslands

or meadows (Scott 1986). They require nectar resources provided by wild flowers, and

they must have access to mates to fertilize eggs (Wiklund 1977). Female butterflies also

require oviposition sites that are suitable for larval feeding. Females of many

Lepidopteran species facilitate larval search for host plants by preferentially alighting and

selectively ovipositing on suitable host plants (Haribal and Renwick 1998) and it is

generally believed that Lepidopteran larvae have little ability to locate larval host plants in

the early stages (Singer 1984, Mayhew 1997).

Status of Butterflies in Canada

Conservation of individual species requires maintenance of viable populations across their

natural geographic range. Viable populations must be sufficiently large to ensure their

persistence over a relatively long period of time. For many invertebrate species

quantifying viable population sizes is a daunting task because scientific studies of non-pest

invertebrate species are rare. Individual collection records have contributed to the

construction of accurate range maps for most butterfly species. From these maps it is

possible to identify both species and areas of conservation concern (Layberry *et al.* 1998).

Describing a viable population, however, is still impossible for most butterfly species. The

official status of most butterflies can not be determined (is indeterminate) due to the lack

of sufficient scientific information. It is evident that more ecological studies of butterflies

in Canada are required to identify species status and improve the chances of protection of

rare species in Canada. This thesis identifies the key habitat requirements of a native

Lepidopteran species, the alpine butterfly, *Parnassius smintheus* and endeavours to define

habitat suitability for this species.

Study Organism: *Parnassius smintheus*

Parnassius smintheus (Lepidoptera, Papilionidae, Parnassiinae, Doubleday (1847)) has a broad distribution in Western North America. Its distribution is constrained by that of its preferred larval host plant, lance-leaved stonecrop, *Sedum lanceolatum* (Crassulaceae). Larvae of *P. smintheus* are monophagous but have been reported to feed on other species of *Sedum* in areas where *S. lanceolatum* is not found (Fisher 1981, Scott 1986, Sperling and Kondla 1991).

Larvae of *P. smintheus* gather nutrients and the cyanoglycoside, sarmentosin, from their food plants (Nishida 1995). This bitter compound has been found in the tissues of all life-stages of *P. apollo* and *P. phoebus* and is believed to play a role in predator defense (Nishida 1995). It is postulated that larvae are aposematically coloured as bright yellow dots are distributed in parallel rows down the length of their black bodies. Due to their solitary feeding habitat and the complexity of the herbaceous layer in alpine environments, larvae are difficult to find and study. For this reason there are few natural history accounts of the immature stages of *P. smintheus* (*e.g.*, Edwards 1885).

Adult *P. smintheus* are large, conspicuous fliers and are sexually dimorphic. Females are generally larger than males and their wing cuticle is transparent; females on the ground are difficult to find because of their wing colour. Although they nectar feed, females fly less frequently than do males, crawling instead on the vegetation and soil surface, presumably

in search of oviposition sites. Males have white scales and patrol meadows for nectar flowers and virgin females. Upon encountering an unmated female, a male will grab her and attempt to mate with her. Mating can take up to six hours while males deposit a sphragis, or waxy pouch, on the female abdomen. Sphragis-bearing females are assumed to have successfully mated only once and are unable to mate again because of interference caused by the sphragis (Layberry *et al.* 1998). Virgin females are seldom seen in the field.

Female *P. smintheus* do not selectively oviposit on the larval host plant. Females have been observed depositing eggs instead on adjacent non-host plant vegetation, soil, rocks and sticks (Scott 1986). Whatever the reasons for this oviposition strategy, it has serious consequences for hatching early-instar larvae. To ensure survival immature *P. smintheus* must move from egg-laying sites to find a suitable host plant.

P. smintheus is non-migratory and overwinters in the egg stage (Layberry *et al.* 1998). Larvae emerge in the spring (Fig. 1-1) soon after snow-melt and begin feeding on *Sedum lanceolatum* rosettes (personal observation). Larvae pupate in the leaf litter, gravel or rocks lying near the soil surface and do not spin a cocoon. Rather they gather some silk around them to attach themselves to the surrounding substrate (Layberry *et al.* 1998). Pupae are light brown and camouflaged in the litter layer. Adults emerge in early July to late August in subalpine and alpine areas. Adults can live for more than three weeks (Roland *et al. in press*) and have been seen flying well into September (Bird *et al.* 1995).
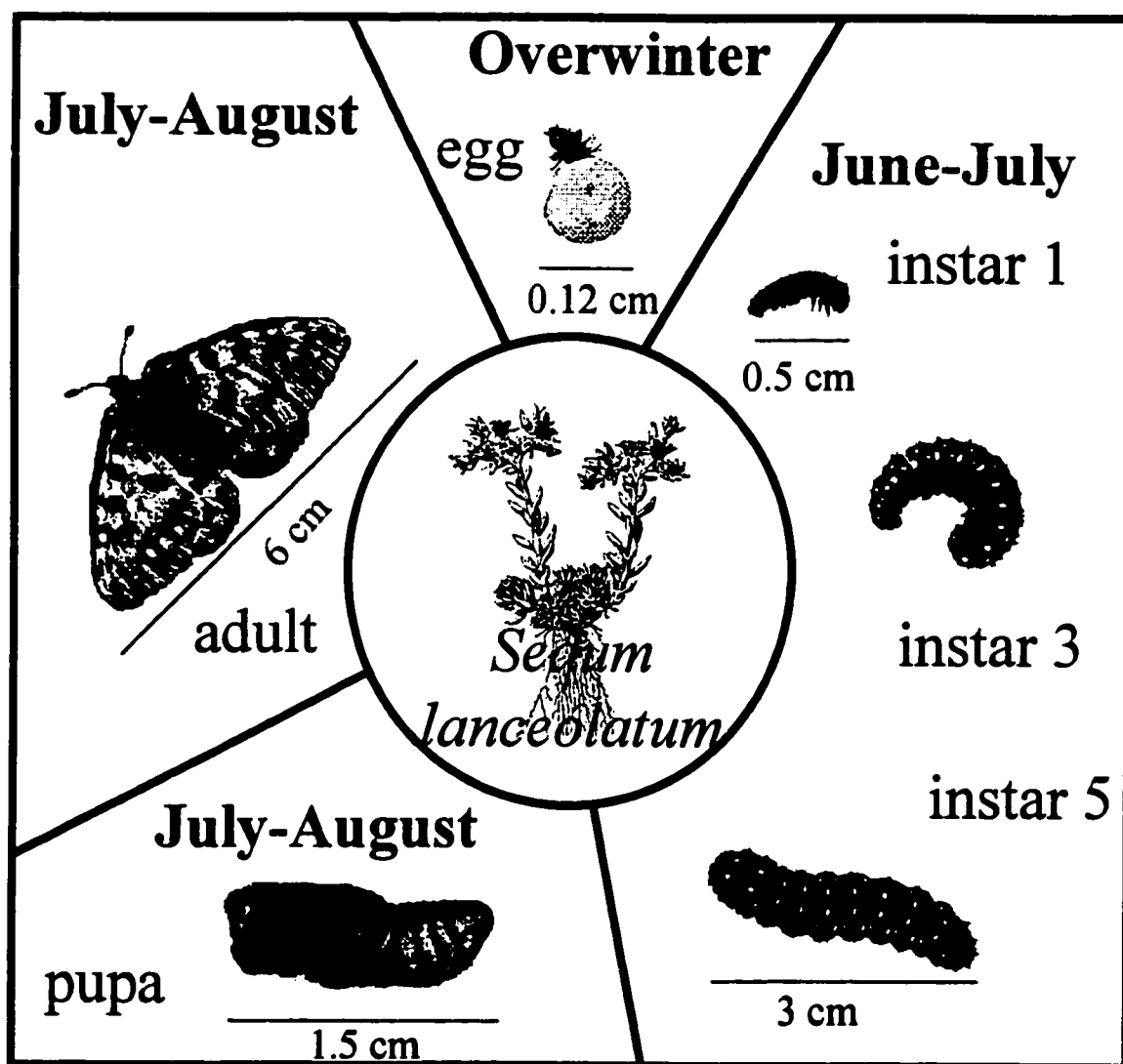
Fig. 1-1. Schematic life-cycle and phenology of *Parnassius smintheus* on Jumpingpound Ridge. The drawing of the larval host plant, *Sedum lanceolatum*, is taken from Clausen (1975).

P. smintheus is regionally abundant in North America. Populations of *P. smintheus* should

however, be monitored because of the poor population status of European congeners.

Due to severe fragmentation and loss of habitat, *P. apollo* and *P. mnemosyne* are

endangered or threatened over most of their range (Geyer and Dolck 1995, Sánchez-

Rodríguez and Baz 1996, Meglécz *et al.* 1997, Deschamps-Cottin *et al.* 1997). *P.*

smintheus may be a good candidate for monitoring subalpine and alpine meadow habitat in

the province of Alberta, because of its habitat specificity, its regional abundance and the

sensitivity of its congeners to changes in habitat composition and structure.

Populations of *Parnassius smintheus*

Roland *et al.* (*in press*) and Keyghobadi *et al.* (*in press*) studied populations of *P.*

smintheus in a series of sub-alpine meadows on Jumpingpound Ridge, Kananaskis

Country, Alberta, using mark-recapture and genetic techniques, respectively. Although

their findings suggest that *P. smintheus* populations along Jumpingpound Ridge are

connected by some movement of individuals between meadows, it is clear that intervening

forests impede movement of *P. smintheus* to a large degree. Based on their findings it is

anticipated that increasing distances between meadows, caused by rising treeline, will

further isolate populations of *P. smintheus*. It is recognized that the ability of organisms

to disperse between patches of suitable habitat is critical to the survival of populations that

are spatially structured (Harrison 1989, Baguette and Nève 1994, Kuussaari *et al.* 1996,

Nève *et al.* 1996, Förare and Solbreck 1997, Mousson *et al.* 1999).

Meadows on Jumpingpound Ridge support different population sizes and densities of *P.*

smintheus (Roland *et al. in press*), suggesting that meadows vary in quality. Variation in

habitat quality can influence the dynamics of spatially structured populations (Moilanen

and Hanski 1998) and degradation of habitat quality has been identified as the leading

cause of butterfly extinctions (Hanski and Thomas 1994). Therefore, understanding what

constitutes quality of meadows for *P. smintheus* is important for understanding their

population dynamics and for predicting how changes to habitat will affect their long-term

persistence.

Overview of Thesis

The objectives of this thesis are to describe habitat suitability and habitat quality of

subalpine and alpine meadows for *P. smintheus*, in particular by the inclusion of an

examination of the behavioural ecology of both adult females and larvae, and a more

complete understanding of the resource requirements of this species. A general overview

is provided in Figure 1-2.

Adult female butterflies are expected to recognize and search for suitable egg-laying sites

to ensure survival of their relatively immobile offspring. In many species adult females do

consider the suitability and quality of oviposition sites, which may translate into their

greater abundance in suitable high-quality areas, and their dispersal from low-quality areas
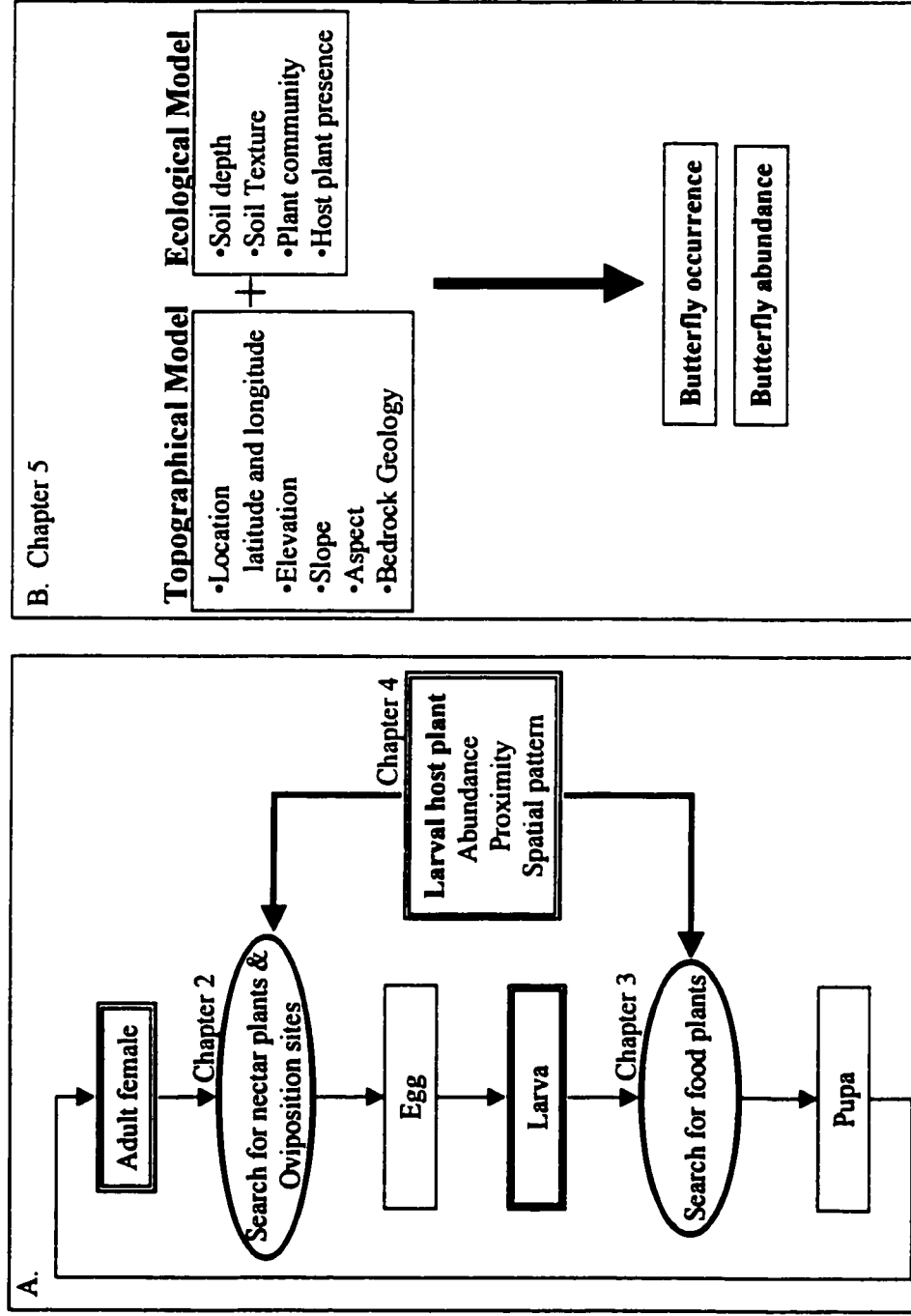
Fig. 1-2. Outline of thesis. A. Investigating how adult females and larvae of the alpine butterfly, *Parnassius smintheus* respond to the larval host plant, *Sedum lanceolatum*. B. Using both topographical and ecological characteristics of meadows to describe the patterns of occurrence and abundance of *P. smintheus* butterflies.

or non-habitat. In some species, however, adult females do not selectively oviposit on suitable larval host plants. Female *P. smintheus* fall into the category of "haphazard" egg layers; they rarely oviposit on the plants on which their offspring feed. The objective of the second chapter is to determine if female *P. smintheus* movement and egg-laying behaviours change in response to differences in habitat suitability and habitat quality.

Chapter 3 deals with the natural history, resource requirements and behaviour of larval *P. smintheus*. It is known that Lepidopteran larvae in general disperse much smaller distances than do the adults. Therefore, selection of suitable habitat is the responsibility of the adult. In species where females do not selectively oviposit on suitable host plants, larval mobility and search ability are therefore critical. Mobility and search ability were observed in the field and quantified in the laboratory.

The role of host plant (*Sedum lanceolatum*) abundance and spatial patterning in determining habitat quality of meadows for *P. smintheus* is explored in Chapter 4. The abundance of required resources is often considered a measure of habitat quality, but the effect of spatial patterning of the required resources in determining habitat quality is rarely quantified. Adult female oviposition behaviour and larval feeding behaviour are shown to be related directly to the density and spatial pattern of *S. lanceolatum*.

Finally, Chapter 5 develops topographical and detailed site variable models that describe patterns of occurrence and abundance of *P. smintheus*. Models of habitat suitability and quality can be used as tools for population ecologists and landscape managers to make land use and planning decisions. Although large vertebrates have traditionally been used for these decisions it is now recognized that non-vertebrates are critical components of the ecological integrity of natural areas and that they can provide additional information on habitat at a fine spatial scale. The development of models such as these is necessary to assess the population status of invertebrates and improve present management practices.

LITERATURE CITED

Baguette, M. and G. Nève. 1994. Adult movements between populations in the specialist butterfly *Proclossiana eunomia* (Lepidoptera, Nymphalidae). Ecological Entomology 19:1-5.

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

Chew, F.S. 1975. Coevolution of pierid butterflies and their cruciferous foodplants. Oecologia 20:117-127.

Clausen, R.T. 1975. *Sedum* of North America North of the Mexican Plateau. Cornell University Press, Ithaca, New York, USA.

Deschamps-Cottin, M., M. Roux and H. Descimon. 1997. Larval foodplant efficiency and laying preferences in *Parnassius apollo* L. (Lepidoptera, Papilionidae). Life Sciences 320:399-406.

Edwards, W.H. 1885. Description of some of the preparatory stages of *Parnassius smintheus*, Doubl., and of *P. clodius*. The Canadian Entomologist 17:61-65.

Ehrlich, P.R. and P.H. Raven. 1964. Butterflies and plants: a study in coevolution. Evolution 18:586-608.

Fisher, M.S. 1981. Superfamily Papilionidae Latreille, 1809 (Parnassians, Swallowtails). *in* Butterflies of the Rocky Mountain States, C.D. Ferris and F.M. Brown *editors*. University of Oklahoma Press, Norman, Oklahoma, USA. pages 175-193.

Förare, J. and C. Solbreck. 1997. Population structure of a monophagous moth in a patchy landscape. Ecological Entomology 22: 256-263.

Geyer, A. and M. Dolck. 1995. Okologie und schutz des apollofalters (*Parnassius apollo* L.) in der Frankenalb. Vortrage der Entomologentagung in Gottingen 27:1-6.

Hanski, I. and M. Gilpin. 1991. Metapopulation dynamics: brief history and conceptual domain. Biological Journal of the Linnean Society. 42:3-16.

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

Haribal, M. and J.A.A. Renwick. 1998. Differential postalightment oviposition behaviour of monarch butterflies on *Ascelpias* species. Journal of Insect Behavior 11:507-538.

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

Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. Biological Journal of the Linnean Society. 42:73-88.

Keyghobadi, N., J. Roland, and C. Strobeck. *In press*. Influence of landscape on population genetic structure of the alpine butterfly *Parnassius smintheus* (Papilionidae). Molecular Ecology 83.

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

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

Mayhew, P.J. 1997. Adaptive patterns of host-plant selection by phytophagous insects. Oikos 79:417-428.

Meglécz, E, K. Pecsenye, L. Peregovits and Z. Varga. 1997. Effects of population size and habitat fragmentation on the genetic variability of *Parnassius mnemosyne* in NE Hungary. Acta Zoologica Academiae Scientiarum Hungaricae 43:183-190.

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

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

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

Nishida, R. 1995. Sequestration of plant secondary compounds by butterflies and moths. Chemoecology 4:127-138.

Pyle, R., M. Bentzien and P. Opler. 1981. Insect conservation. Annual Review of Entomology 26:233-258.

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

Sánchez-Rodríguez, J.F. and A. Baz. 1996. Decline of *Parnassius apollo* in the Sierra de Guadarrama, Central Spain (Lepidoptera: Papilionidae). Holarctic Lepidoptera 3:31-36.

Scott, J.A. 1986. The butterflies of North America: a natural history and field guide. Stanford University Press, Stanton, California, USA.

Singer, M.C. 1984. Butterfly-hostplant relationships: host quality, adult choice, and larval success. Pages 82-88 *in* R. Vane-Wright and P.R. Ackery, editors. The Biology of Butterflies. Academic Press, New York, USA.

Sperling, F.A.J. and N.G. Kondla. 1991. Alberta swallowtails and parnassians: natural history, keys, and distribution. Blue Jay 49:183-192.

Weiss, S.B., D.D. Murphy, and R.R. White. 1988. Sun, slope, and butterflies: topographic determiants of habitat quality for *Euphydryas editha*. Ecology 69:1486-1496.

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

Chapter 2

HABITAT SUITABILITY INFLUENCES FEMALE MOVEMENT AND EGG-LAYING

BEHAVIOUR IN THE ALPINE BUTTERFLY *PARNASSIUS SMINTHEUS*

"...efficient searching and accurate assessment of resources are crucial to an individual's

survival chances and reproductive potential," (Bell 1991).

INTRODUCTION

Butterfly population size and distribution are constrained by the availability of suitable

habitat. Suitable habitat contains all the resources required for the survival of a population

for many years (Hanski and Thomas 1994), and may not be continuous over the total

spatial extent of a population, existing instead as fragments or patches. Research on

butterfly population dynamics has shown that both quality and connectivity between

suitable habitat patches are important for ensuring the persistence of populations (Harrison

et al. 1988, Thomas et al. 1992, Hanski and Thomas 1994, Hanski et al. 1996). Habitat

quality, in the context of butterflies, has traditionally been equated with the abundance of

adult nectar plants or larval food plants, or both, and deterioration in habitat quality has

been identified as the main cause of butterfly extinctions (Hanski and Thomas 1994). In

spatially-structured populations, dispersal behaviour, which is the product of individual

decisions to leave a patch or not, can mediate the effects of habitat quality on populations

but is dependent on the connectivity or on the degree of isolation of habitat patches in the

landscape (Harrison 1991). Intervening non-habitat can impede dispersal of individuals

between patches of suitable habitat, thereby reducing the connectivity or increasing the

isolation of suitable habitat patches in the landscape. Niemenen (1996) studied movement

rates of several species of moth and butterfly among islands and found that emigration and

immigration were affected by habitat patch isolation and by various physical traits of the

species considered. Other studies have shown that the persistence of spatially-structured

populations is determined, in part, by the ability of individuals to cross unsuitable habitat.

By moving between suitable habitat patches they can recolonize patches where the population was absent or extirpated (Harrison 1989, Baguette and Nève 1994, Kuussaari *et al.* 1996, Nève *et al.* 1996, Förare and Solbreck 1997, Mousson *et al.* 1999). It has been acknowledged that an understanding of the dispersal abilities of a species is required prior to predicting how the spatial arrangement of habitat patches can affect population structure or survival (Fahrig and Paloheimo 1988, Ruckleshaus *et al.* 1997, Moilanen and Hanski 1998).

Colonization of extinct habitat patches must be done by females, because it is their decision when and where to oviposit. From an evolutionary perspective, female Lepidoptera are expected to choose to oviposit on plant species that maximize growth and survival of their larvae (Thompson and Pellmyr 1991). It would therefore be advantageous for females to assess the suitability and quality of habitats for their hatching larvae, to respond positively to the abundance and quality of larval resources. Such assessments would promote residency in suitable, high-quality meadows and dispersal from unsuitable or poor-quality meadows. Unlike adult butterflies, hatching larvae are restricted to searching an area within a few metres of their hatching site (Renwick and Chew 1994). As a result, early larval survival depends almost entirely on female search behaviour and selection of oviposition sites (Root and Kareiva 1984). Females of several species of moths and butterflies can orientate to the host plants during flight and accurately assess landing sites for oviposition (Thompson and Pellmyr 1991). Assessment

of landing sites for oviposition is very species-specific and may involve a combination of physical, chemical and visual cues from landing sites (Thompson and Pellmyr 1991, Honda 1995). Females of many species "drum" the plant surface with some or all of their tarsi, antennae, ovipositor or proboscis prior to making a decision to oviposit or not (Honda 1995).

Fine-scale search and oviposition behaviours result in a tight link between host plant distribution and adult butterfly distribution. Thomas and Singer (1987) found that *Euphydryas editha* females released in habitats with and without their preferred host plant, were more likely to disperse from those without. In the closely related *Euphydryas anicia* it was found that females dispersed faster from areas with no hosts compared to areas with many hosts (Odendaal *et al.* 1989). Similarly, for the endangered Fender's blue (*Icaricia icarioides fenderi*), females alter their dispersal behaviour depending on habitat type. They fly greater distances and cover more ground in areas without the host plant (Schultz 1998). In all three of these species, females search for and selectively oviposit on suitable host plants. In some Lepidopteran species however, females do not lay their eggs on suitable host plants (Scott 1986). In these species larval establishment on suitable food plants depends on adult oviposition close to host plants and larval ability to detect and move to these plants. This paper investigates the influence of habitat quality, measured indirectly as the abundance of adult butterflies and directly as the abundance of the larval host plant, on female movement and oviposition behaviour of a butterfly whose

females have been described as "haphazard" egg-layers (Scott 1986).

The alpine butterfly *Parnassius smintheus* has monophagous larvae which feed only on lance-leaved stonecrop, *Sedum lanceolatum*(Bird *et al.* 1995). The distribution of *P. smintheus* in Alberta is restricted to the subalpine and alpine meadows where the larval host plant is found (Sperling and Kondla 1991). Studies of *P. smintheus* population dynamics on Jumpingpound Ridge, Alberta, have produced two population-movement models of *P. smintheus* (Keyghobadi *et al. in press*, Roland *et al. in press*) which demonstrate, using genetics and mark-recapture techniques respectively, that intervening forests impede movement of *P. smintheus* butterflies and thus reduce the connectivity of the regional landscape. Treeline rise in recent decades has reduced the size of the Jumpingpound Ridge meadows (Roland *et al. in press*); recolonization of increasingly isolated patches of suitable habitat may become critical to the persistence of *P. smintheus* at sites like Jumpingpound Ridge (Fig. 2-1). Although populations of *P. smintheus* are not endangered, closely related European species of *Parnassius*, including *P. mnemosyne* and *P. apollo*, are declining and endangered in many portions of their range, due to the loss and fragmentation of suitable habitat (Geyer and Dolck 1995, Sánchez-Rodríguez and Baz 1996, Meglécz *et al.*1997, Deschamps-Cottin *et al.* 1997). Predicting how physical changes to suitable habitat patches on Jumpingpound Ridge will affect populations of *P. smintheus* requires an understanding of how female *P. smintheus* make movement decisions.
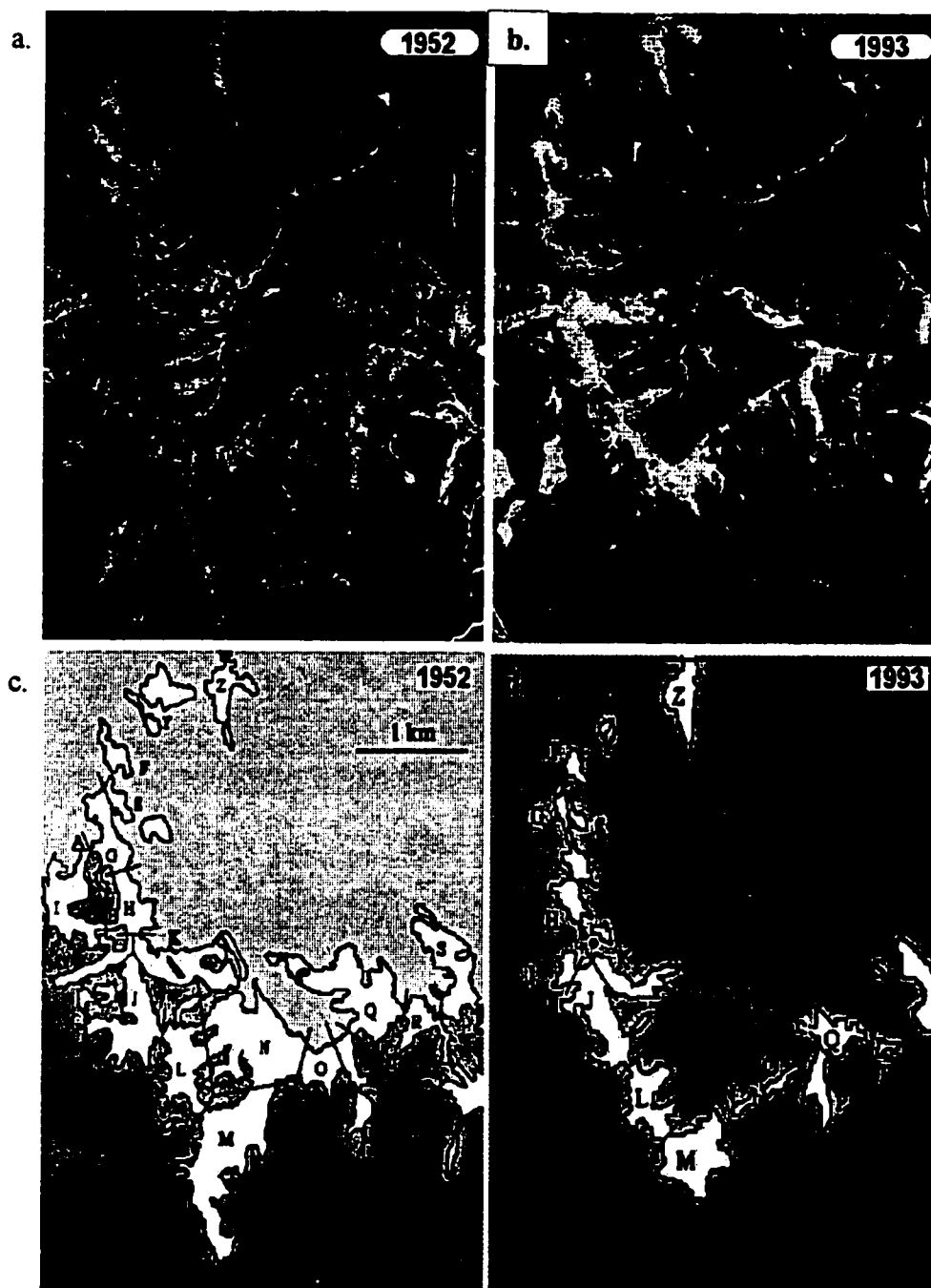
Fig. 2-1. Rise in treeline over the past four decades is evident from air photos taken on Jumpingpound Ridge, Kananaskis Country, Alberta (50°57'N, 114°55'W) in 1952 (a) and 1993 (b). Treeline (or meadow perimeters), as interpreted from the air photos, are represented by the lines for 1952 (c) and 1993 (d). Meadows are becoming smaller and increasingly isolated from one another (from Roland *et al. in press*).

The strong and highly significant correlation between adult population size and abundance of the larval host plant in Jumpingpound Ridge meadows, discovered in Chapter 4, suggests that there is a tight link between the two, even though females do not place their eggs directly on the host plant. If female *P. smintheus* respond to local larval host plant abundance and can thus determine meadow suitability for developing larvae, it is expected that females would favour the neighbourhood of the host plant as a landing site and make reproductive investments only in those meadows containing abundant host plants. Meadows on Jumpingpound Ridge support different population sizes and densities of *P. smintheus* (Roland *et al. in press*), suggesting that not all suitable meadows are of equal quality for *P. smintheus* (Table 2-1). If female *P. smintheus* can assess the quality of meadows, it is expected that females would lay more eggs in meadows with a higher density of the host plant. These behavioural patterns would require flight behaviours that tend to retain butterflies in high-quality meadows, and result in dispersal from low-quality or non-habitat meadows. In this study I investigate female *P. smintheus* landing site selection, estimate the relative quality of three different meadows, and conduct behavioural studies to identify how differences in habitat quality affect their movement and reproductive investment.

OBJECTIVES

1. To determine if *P. smintheus* females orientate to the host plant, *S. lanceolatum*, during flight and alight on available flower species randomly or if they favour *S.*

Table 2-1. The area of Jumpingpound meadows (ha) and *Parnassius smintheus* 1995 population estimates using Craig's method (from Roland *et al. in press*). The values generated from Craig's method provide indices of abundance and not absolute estimates of abundance. Population density of meadows is calculated by dividing population size by meadow area.

Meadow	Meadow Area (ha)	Population Size	Population Density (#/ha)
F	3.66	31.6	8.6
g	2.99	42.4	14.2
G	10.33	60	5.8
H	3.4	4	1.2
I	5.03	1	0.2
J	31.9	3	0.1
K	9.75	18.3	1.9
L	22.56	9	0.4
M	31.13	26.5	0.9
N	1.54	0	0
O	2.83	4.3	1.5
P	9.39	10	1.1
Q	12.42	6.6	0.5
R	1.56	6.9	4.4
S	18.35	1	0.1
Y	0.98	5.8	5.9
Z	12.2	58	4.8

lanceolatum as a landing site.

2. To assess if female *P. smintheus* fly randomly or if they alter their flight behaviour in different quality habitats, thus promoting residency in high quality meadows and dispersal from low-quality and non-habitat meadows.

3. To explore the effect of habitat suitability and quality on *P. smintheus* egg-laying behaviour.

METHODS

Study Area

Studies were conducted in the foothills of the Canadian Rocky Mountains on Jumpingpound Ridge, Kananaskis Country, Alberta. Jumpingpound Ridge is a chain of subalpine meadows separated from each other by intervening forest of lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) (Fig. 2-1d). Vegetation of the meadows is dominated by white mountain avens (*Dryas octopetala* ssp. *hookeriana*), grasses, sedges and other wildflowers. All meadows have at least some larval host plant (*S. lanceolatum*) in them.

Orientation to Host Plant During Flight

Female *P. smintheus* were caught on sunny days from July 6, 1997 to August 12, 1997 in meadow G. Individuals were marked with a three letter identification code and their mating status was assessed by the presence or absence of a sphragis, laid down on the

female abdomen by the male during mating (Scott 1986). Mated females were followed at a distance of one to two metres. Care was taken not to pass observer shadow over the butterfly because this stimulates premature take-off and anti-predator flight behaviour. Landing sites were marked with sequentially numbered clothes pins (Stanton 1982), until females could no longer be followed. Flight paths were later mapped by recording the straight-line distance and the compass angle between consecutive landing sites. Stanton (1982) defines preference as an instance where resources are utilized more often than would be predicted from the frequency with which foragers encounter and perceive them. In order to assess preference in *P. smintheus*, landing sites that were flowers were compared to all available flowering nectar plants located along flight paths. All available nectar plants within 1.5 metres on either side of the flight path were identified to species and tallied; all plants including those with multiple flower heads were counted as one plant except for legumes (*Hedysarum sulphurescens* and *Oxytropis sericea*). Due to the size of the legume inflorescences, each was considered as one plant.

Collection of flight path data was very time-consuming and therefore only four full flight paths were recorded. Data on landing choice from a total of four observed flight paths were combined. Preference was estimated using a G-test and several subdivided G-tests were conducted to determine if females landed more than, less than or as frequently as expected, on each of the individual flower species. The alpha level for the multiple subdivided G-tests was adjusted for experimentwise error (Sokal and Rohlf 1998).

Habitat Quality

Data on larval host plant density (Chapter 4), butterfly population indices and individual

movements of *P. smintheus* (Roland *et al. in press*), were used to select three meadows of

different quality for female *P. smintheus* behavioural observations: an unsuitable or non-

habitat meadow on Powderface Trail (clear cut), a suitable meadow of poor-quality

(meadow J) and a suitable meadow of good-quality (meadow G) (Table 2-2). All three

meadows had suitable and abundant nectar resources for female *P. smintheus*.

Table 2-2. Assessing quality of meadows for *P. smintheus*. Movement data are from the
1995 mark/recapture session conducted by Roland *et al.* (*in press*). The number of
individuals that were marked and recaptured in the same meadow (residents), the number
of individuals marked in that meadow and recaptured in another (emigrants) and the
number of individuals marked in another meadow that were recaptured in the indicated
meadow (immigrants). The mean density of larval host plants, *Sedum lanceolatum*, is
from mapping work conducted in 1998 for Chapter 4.

Meadow	Residents	Emigrants	Immigrants	*Sedum* (plants/m^2)
Non-Habitat	0	0	0	0
Poor-Quality (J)	1	2	1	4.1
Good-Quality (G)	130	11	9	5.7

Effect of Habitat Quality on Movement

Females were collected, marked with unique codes, and kept in outdoor cages with a

nectar source. Females were released in one of three meadows on sunny days between

July 14, 1998 and August 8, 1998. To standardize for the influence of the release site on

female behaviour, females were released by observers onto suitable nectar flowers.

Females were followed and paths marked as described above. At each landing site, post-alighting behaviours were recorded, including: stationary (females did not move; includes basking with wings open), crawling (females remain in contact with the substrate but move over the substrate using their legs only), abdominal arch (females arched abdomen and contacted the substrate with the posterior end of their abdomen), oviposition (confirmed by presence of an egg), and nectar feeding (females probed flowers with proboscis). Compass angles were converted to a turning angle for each step in the path traversed (turn angle $step_x$=compass angle $step_{x+1}$-compass angle $step_x$). The number of steps was limited to eight to ensure an equal sample for each female.

Testing for random movement

Turn angles and step lengths in the three separate habitats can be used to estimate whether females move randomly or if they respond to differences in habitat quality and move differently in the three habitats. Karieva and Shigesada (1983) proposed a simple method for comparing the observed rate of dispersal (mean net displacement squared) of organisms to a correlated random walk (CRW). An assumption of CRW is that organisms behave as they would in a first-order Markov chain model. Movement decisions (turn angle and step length), for organisms which move in a first-order Markovian manner, depend only on the preceding step. Each turn angle and step length is dependent on the preceding turn angle and step length (Turchin 1998). Provided that the distribution of turn angles is normal and symmetrical around zero, the CRW represents the random

dispersal of an organism. Therefore, any observed deviations in the rate of dispersal from the CRW prediction indicates that there are either serial correlations in step length and turn angle at a lag of more than one step or that the rate of dispersal of an organism is more or less than random. This method allows for comparison of movement paths of conspecifics in different environments (Cane 1978, Root and Karieva 1984, Turchin 1998).

I compared the average movement rates, the mean net displacement squared, observed for females to a CRW prediction for each of the three habitats. It is often difficult to demonstrate whether or not organisms are moving in a Markovian fashion (Root and Karieva 1984). Tests for serial correlations in movement behaviours were conducted to determine whether *P. smintheus* females met the assumptions for the CRW model separately for all habitats. Turn angles were reduced to right (R) and left (L) turn directions and were analysed using G-tests to determine if there was a significant interaction between turn direction and its previous turn direction at a lag of one, two and three steps. Correlation analyses were used to determine whether a given step length was correlated with the steps preceding it at a lag of one, two and three steps.

Another approach for comparing observed displacements to random displacements is the bootstrap method. Unlike the CRW model, this method provides an estimate of statistical significance and makes no assumptions about the distribution of the test statistic (Turchin

1998). Simulations of 1000 flight paths of eight steps for each habitat were compared to

the observed mean net displacements for the respective habitats. The simulated paths for

the non-habitat meadow were generated by randomly drawing individual step lengths and

turn angles (with replacement) from the observed step lengths and turn angles in the non-

habitat meadow. Ninety-five percent confidence envelopes were generated from the

simulations and compared to the observed mean net displacements. If observed mean net

displacements fell above or below the confidence envelopes, females were considered to

have moved respectively more or less than expected from random. This procedure was

repeated for all habitats.

Emigration and Habitat Quality

Mean step lengths and turn angles for each female were used to compare effects of habitat

quality on movement behaviour. Use of mean turn angle was based on the fact that the

distribution of all turn angles for each habitat were normal and centred around zero, thus

simplifying turn angle analyses (Odendaal *et al.* 1989). Mean distance per step, and mean

turn angle per step were later compared between good-quality, poor-quality, and non-

habitat habitats using analysis of variance (ANOVA) tests, after testing for equality of

variances (Levene 1960). Mean distance per step and mean turn angle per step were

combined for the poor- and good-quality meadows and compared to the non-habitat

meadow using an ANOVA, to determine whether suitability (instead of meadow quality)

is affecting female behaviour. As a more direct comparison of emigration in the three

different habitats, the net displacements of butterflies for one to eight steps and one to

twenty steps were compared using repeated measures ANOVA (Schultz 1998). Repeated

measures ANOVA allows one to analyze data collected on the same individual three or

more times and to test for interaction between different factors (Zar 1996). In this study

both habitat quality and step number are factors. The net displacement data were

combined for poor- and good-quality meadows and repeated measures ANOVA was

conducted comparing net displacements in suitable (poor- and good-quality) and

unsuitable (non-habitat) meadows after 8 and 20 steps.

Oviposition and Habitat Quality

P. smintheus lay eggs singly on a variety of substrates (Scott 1986). I recorded the

number of ovipositions for each of the three meadow types during 1998 flight path

observations. The total number of eggs laid along each flight path was compared among

habitat types. To control for the individual variation in the number of oviposition

opportunities I compared the proportion of landings for each female, x, that resulted in

oviposition (P_x):

$$P_x = \frac{O_x}{L_x} \qquad (1)$$

where O_x is the number of landings with oviposition for female x and L_x is the total number

of landings for female x. I also compared net displacement between successive

ovipositions for the poor- and good-quality meadows to determine if females fly greater distances in search of suitable ovipositions sites in the poor quality meadow. Due to small sample sizes and unequal variances between meadows, the non-parametric Kruskal-Wallis test was used. To determine if habitat suitability affects oviposition behaviour, the number of eggs laid and proportion of landings that resulted in oviposition in the poor- and good-quality meadows were combined and compared to the non-habitat meadow using non-parametric the Mann-Whitney U tests. Net displacement between successive ovipositions was also compared using a Mann-Whitney U test.

Natural ovipositions along flight paths in 1998 were supplemented with oviposition cage studies in 1997 and 1998. To determine if females oviposit in response to the larval host plant, females were retained in meadow G for 24 hours in netted cages (Coleman™ food cover: 32 cm x 32 cm at base and 20 cm high in the centre) with or without *S. lanceolatum*. Difference in the number of eggs laid in the presence or absence of *S. lanceolatum* was determined using a Mann-Whitney U test. The number of eggs laid and their locations within the cage (plant species or substrate) were recorded.

RESULTS

Orientation to Host Plant During Flight

Female *P. smintheus* did not land in random locations (G=51.1; p=0.00002). However, all landing sites were proportionate to their availability except *Senecio canus* (Prairie

Groundsel), which was landed on more than expected (G=16.8, p=0.0004) and *Galium*

boreale which was landed on less than expected (G=14.9, p=0.0001) (Table 2-3).

Table 2-3. Subdivided G-test results for testing the interaction between the number of available nectar plants of each species available along flight paths and the number of landings on each species. Significant results indicate that females landed more or less often than expected than if they had landed randomly on all available flowers. Preference indicates that females landed more often than expected and avoidance indicates that females landed less often than expected.

Plant Species	Landings/Available	G	Prefer/Avoid
Oxytropis sericea	0	0.06	
Stellaria longipes	0	0.06	
Potentilla diversifolia	0	0.06	
Erigeron peregrinus	0	0.17	
Agoseris glauca	36166	1.78	
Castilleja spp.	0	0.62	
Comandra umbellata	0	0.74	
Senecio canus	8/51	16.8**	prefer
Zigadenus elegans	0	1.31	
Hedysarum sulphurescens	1/40	0.01	
Solidago multiradiata	36245	4.17*	prefer
Rhinanthus minor	0/73	4.23*	avoid
Achillea millefolium	3/94	0.06	
Potentilla fruticosa	8/132	4.58*	prefer
Galium boreale	0/240	14.9**	avoid
Sedum lanceolatum	10/307	0.33	
Aster sibiricus	3/309	6.0*	avoid

**Chi square (corrected for multiple comparison) is significant at p<0.01.
*Chi squre (not corrected for multiple comparison) is significant at p<0.05.

Effect of Habitat Suitability and Quality on Movement

Testing for random movement

There were no significant correlations between successive moves for turn angle nor for step length in the non-habitat meadow, but there were significant correlations for these in both the poor- and good-quality meadows at a lag of one step (Table 2-4). These results suggest that females behave as they would in a first-order Markov chain in the two butterfly meadows. Observed deviations of female net displacement squared in the two butterfly meadows suggest that females displace further than expected from CRW predictions (Fig. 2-2) and those noted in the non-habitat meadow may be produced by the non-Markovian manner of movement. Bootstrap simulation (Fig. 2-3) suggests that net displacement of females does not differ from random in the non-habitat meadow. After five moves the observed net displacement is greater than the bootstrap prediction in the poor-quality butterfly habitat. In the good-quality meadow the observed mean net displacement remains near the upper bounds of the bootstrap prediction but does not differ significantly from the predicted net displacement. In general, there is more movement in the poor- and good-quality meadows than expected from the distribution of turn angles and step lengths observed.

Emigration and Habitat Quality

There were no significant differences in the mean step length among the three habitats, although step lengths were greatest in non-habitat ($F_{2,30}$=2.13, p=0.14, power<0.10) (Fig.

2-4). When step length data were combined for the two butterfly meadows there was still

no significant effect of habitat suitability on step lengths ($F_{1,30}=1.64$, $p=0.21$, power<0.10).

Table 2-4. Effects of three meadow habitats (non-habitat, poor-quality and good-quality meadows) on the assumption of the Correlated Random Walk model for movement. Serial correlation testing of turn direction (Right vs. Left) and step length (L_x) at a lag of 1, 2 and 3 steps. The G statistic is from the log likelihood ratio and r is Pearson's correlation coefficient. * indicates significant autocorrelation at $p<0.05$. Females meet the assumption of CRW in the poor- and good-quality butterfly meadows, but violate the assumption in the non-habitat meadow.

Meadow	Lag 1 step		Lag 2 steps		Lag 3steps	
	R vs. L	L_x vs. L_{x-1}	R vs. L	L_x vs. L_{x-1} +L_{x-2}	R vs. L	L_x vs. L_{x-1} +L_{x-2} +L_{x-3}
Non-Habitat	G=0.03	r= 0.11	G=0.05	r= 0.31	G=0.36	r= 0.15
Poor-Quality	G=4.18*	r= 0.14	G=0.93	r= 0.17	G=0.16	r= 0.12
Good-Quality	G=1.63	r= 0.44 *	G=3.26	r= 0.40 *	G=1.37	r= 0.14
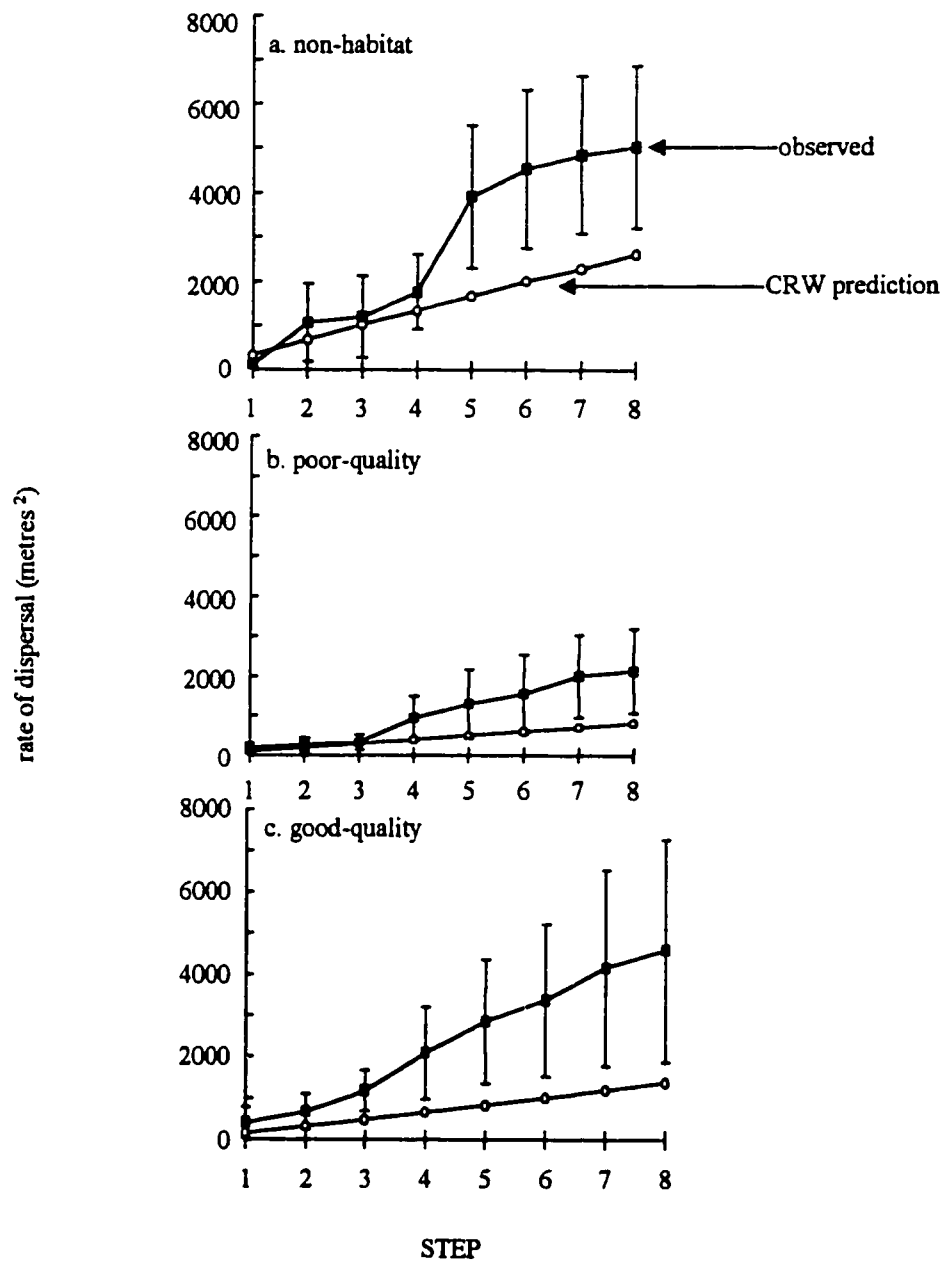
Fig. 2-2. Observed mean net displacement (rate of dispersal) with standard error bars and the expected mean net displacement squared from the Correlated Random Walk Model for the non-habitat meadow (a), the poor-quality meadow (b), and the good-quality meadow (c). Females exceeded the CRW model predictions after 4, 6 and 2 steps in the non-habitat, poor-quality, and good-quality meadows, respectively.
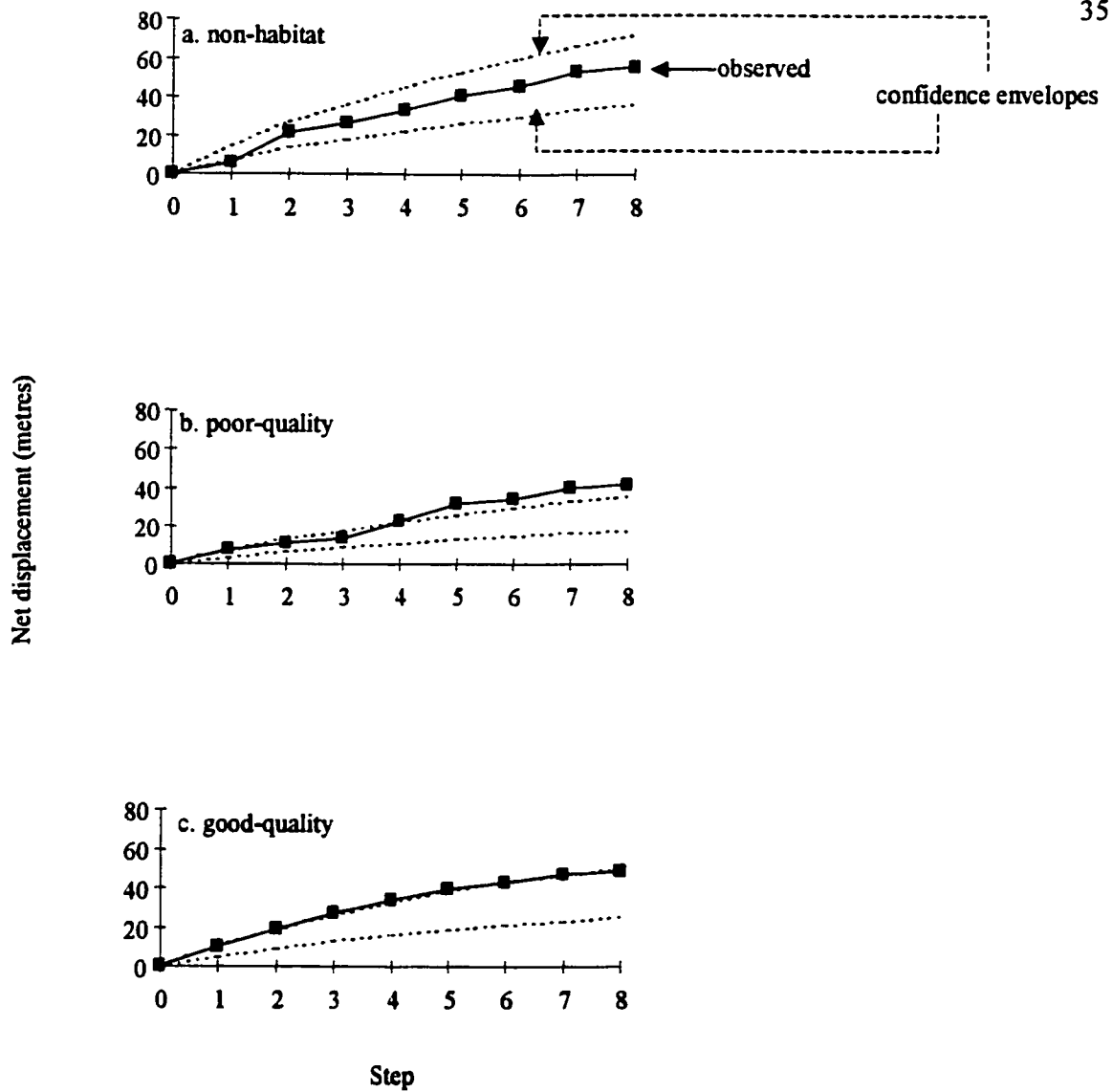
Fig. 2-3. Observed mean net displacement (m) of female *P. smintheus* plotted with 95% confidence envelopes from simulated flight paths for: (a) the non-habitat meadow; (b) the poor-quality meadow; and, (c) the good-quality meadow. Where the observed net displacement is greater than the upper confidence envelope females displaced further than expected from random and where the observed net displacement is within the confidence envelopes females displaced as expected from random. Females appeared to displace randomly in the non-habitat meadow and displaced further than expected in the two butterfly meadows.
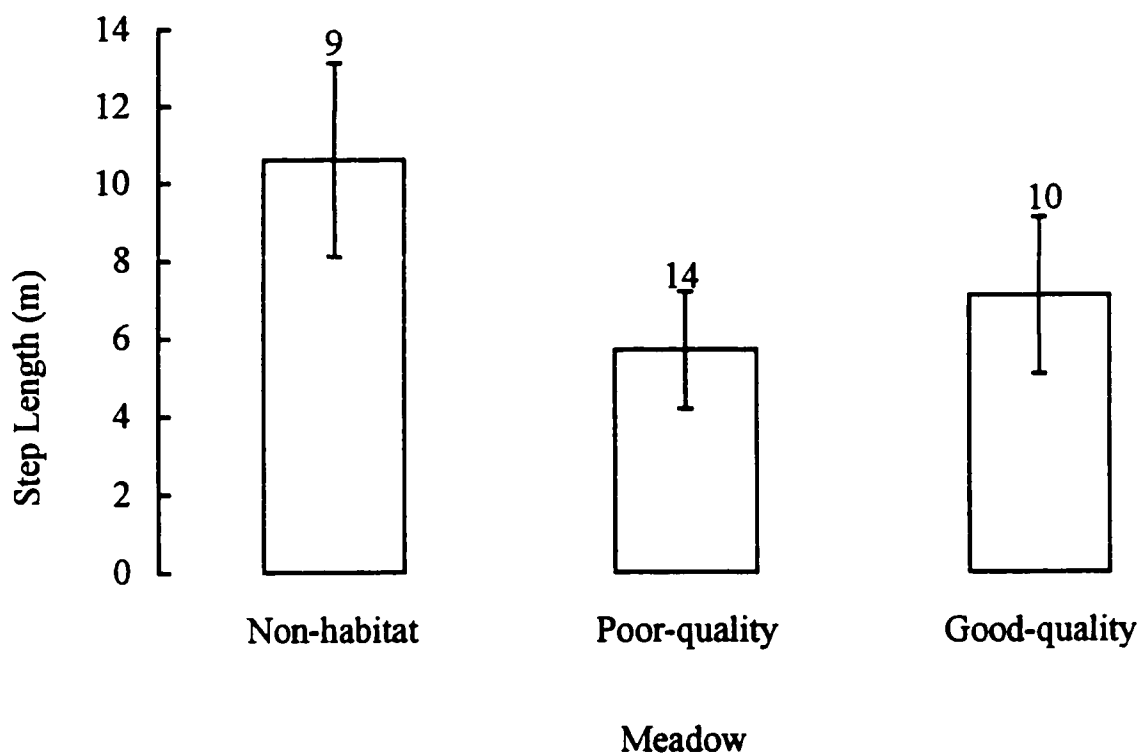
Fig. 2-4. The mean step length (m) for female *P. smintheus* released in the three meadow habitats, calculated from the mean step lengths of the first eight steps of each female. The number of females observed in each of the treatments is recorded at the top of the standard error bars. There was no significant effect of habitat quality on mean step length, p=0.14.

Mean absolute turning angles approximated a normal distribution in each of the three

habitats and variances for the absolute turn angles were similar among the three release

sites (p=0.35). Females tended to turn more sharply in the good-quality meadow, but

there was no significant effect of habitat quality on turn angle ($F_{2,28}$=1.65, p=0.21,

power<0.10) (Fig. 2-5) nor was there a significant effect of habitat suitability on turn angle

($F_{1,28}$=0.45, p=0.51, power<0.10).

Females moved consistently further at each step in the non-habitat than in the poor- and

good-quality butterfly meadows (Fig. 2-6). There were no significant effects of habitat

quality (p=0.63) nor was there any interaction between step number and habitat quality

(p=0.88) on net displacement during the first eight steps using repeated measures

ANOVA. When data were combined for the poor- and good-quality butterfly meadows

and compared to the non-habitat meadow, there was no effect of habitat suitability on net

displacement (p=0.56).

Using all twenty steps, there was no significant effect of habitat quality on net

displacement (p=0.13). Despite the small sample size, there was a marginally significant

interaction between step number and habitat quality (p=0.05) on mean net displacement.

When data were combined for poor- and good-quality butterfly meadows and compared

to the net displacements in the non-butterfly meadow there was a significant effect of

habitat suitability (p=0.044) on net displacement and there was a significant interaction
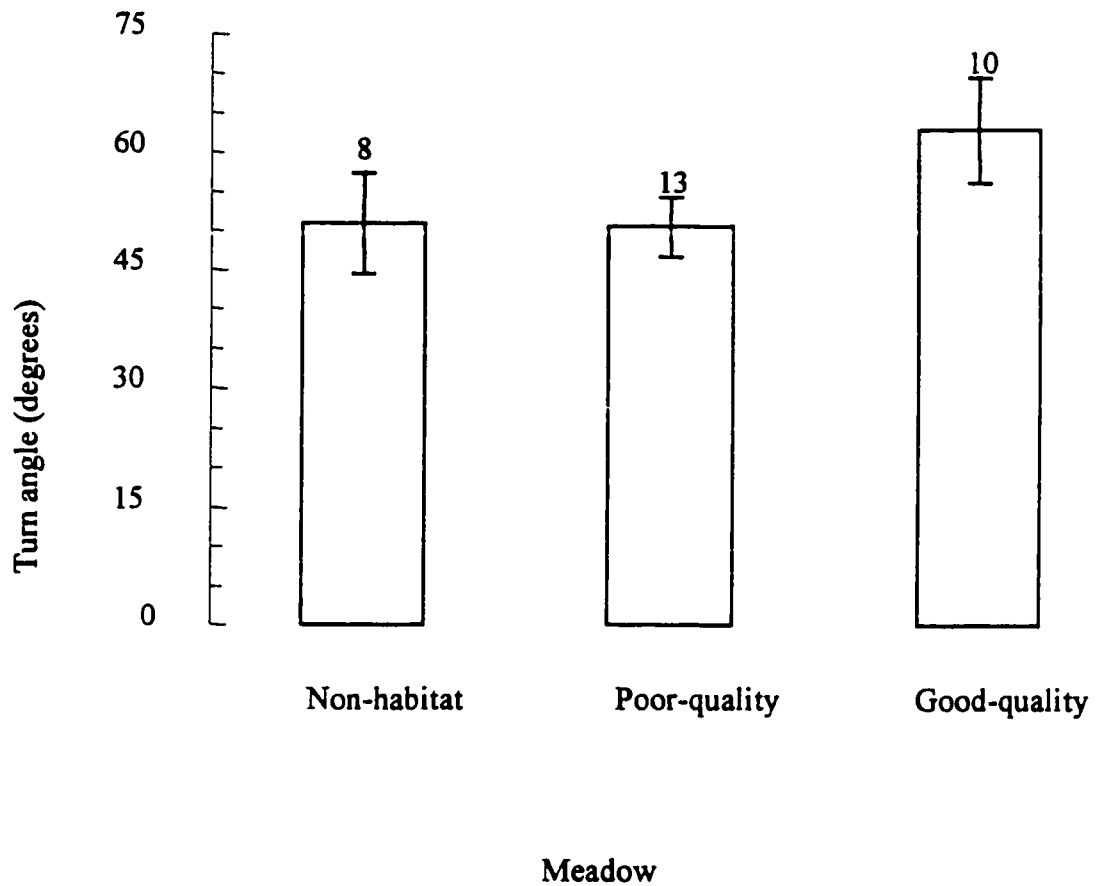
Fig. 2-5. The mean absolute turn angle (degrees) of female *P. smintheus* in the three meadow habitats, calculated from the mean absolute turn angle for the first eight steps of each female. The number of females observed in each of the treatments is recorded at the top of the standard error bars. There was no significant effect of habitat quality on turn angle, $p=0.21$.
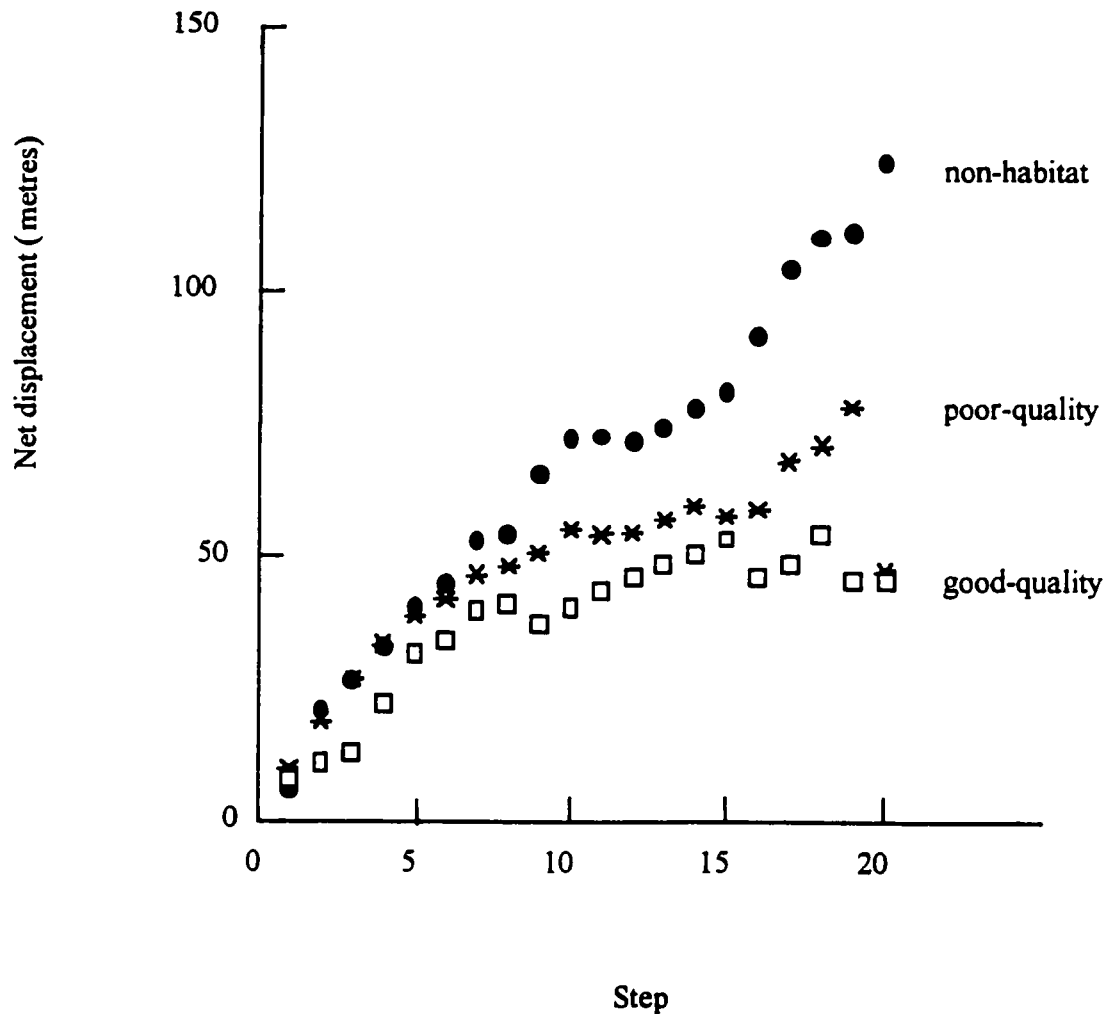
Fig.2-6. The mean net displacements (m) of female *P. smintheus* released in the three meadow habitats. The sample sizes for the different habitats after 8 and 20 steps are: non-habitat, 9 and 6; poor-quality, 14 and 8; and good-quality, 10 and 5. There was no significant effect of habitat quality after 8 steps (p=0.63) nor after 20 steps (p=0.13). There was a significant interaction between step number and habitat quality after 20 steps; p=0.05.

between step number and habitat suitability (p=0.012). This suggests that in all cases

there was greater displacement with step length in the non-habitat meadow.

Oviposition and Habitat Suitability and Quality

Females laid the most eggs in the good-quality meadow (Fig. 2-7). While there was no

statistically significant effect of meadow quality on the number laid (H=5.35, p=0.07) nor

in the proportion of landings that resulted in oviposition (H=4.8, p=0.09), these values

approached statistical significance. In suitable (poor- and good-quality) meadows

significantly more eggs were laid by females than in the unsuitable (non-habitat) meadow

(U=93, p=0.047). There was almost a significant effect of habitat suitability on the

proportion of landings that resulted in oviposition (U=100, p=0.083). There was no

difference in the net displacement between successive oviposition events in the poor- and

good-quality meadow (U=130, p=0.93) (Fig. 2-8). Only two out of forty-seven (4.3%)

ovipositions observed during flight follows were on *S. lanceolatum* (Appendix A contains

detailed oviposition site information). Females laid more eggs in cages when *S.

lanceolatum* was present in 1997 (U=5.5; p=0.009) and 1998 (U=11; p=0.012) (Fig. 2-9).
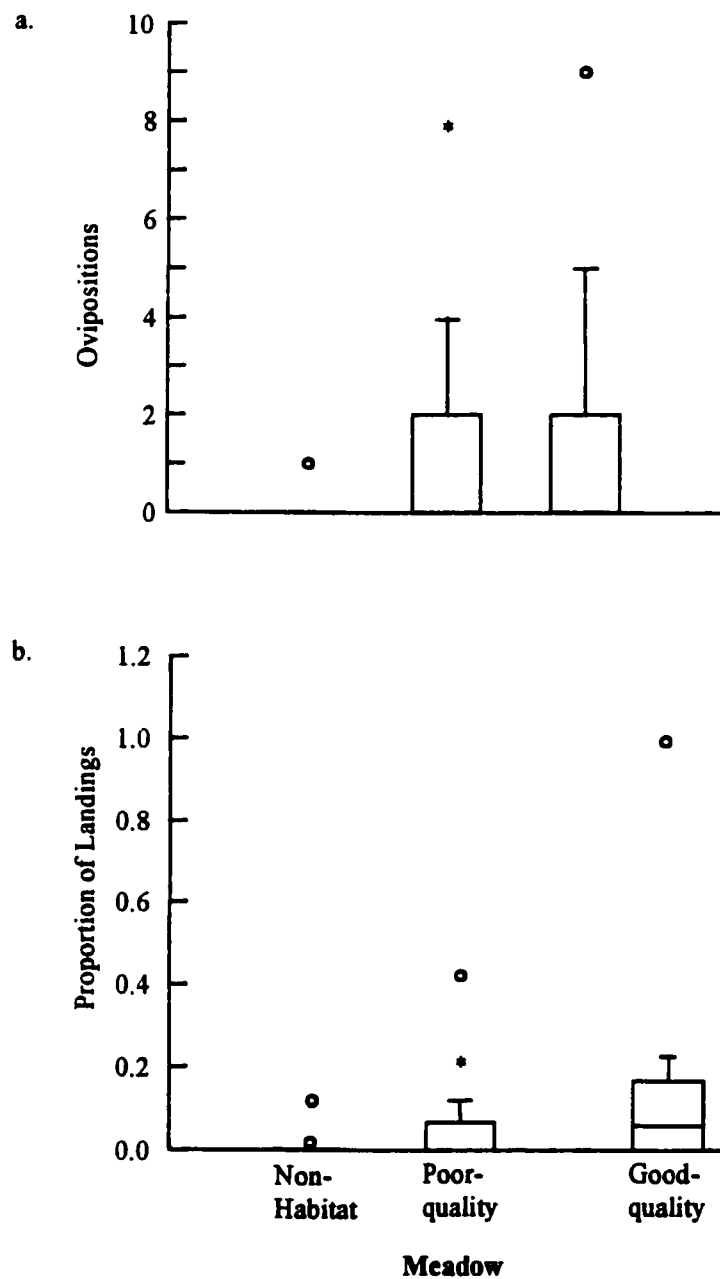
Fig. 2-7. Box and whisker plots for: (a) the number of ovipositions observed in the three meadows during flight path observations; and, (b) the proportion of landings which resulted in ovipositions. There was no significant effect of habitat quality on the number of ovipositions observed (p=0.07) nor on the proportion of landings which resulted in ovipositions (p=0.09). * and o are outliers and extreme outliers.
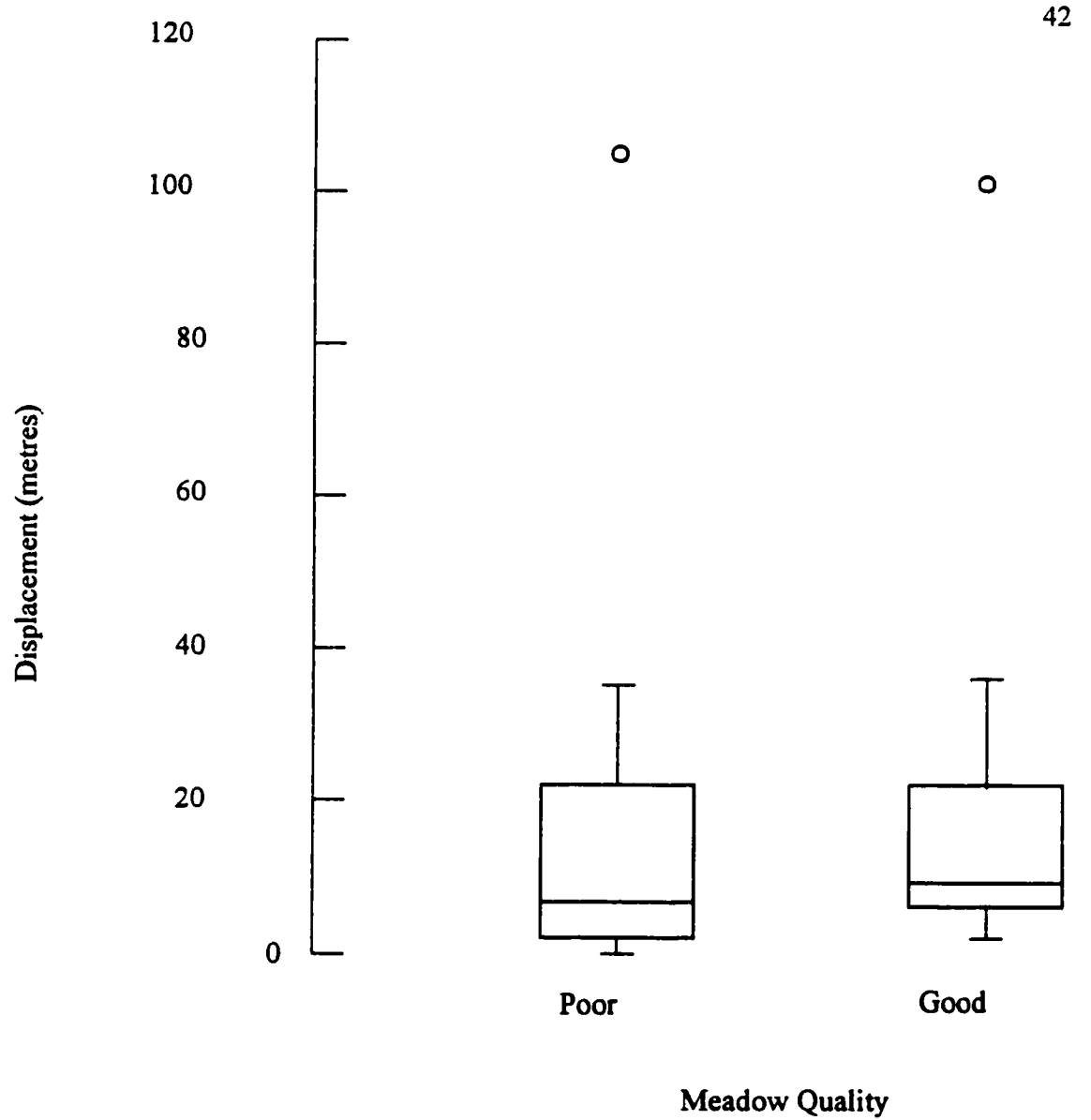
Fig. 2-8. Box and whisker plots of net displacement (m) between successive ovipositions in the two butterfly meadow treatments. There was no significant effect of habitat quality on displacement between ovipositions; p=0.93.
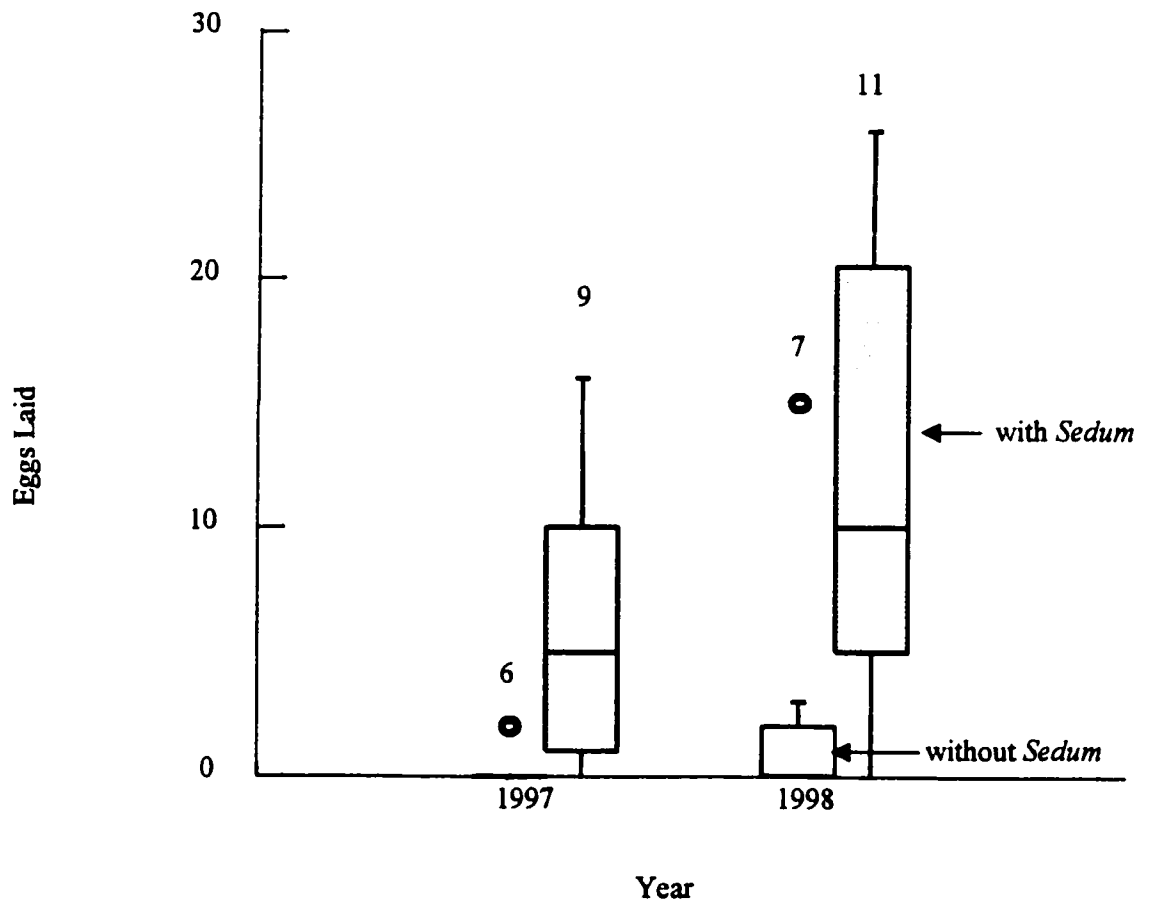
Fig. 2-9. Box and whisker plots of number of eggs laid in 1997 and 1998 for females caged for 24 hour with *Sedum lanceolatum* (stippled) and without *S. lanceolatum* (empty). Sample sizes are indicated above the plots. There was a significant effect of *S. lanceolatum* presence in both 1997 (p=0.009) and 1998 (p=0.012).

DISCUSSION

Female *P. smintheus* nectar-feed on flowers of a variety of plant species and although

females alighted frequently on the larval host plant, *S. lanceolatum*, they did not prefer it

as a landing site. The results indicate that *S. lanceolatum* was abundant along flight paths

in this study and that females landed opportunistically on this ample nectar source. This is

further supported by the few significant departures from the random expectation of

landings on the other flower species. The preference detected for *Senecio canus* may be

attributed to some characteristic of this plant for example, its physical structure, its

apparency, or the quality of its nectar. *Senecio canus* is a tall plant, between one and four

decimetres tall; it stands above much of the surrounding vegetation and has a large

composite flower head with bright yellow ray flowers (Moss 1994). Flower

characteristics were not measured but may be of interest for further study of search

behaviour and learning in *P. smintheus*. Stanton (1982) found that *Colias philodice*

eriphyle butterflies confused their preferred host plant, *Vicia americana*, with two other

legumes, *Lathyrus leucanthus* and *Astragalus decumbens*, and postulated that it was due

to their similarities in leaf shape and size. In a survey of Swedish butterflies in the field

Wiklund (1984) noted that species most successful at alighting on host plants, had host

plants that extended above the surrounding vegetation or were brightly coloured, and

were therefore more apparent to searching females. In laboratory experiments it has been

shown that *Papilio xuthus* butterflies can learn to feed on different coloured flowers

depending on nectar reward (Kinoshita *et al.* 1999). Because floral phenology and

learning affect landing frequencies in other butterfly species (see also Stanton 1984,

Renwick and Chew 1994), a larger sample of flight paths over the entire *P. smintheus*

flight period may identify seasonal landing site preferences. *P. smintheus* on

Jumpingpound Ridge are known to live up to twenty days (Roland *et al. in press*) and are

active during sunny hours. Therefore, the flight path observations in this study represent a

small portion (5 to 38 minutes) of the lifetime activities of a female.

Observed rates of net displacement in all meadows were greater than CRW model

predictions and indicate that females either have greater movement rates than expected

from random or that they do not behave in a Markovian manner. Independent calculations

for serial correlation in turn angle and step length show that females do not behave in a

first-order Markovian manner in the non-habitat meadow. This suggests that females in

the poor- and good-quality meadows move further than expected from the CRW

prediction. Results from the bootstrap simulation of "random" net displacements indicate

that females behave differently in non-habitat and habitat meadows. Females conformed

more closely to "random" net displacement expectations in the non-habitat meadow than

in the habitat meadows, where females tended to displace further than expected. Female

P. smintheus movements in poor- and good-quality habitat meadows were serially

correlated and resulted in greater displacements than expected (CRW and Bootstrap),

suggesting that females direct their movements in these two suitable meadows. This

directedness is perhaps in response to the spatial distribution of resources, including nectar

plants or the larval host plant, *S. lanceolatum*. Brommer and Fred (*in press*)

demonstrated that the distribution and isolation of adult nectar resources and larval host

plant patches affect the movement of adult *P. apollo*. The seemingly uncorrelated

movement behaviours of females in the non-habitat meadow in my study and the bootstrap

simulation results suggest that females *P. smintheus* move randomly and that their

movement is not directed in the non-habitat meadow. These findings are similar to those

for *Euphydryas editha bayensis* butterflies, which exhibit random flight in non-habitat and

more directed flight within 50 metres of habitat (Harrison 1989).

The lack of significant differences in step length and turn angle behaviours between

habitats results in part from the extremely low power of the analyses. However, females

did tend to turn more sharply and have smaller step lengths in the good-quality meadow

than in the non-habitat meadow. Both of these patterns were expected and have been

noted in other species of butterfly *Colias philodice eriphyle* (Stanton 1982) and

Euhpydryas editha (Odendaal *et al.* 1989). The combined effect of these two behaviours

resulted in greater net displacements in the non-habitat meadow than in the poor- and

good-quality butterfly meadows. The net displacement continued to increase in the non-

habitat meadow with increased number of steps. In contrast the net displacement leveled

off in the butterfly meadows after approximately ten steps. This finding conforms to the

results for the Fender's Blue (Schultz 1998) where the net displacement was greatest for

butterflies moving in non-habitat. Movement observations indicate that females perceive

the non-habitat meadow as different from either of the two butterfly meadows.

Movement patterns discussed above are reflected in the natural oviposition observations, despite the absence of a statistically significant effect of habitat quality on the number and proportion of landings that resulted in oviposition. The observation that almost all ovipositions occurred in suitable (poor- and good-quality) meadows supports the original hypothesis that females will retain eggs and travel greater distances between ovipositions in non-habitat meadows. It is interesting to note that the distances traveled between oviposition events in the two butterfly meadows were similar. This observation suggests that females in habitats containing the larval host plant will oviposit at regular intervals, regardless of host plant density. Detection of these patterns was hampered by small sample size and hence, low power.

Caged experiments on oviposition support the pattern of retention of eggs by females in non-habitat. These experiments also indicate that some chemical or physical cue, or both, from the larval host plant stimulates oviposition, despite the fact that the actual oviposition occurs off of the host plant. Females are therefore capable of assessing the suitability of a meadow for their larval offspring, and may detect and search for *S. lanceolatum* oviposition cues during flight, or upon landing. In a survey of the chemical mediation of oviposition in Lepidoptera, Honda (1995) stated that chemicals from host plants often help attract ovipositing females. More detailed behavioural and physiological

experimentation is required to identify what is eliciting oviposition response in *P. smintheus* females.

Understanding why *P. smintheus* oviposit off of the host plant requires further study and a more detailed understanding of their biology and that of *S. lanceolatum*. This phenomenon has been observed in other butterflies: including other *Parnassius* sp., *Speyeria* sp., *Boloria* sp., and the families Satyrinae and Hesperiinae (Scott 1986). The following reasons have been postulated for ovipositions off of the host plant: (1) inability of female to locate larval host plants (Stanton 1982); (2) avoidance of exposure of eggs to predator/parasite complex associated with host plant (Dethier 1959, Singer 1984, Mappes and Kaitala 1995); (3) evolution of a shift to a new host plant species (Wiklund 1975); and, (4) the cause or consequence of mobility of newly hatched larvae (Chew 1977). Species that overwinter as eggs and whose larvae feed on herbaceous host plants, often oviposit off the host plant (Wiklund 1984) and oviposition site selection on the host plant may not be as critical for species with overwintering eggs or larvae where parts of the host plant senesce (Scott 1986). *P. smintheus* overwinter in the egg stage and although *S. lanceolatum* is a perennial plant, its flowering stalk senesces. The spatial distribution of *S. lanceolatum* does not vary greatly from year to year because it is a perennial and may live many years (Clausen 1975), therefore, oviposition in the proximity, or on senescing portions of *S. lanceolatum* remains advantageous for *P. smintheus*.

Both *P. smintheus* (this study) and *P. apollo* (Deschamps-Cottin *et al.* 1997) females

preferred ovipositing on the artificial substrates presented to them. *P. apollo* laid the

majority of eggs on walls and tissue paper rather than the host plant and *P. smintheus* laid

the majority of eggs on the screening of the enclosure. *P. apollo* did, however, oviposit

proportionately more often on the host plant than did *P. smintheus* (Table 2-5). The

similarities in oviposition behaviours detected in *P. smintheus* and *P. apollo* mentioned

above, and the observations that *P. clodius* oviposit on or near its host plant *Dicentra*

formosa (McCorkle and Hammond 1985) and that *P. mnemosyne* scatter their

complement of eggs over a wide area where the larval host plants (*Corydalis cava* and *C.*

solida) are found (Meglécz 1998), suggest that there may be evolutionary constraints on

oviposition behaviours within this genus.

Table 2-5. The percentage of eggs laid on artificial, host plant, and other substrates in the caged oviposition experiments for *Parnassius apollo* and *Parnassius smintheus*. Percentages were calculated from a total of 1696 oviposition events by 25 *P. apollo* females. For *P. smintheus* estimates were calculated from 70 eggs laid by 11 females in 1997 and 130 eggs laid by 10 females in 1998. *P. apollo* was only exposed to host plant and artificial substrate whereas *P. smintheus* females were in contact with alternative nectar source, soil and other plants. Data for *P. apollo* was taken from Deschamps-Cottin *et al.*(1997).

Egg laying Site	*Parnassius apollo*	*Parnassius smintheus*	
		1997	1998 Season
Artificial Substrate	68.8	81.9	88.5
Host plant	31.2	2.8	1.5
Other	-	15.3	10

Given that female *P. smintheus* do respond to the presence of the larval host plant, the absence of *S. lanceolatum* in the non-habitat meadow may explain the consistently greater net displacement of females released in the non-habitat meadow than of females released in the two butterfly meadows. Although there were different densities of *S. lanceolatum* in the poor- and good-quality butterfly meadows, female flight behaviour was similar and net displacements between ovipositions were almost identical. Females may respond to the host plant at a fairly coarse scale and consider habitats with *S. lanceolatum* as suitable habitat and yet not discern finer scale differences in quality of habitat (concentrations of *S. lanceolatum*); again, because they do not respond directly to the host plant. It should also be noted that the difference in *S. lanceolatum* density was not very large in the butterfly meadows (Table 2-2).

The results from this study suggest that female *P. smintheus* can assess meadow suitability. This response likely plays an important role in determining the distribution of populations in the landscape because female butterflies will: (1) tend to remain within habitat containing the larval host plant and displace at faster rates in non-habitat (meadows not containing *S. lanceolatum*); and, (2) oviposit in habitats containing variable densities of the host plant and retain eggs in non-habitat. The results support the findings from mark/recapture work by Roland *et al.* (*in press*) that *P. smintheus* adults on Jumpingpound Ridge are fairly sedentary and do not move often between patches of suitable habitat, and further indicates that females encountering non-habitat will likely

emigrate from it. These findings will provide meaningful information on movement in *P.*

smintheus females for current physical models of the population dynamics for this species

(Keyghobadi *et al. in press*, Roland *et al. in press*).

LITERATURE CITED

Baguette, M. and G. Nève. 1994. Adult movements between populations in the specialist butterfly *Proclossiana eunomia* (Lepidoptera, Nymphalidae). Ecological Entomology 19:1-5.

Bell, W.J. 1991. Searching behaviour: the behavioural ecology of finding resources. Chapman and Hall, London, UK.

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

Brommer, J.E. and M.S. Fred. 1999. Movement of the Apollo butterfly, *Parnassius apollo*, related to host plant and nectar plant patches. Ecological Entomology *In press*.

Cane, V.R. 1978. On fitting low-order Markov chains to behaviour sequences. Animal Behaviour 26:332-338.

Chew, F.S. 1977. Coevolution of pierid butterflies and their cruciferous foodplants. II. The distribution of eggs on potential foodplants. Evolution 31:568-579.

Clausen, R.T. 1975. *Sedum* of North America North of the Mexican Plateau. Cornell University Press, Ithaca, New York, USA.

Deschamps-Cottin, M., M. Roux and H. Descimon. 1997. Larval foodplant efficiency and laying preferences in *Parnassius apollo* L. (Lepidoptera, Papilionidae). Life Sciences

320:399-406.

Dethier, V.G. 1959. Egg laying habits of Lepidoptera in relation to available food. Canadian Entomologist 91:554-561.

Fahrig, L. and J. Paloheimo. 1988. Effect of spatial arrangement of habitat patches on local population size. Ecology 69:468-475.

Förare, J. and C. Solbreck. 1997. Population structure of a monophagous moth in a patchy landscape. Ecological Entomology 22:256-263.

Geyer, A. and M. Dolck. 1995. Okologie und schutz des apollofalters (*Parnassius apollo* L.) in der Frankenalb. Vortrage der Entomologentagung in Gottingen 27:1-6.

Hanski, I., A. Moilanen, T. Pakkala, and M. Kuussaari. 1996. The quantitative incidence function model and persistence of an endangered butterfly metapopulation. Conservation Biology 10:578-590.

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

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

Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. Biological Journal of the Linnean Society 42:73-88.

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

Honda, K. 1995. Chemical basis of differential oviposition by Lepidopterous insects. Archives of Insect Biochemistry and Physiology 30:1-23.

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

Keyghobadi, N., J. Roland, and C. Strobeck. *In press.* Influence of landscape on population genetic structure of the alpine butterfly *Parnassius smintheus* (Papilionidae). Molecular Ecology 83.

Kinoshita, M., N. Shimada, and K. Arikawa. 1999. Colour vision of the foraging swallowtail butterfly *Papilio xuthus*. The Journal of Experimental Biology 202: 95 - 102.

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

Levene, H. 1960. Robust tests for equality of variance. Pages 278-292 *in* I. Olkin, editor. Contributions to Probability and Statistics. Stanford University Press, Palo Alto, California, USA.

Mappes, J. and A. Kaitala. 1995. Host-plant selection and predation risk for offspring of the parent bug. Ecology 76:2668-2670.

McCorkle, D.V. and P.C. Hammond. 1985. Observations on the biology of *Parnassius clodius* (Papilionidae) in the Pacific Northwest. Journal of the Lepidopterists' Society 39:156-162.

Meglécz, E, K. 1998. Population structure and variability of *Parnassius mnemosyne* (L.)(Lepidoptera) populations in the Carpathian Basin. PhD Thesis. Department of Evolutionary Zoology and Humanbiology, Kossuth Lajos University, Debrecen.

Meglécz, E, K. Pecsenye, L. Peregovits and Z. Varga. 1997. Effects of population size

and habitat fragmentation on the genetic variability of *Parnassius mnemosyne* in NE Hungary. Acta Zoologica Academiae Scientiarum Hungaricae 43:183-190.

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

Moss, E.H. 1994. The Flora of Alberta, *second edition*. Revised by J.G. Packer. University of Toronto Press, Toronto, Ontario, Canada.

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

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

Nieminen, M. 1996. Migration of moth species in a network of small islands. Oecologia 108:643-651.

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

Renwick, J. and F. Chew. 1994. Oviposition behaviour in Lepidoptera. Annual Review of Entomology 39:377-400.

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

Root, R.B. and M. Kareiva. 1984. The search for resources by cabbage butterflies (*Pieris*

rapae): ecological significance of Markovian movements in a patchy environment. Ecology 65:147-165.

Ruckelshaus, M., C. Hartway, and P. Kareiva. 1997. Assessing the data requirements of spatially explicit dispersal models. Conservation Biology 11:1298-1306.

Sánchez-Rodríguez, J.F. and A. Baz. 1996. Decline of *Parnassius apollo* in the Sierra de Guadarrama, Central Spain (Lepidoptera: Papilionidae). Holarctic Lepidoptera 3:31-36.

Schultz, Cheryl. 1998. Dispersal behavior and its implications for reserve design in a rare Oregon butterfly. Conservation Biology 12: 284-292.

Scott, J.A. 1986. The butterflies of North America: a natural history and field guide. Stanford University Press, Stanton, California, USA.

Singer, M.C. 1984. Butterfly-hostplant relationships: host quality, adult choice, and larval success. Pages 82-88 *in* R. Vane-Wright and P.R. Ackery, editors. The Biology of Butterflies. Academic Press, New York, USA.

Sokal, R.R. and F.J. Rohlf. 1998. Biometry, third edition. W.H. Freeman and Company. New York, USA.

Sperling, F.A.J. and N.G. Kondla. 1991. Alberta swallowtails and parnassians: natural history, keys, and distribution. Blue Jay 49:183-192.

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

Stanton, M.L. 1984. Short-term learning and the searching accuracy of egg-laying butterflies. Ecology 32:33-40.

Thomas, C. and M. Singer. 1987. Variation in host preference affects movement patterns within a butterfly population. Ecology 68:1262-1267.

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

Thompson, J.N. and O. Pellmyr. 1991. Evolution of oviposition behaviour and host preference in Lepidoptera. Annual Review of Entomology 36:65-89.

Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates Incorporated, Sunderland, Massachusetts, USA.

Wiklund, C. 1975. The evolutionary relationship between adult oviposition preferences and larval host plant range in *Papilio machaon*. Oecologia 18:185-197.

Wiklund, C. 1984. Egg-laying patterns in butterflies in relation to their phenology and the visual apparency and abundance of their host plants. Oecologia 63:23-29.

Zar, J.H. 1996. Biostatistical Analysis, *third edition*. Prentice Hall, Upper Saddle, New Jersey, USA.

Chapter 3

PARNASSIUS SMINTHEUS LARVAE CAN MITIGATE OVIPOSITION "ERRORS" OF ADULT FEMALES

"The tiny world of the larva, a single plant or even a single leaf, contrasts with the world

of the adult, which may be several hectares (or acres) to several kilometres squared in

extent, or even larger," (Scott 1986).

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INTRODUCTION

Most butterflies have phytophagous larvae which specialize on one or a few closely related species of plant (Ehrlich and Raven 1964, Chew 1975, Singer 1984). Larval survival, therefore, depends on their establishment on a suitable host plant. Larvae of the alpine butterfly *Parnassius smintheus* are monophagous, feeding solely on lance-leaved stonecrop, *Sedum lanceolatum* Torr. (Crassulaceae), over much of their range, including Alberta (Fisher 1981, Scott 1986, Sperling and Kondla 1991). *Parnassius* sp. larvae not only obtain nutrients from *Sedum* sp. plants, they also sequester the cyanoglycoside, sarmentosin, into their tissues (Nishida 1995). This bitter compound has been found in eggs and adult butterflies of *P. phoebus* and *P. apollo* and is believed to play a role in predator defence (Nishida 1995). Although females of some Lepidopteran species facilitate larval search for host plants by preferentially alighting on and selectively ovipositing on suitable host plants (Haribal and Renwick 1998), *P. smintheus* females do not oviposit directly on the host plant (Chapter 2). These "errors" in oviposition site selection by *P. smintheus* females mean that newly-hatched larvae must move to find a suitable host plant. It is generally thought that Lepidopteran larvae have little ability to locate larval host plants in the early stages (Singer 1984, Mayhew 1997). Factors influencing *P. smintheus* larval search success may, therefore, have important implications for habitat suitability and habitat quality.

Successful establishment of *P. smintheus* larvae on *S. lanceolatum* depends on factors

internal and external to the larvae. Internal factors which contribute to larval search

success are larval mobility and larval search ability. For many species little is known of

these internal factors (Dethier 1959). Due to their small size and mode of locomotion

Lepidopteran larvae are limited to the area within tens of metres of their hatching site,

except species that "balloon". Search ability refers to the ability of individuals to detect

and orientate to the host plant according to physical cues (tactile and visual) or chemical

cues (olfactory and gustatory) associated with the host plant (Bell 1991). Tactile setae

physically allow them to perceive the substrate and surrounding environment and are

distributed on larval antennae, mouth, head and body (Scott 1986). Chemical receptors

for smell and taste are located on larval antennae, mouth parts, head surface, legs, last

prolegs and body (Scott 1986). Research of Lepidopteran vision has demonstrated that it

is difficult to quantify its role in host plant search. It is known that larval eyes, consisting

of two sets of six lateral ocelli (or stemmata) lying on either side of the head, can

distinguish UV and colour (Weiss *et al.* 1944, Ishikawa 1969, Saxena and Goyal 1978).

Lateral ocelli are all structurally similar but may vary within individuals, between

individuals of the same species, and between species (Dethier 1942, Singleton-Smith and

Philogène 1981). It was originally believed that Lepidopteran eyes could not function at

distances greater than a few centimetres (Dethier 1959). This belief is supported by

findings that *Pieris* species larvae are unable to locate food plants more than a few

centimetres away (Chew 1974). Research on gypsy moth (*Lymantria dispar*) larvae

however, has found that individuals can detect forms from 50 cm away and can likely

detect crude shapes up to a distance of three metres (see discussion in Roden *et al.* 1992).

Despite the broad distribution of *P. smintheus* in North America little is known about the

natural history of its larvae; prior to this study no behavioural studies had been conducted

and only three larval instars had even been described (Edwards 1885).

Success of larval search, although dependent on both mobility and search ability, is

complicated by external factors which affect the accessibility or availability of the host

plant to the larvae. External factors which influence the accessibility of the host plant to

the larvae include host plant abundance, distribution, apparency relative to the

surrounding plant community, chemical composition, and the location of the host plant

relative to the hatching site (Dethier 1959, Cain *et al.* 1981, McNeill and Southwood

1978, Slansky 1992). In Chapter 4 the abundance and spatial distribution of the host plant

were studied in Jumpingpound Ridge meadows and related to populations of *P.*

smintheus. It was discovered that the abundance of *S. lanceolatum* is positively correlated

with *P. smintheus* populations, but that the spatial patterning of *S. lanceolatum* does not

vary among meadows. The spatial patterning of feeding damage suggests that larval

feeding is distributed randomly among available *S. lanceolatum* plants (Chapter 4). This

chapter attempts to assess more directly whether larval search and feeding behaviours

exhibited in a laboratory setting are random, or if larvae are attracted to the host plant.

The present study furthers our knowledge of *P. smintheus* natural history and examines

the ability of monophagous larvae to move and to orientate to their host plant. Quantifying

larval mobility and search behaviour may improve our understanding of the habitat

requirements of *P. smintheus* by explaining why suitable meadows support different

population sizes and densities of adult *P. smintheus* on Jumpingpound Ridge, Kananaskis

Country, Alberta (Roland *et al. in press*).

OBJECTIVES

1. To find larval *P. smintheus* in the field, to identify their food plants, to learn more

about their natural history and to determine the number of larval instars.

2. To determine how far naive, first-instar *P. smintheus* are capable of moving to their

host plant in a simple, two-dimensional environment.

3. To assess whether experienced, late-instar *P. smintheus* movement is directional

towards the larval food plant.

METHODS

Study Site, Field Observations and Larval Collections

Larval surveys were conducted in the foothills of the Canadian Rocky Mountains on

Jumpingpound Ridge, Kananaskis Country, Alberta (Fig. 3-1). Jumpingpound Ridge is a

chain of nineteen subalpine meadows separated from each other by intervening forests of

lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*) and subalpine fir
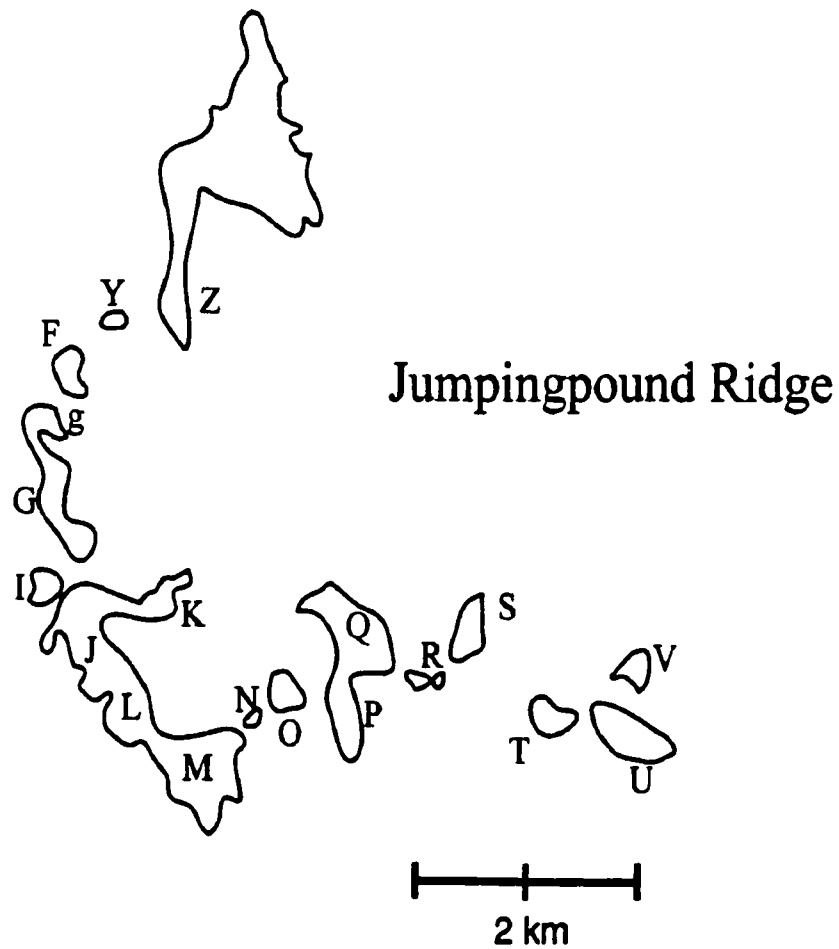
Fig. 3-1. Meadows on Jumpingpound Ridge (50 °57'N, 114°55' W). Meadows above treeline have each been assigned a letter and are separated from one another by different distances through forest.

(*Abies lasiocarpa*). The vegetation of the meadows is dominated by white mountain avens (*Dryas octopetala* ssp. *hookeriana*), grasses, sedges and other wildflowers, and all contain the larval host plant *S. lanceolatum*. During June and July of 1998, meadows on Jumpingpound Ridge were searched for larvae of *P. smintheus*. Larvae were followed and their locations and behaviours were recorded. The substrates and food plants were identified and the parts of the plants consumed were noted. Larvae were collected in the field and brought to the University of Calgary Kananaskis Field Station at Barrier Lake for laboratory experiments on late-instar larvae. Larvae were maintained at room temperature (~19°C) and fed *S. lanceolatum* collected in the Jumpingpound Ridge meadows.

Laboratory Rearing of Larvae

Eggs were collected from mated females in August, 1998, and were kept in a fridge at 4°C until the third week of April 1999, at which time they were placed at room temperature (~19°C) in a petri plate with moist filter paper. During the following week, twenty-two larvae hatched from over forty eggs. These larvae were placed into individual 50 mL SOLO® cups, with a piece of paper for protection from the light and were moved to a growth chamber(16h:8h light:dark regime). Containers were changed regularly to avoid fungal growth and were checked daily for mortality and moultings. Larvae were initially fed a greenhouse species of *Sedum*, *S. sexangulare* (six-sided stonecrop) and later, following a collection of their host plant, *S. lanceolatum*, from Prairie Mountain, Kananaskis Country, Alberta (50°57'N, 114°55'W) on May 9, 1999, they were offered a

choice of either *S. sexangulare* or *S. lanceolatum*.

First-Instar Mobility Study

Eighteen, first-instar larvae were studied within 24 hours of hatching, prior to exposure to

S. lanceolatum. Individuals were released onto a sheet of paper, left to habituate to the

paper for five minutes, and then their locations were recorded over a 5 minute period at

ten-second intervals. Locations were later converted into Cartesian coordinates. Step

lengths were considered the distance moved in a ten second interval and turning angles,

the change in direction, in degrees, between steps. To estimate potential displacement of

newly hatched larvae from the egg-laying site, the following movement behaviours were

summarized: the total distance moved in five minutes, the net displacement from the

beginning of the study period until the end of the study period, the speed when moving

and the turning direction.

Late-Instar Search Ability

Larvae collected in the field in the summer of 1998 were released at distances of 1 cm, 2

cm, 4 cm, 8 cm, 16 cm and 32 cm from a host plant, consisting of a rosette and an

inflorescence. Experiments were conducted in a clear Rubbermaid® container (24 cm by

36cm, and 13 cm deep) lined with coarse soil (1 cm deep) collected in Jumpingpound

Ridge meadows to provide larvae a more natural substrate for crawling (Fig. 3-2). Larvae

were not fed for twenty-four hours prior to experimentation.

Larval paths were transferred directly onto a sheet of paper with a grid 0.5 the scale of the observation arena. Time intervals were recorded at locations along the path where individuals changed direction or behaviour. Each of these locations was assigned a Cartesian coordinate to be used later in movement analysis. Behaviour of late instar larvae included: 1) crawling — larva moving forward and entire body in contact with the substrate; 2) stationary — larva not moving and entire body in contact with the substrate; and 3) head wave — larvae is stationary and the posterior portion of the larva remains in contact with the substrate and the anterior portion is raised above the substrate (at approximately 40 degrees above the substrate) and is moved left or right, or both, before the anterior portion is lowered to the substrate (Fig. 3-3). The time for its head to contact the host plant was also recorded.

I tested whether distance to the host plant affected the probability of larval search success using a logistic regression. The efficiency of larvae to locate host plants at increasing distances was also estimated. Two measures of search efficiency were calculated at each release distance: (a) distance efficiency: the total distance moved by larvae prior to locating and contacting *S. lanceolatum* divided by the straight line distance from the release point to the host plant. Values of 1 would be perfect efficiency, with greater values indicating less efficiency; and (b) time efficiency: the total time between release to locating and contacting *S. lanceolatum* was divided by release distance. Again, larger values indicate poor search efficiency and smaller values greater search efficiency. Search

larval path

release distance

36 cm

24 cm
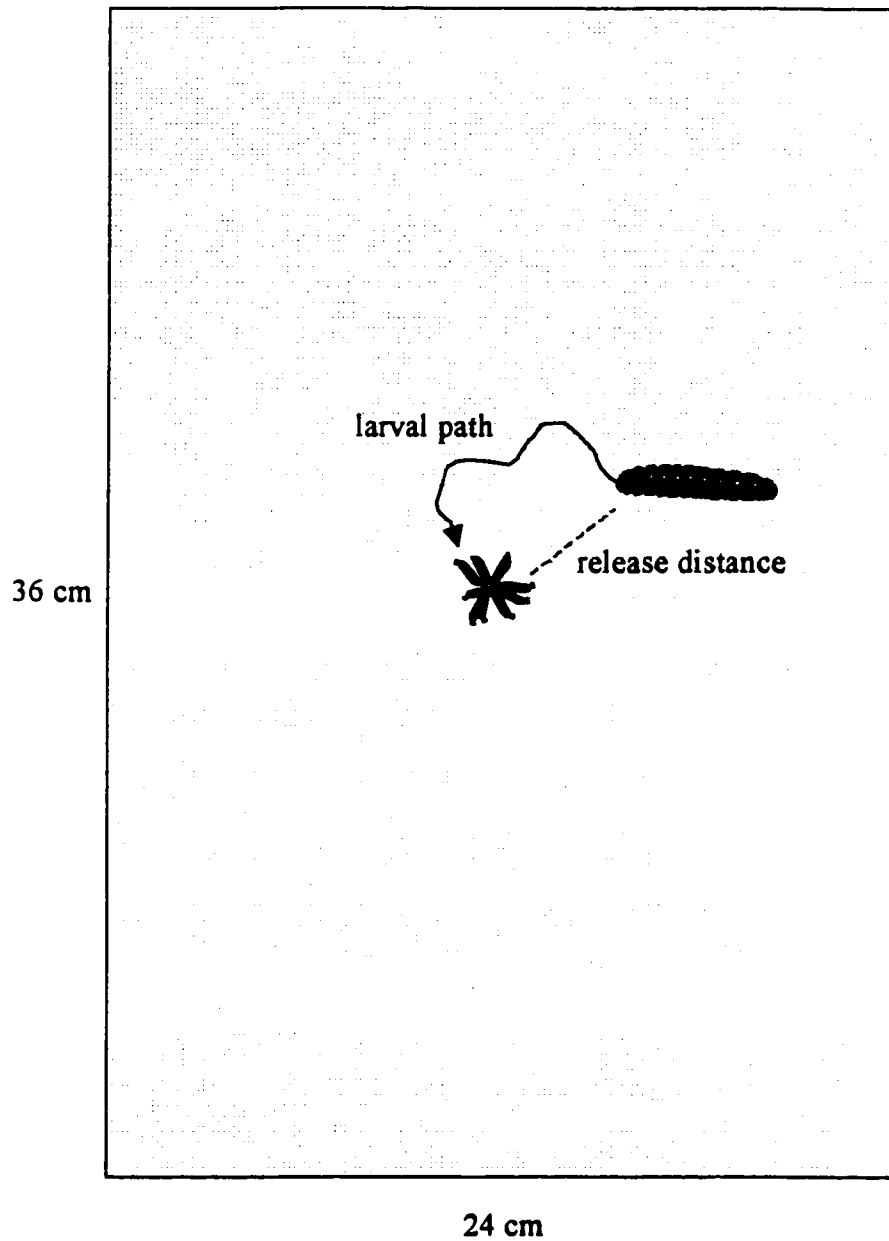
Fig. 3-2. Experimental set-up for late-instar larval search ability experiments. The container was lined with coarse soil, 1 cm deep. The solid line represents the larval search path tracing and the dotted line represents the release distance. Larvae were released at 1, 2, 4, 8, 16 and 32 cm from the host plant, *Sedum lanceolatum*.
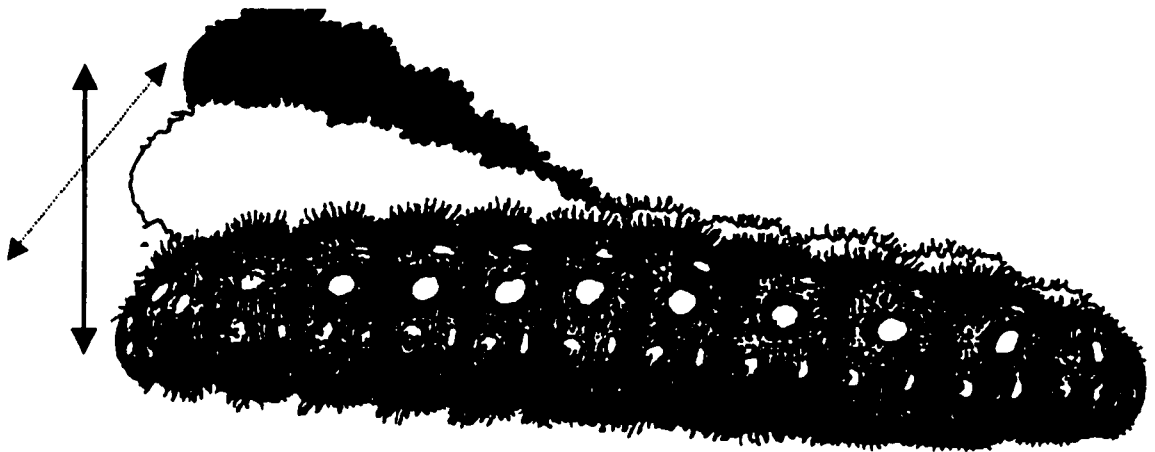
Fig. 3-3. Head-wave behaviour exhibited by late-instar *P. smintheus* larvae. The head and first few segments of the larval body are raised above the substrate moved right or left, or both, and then lowered back down to the substrate. Original black and white sketch of *P. smintheus* larvae is from Bird *et al.* (1995).

efficiencies were plotted against release distance to visually assess if the efficiency of larval search varied with release distance.

I also tested for the directionality of the initial moves of individual larvae. The deviation of the first and second turn angles from the straight line to the host plant were calculated for each individual tested. The mean and median deviation angles for the first and second move of larvae at each distance were calculated (Zar 1996; pages 428-429). For both moves at each distance, a parametric one-sample test for the mean angle and a non-parametric test for the median angle were conducted (Zar 1996; pages 445-446); the null hypotheses were that the mean angle and median angle were not different from zero.

RESULTS

Objective 1: Natural History of *P. smintheus* larvae

Thirty-three late instar larvae (fourth or fifth instars) were located during searches on Jumpingpound Ridge. They were found on a variety of substrates including: *S. lanceolatum*, dead grass, lichens, moss, leaf litter, and soil under rocks. Field observations of larval feeding suggest that larvae consume only the innermost leaves of *S. lanceolatum* infertile and fertile rosettes; they were not observed feeding on any other plant species. One individual placed its mouthparts around a basal leaf of a Saxifrage plant (*Saxifraga bronchialis*) and but did not make any noticeable feeding marks on the leaf.

Larvae were most active during short sunny spells and generally inactive during extended periods of bright sunshine or cloud cover and precipitation events. During a hail storm larvae moved away from their marked locations and could not be relocated. Larvae moved up to 34 cm in any one move and one individual crawled more than 40 cm to reach a *S. lanceolatum* plant for feeding. Some larvae passed over, or near *S. lanceolatum* plants and did not necessarily move to the closest plant to resume feeding.

Five larval instars were identified from laboratory rearing of larvae (Fig. 3-4). In their first instar larvae are entirely black and have abundant setae distributed over their body. In the second instar larvae develop yellow spots which are present in the remaining three instars.

Objective 2: First-Instar Larval Mobility

Out of the 18 larvae tested, thirteen moved during the trials. The summary of movement behaviours for "moving" individuals in the absence of the host plant is provided in Table 3-1. Non-parametric one-sample tests for the median turn angle reveal that only three caterpillars of 13 had a preferred turn direction in the absence of the host plant (Fig. 3-5).
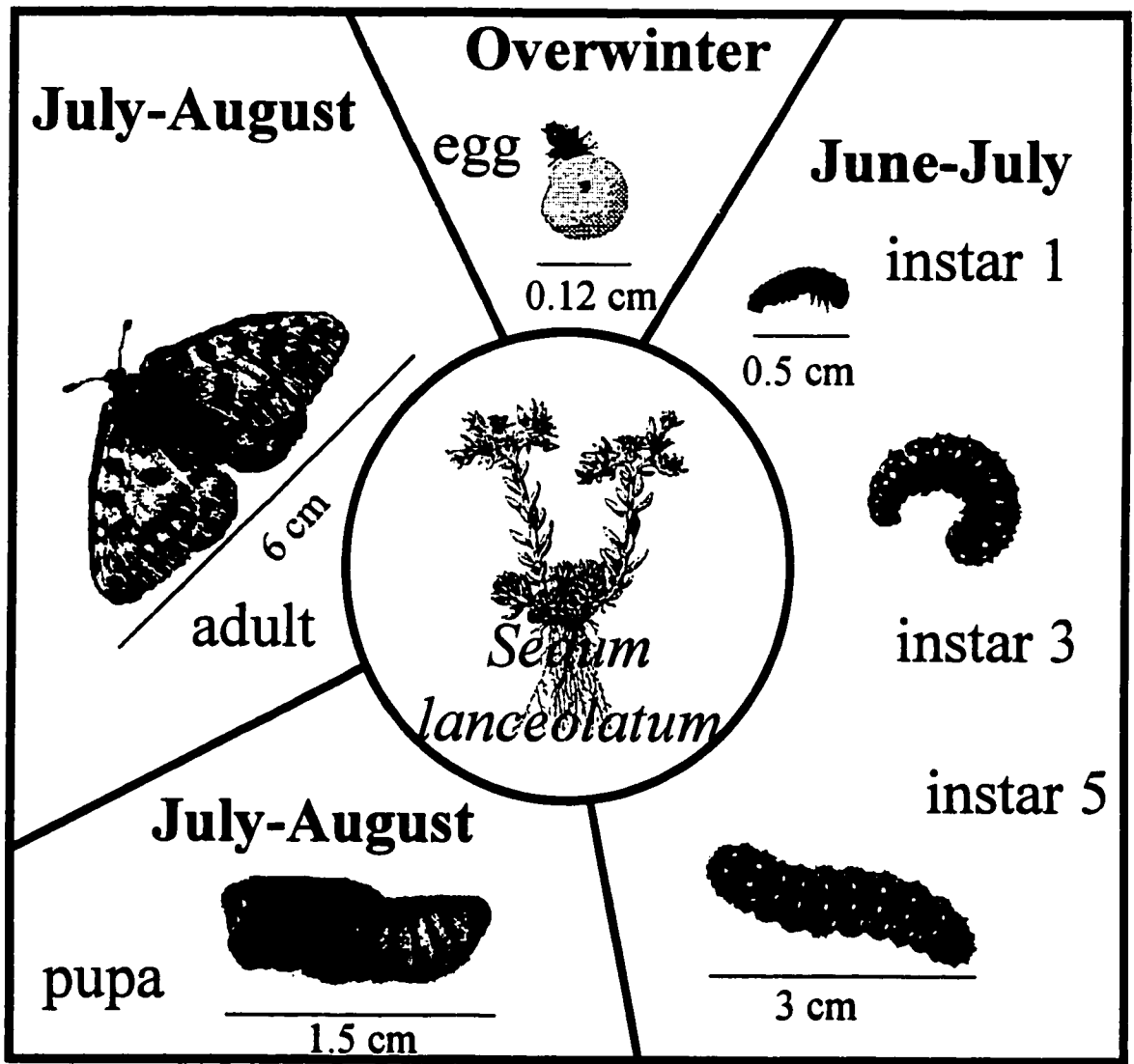
Fig. 3-4. Schematic life-cycle and phenology of *Parnassius smintheus* on Jumpingpound Ridge. The drawing of the larval host plant, *Sedum lanceolatum*, is taken from Clausen (1975).

Table 3-1. Movement behaviour of 13 first-instar larvae of *P. smintheus* in a two-dimensional environment. The range and median value of 10 second intervals, in a five-minute study period, during which larvae were moving, the total distance traveled (cm) during the study period, the net displacement (cm) during the study period, and the speed of movement (cm/sec).

Behaviour	Range	Median
number of intervals moved	4 to 25	10
total distance moved (cm)	1.7 to 19.3	5.1
net displacement (cm)	1.2 to 8.7	1.2
speed of movement (cm/sec)	0.034 to 0.092	0.052
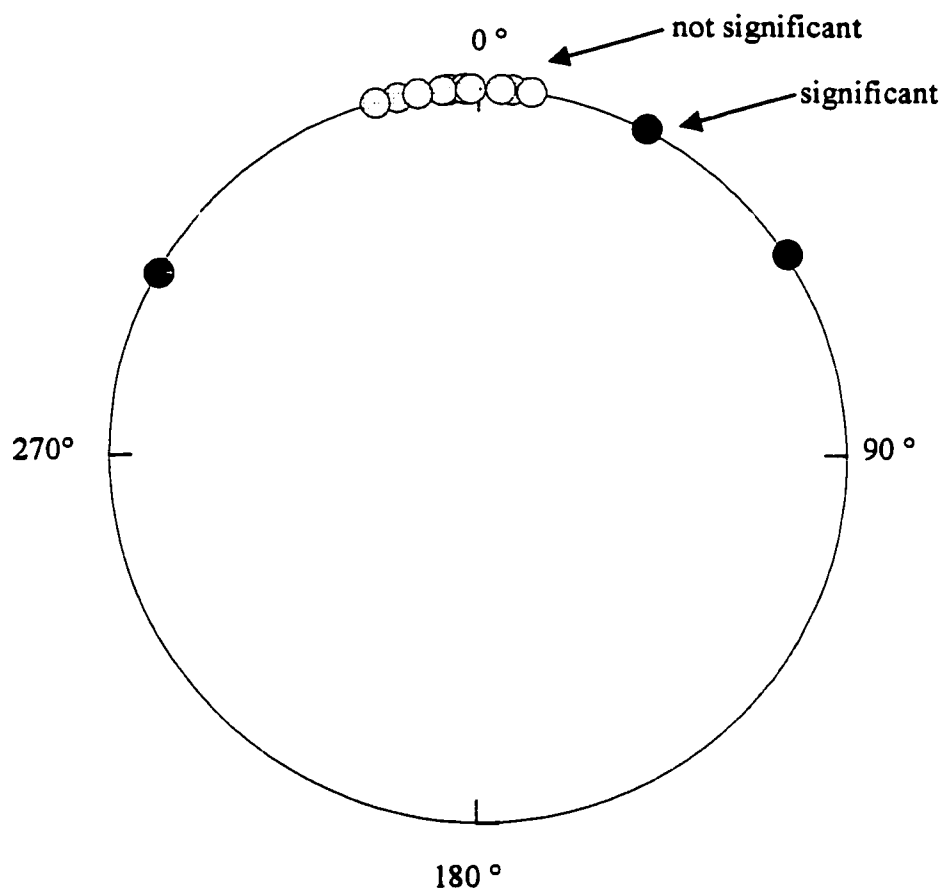
Fig. 3-5. Median turn angles (degrees) summarize turning behaviour of individual first-instar larvae. The solid and open circles represent median turn angles which do differ significantly from zero (p<0.05) and median turn angles which do not differ significantly from zero, respectively.

Objective 3: Late Instar Larval Search Ability

Locating the host plant, *S. lanceolatum*

Individual larvae that intercepted the wall of the enclosure while moving were removed from the following analyses because the enclosure walls may have redirected individuals towards the host plant. Encounter rate with the wall increased with release distance and was greatest for the 32 cm release distance; therefore, releases at 32 cm were removed from analyses. Late-instar larvae placed at different distances from the larval host plant were equally successful at eventually locating the larval host plant (Fig. 3-6), within the arenas provided (distance coefficient=0.047, change in residual deviance=0.503, p=0.48). Removing individuals that hit the wall of the enclosure during search did not affect the outcome of the logistic regression analysis. Both distance efficiency and search efficiency indicate that larvae are more efficient at contacting *S. lanceolatum* plants at greater release distances (Fig. 3-7).

Larval attraction to the host plant, *S. lanceolatum*

The median turn angles of larvae for the first and second move did not differ significantly from zero (p<0.05), which is directly towards the host plant; median turn angles indicate that larval movements were biased towards the host plant at all release distances for the first and second move (Fig. 3- 8 and Fig. 3- 9).
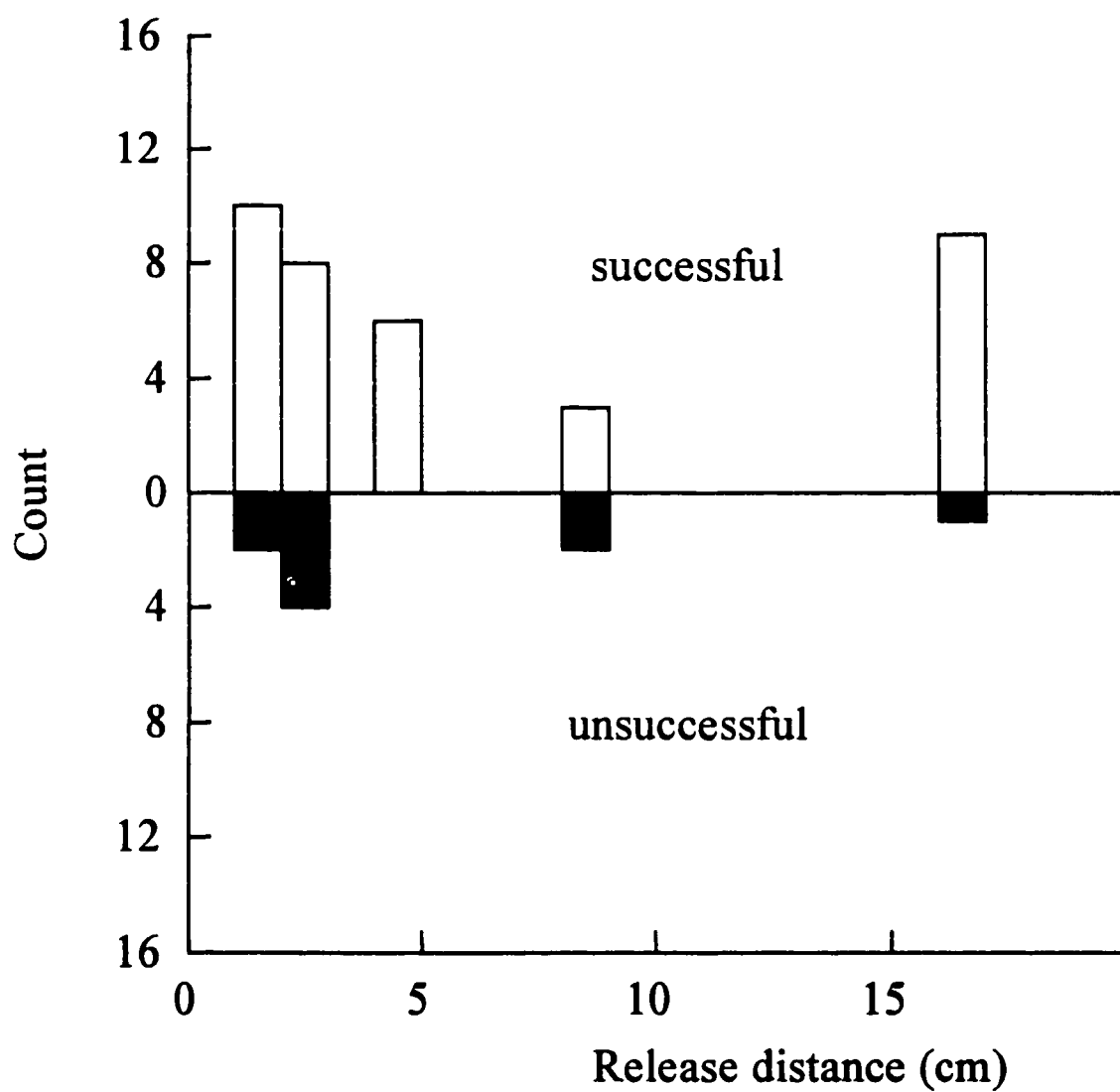
Fig. 3-6. The results of individual late-instar larval searches. Larvae were released at 1, 2, 4, 8 and 16 cm from the host plant. There was no significant effect of release distance on search outcome (p=0.48).
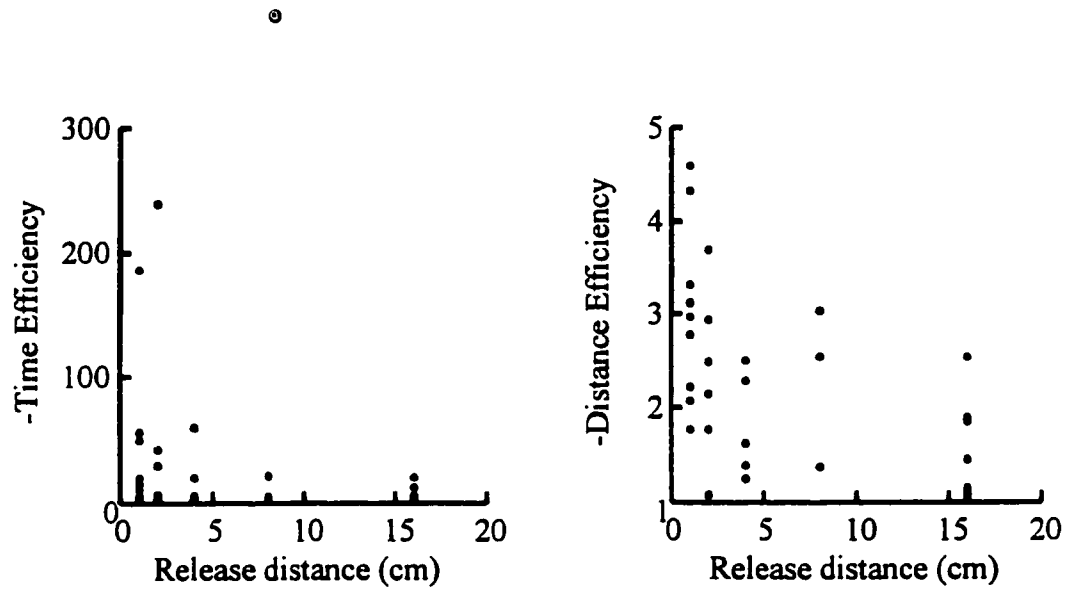
Fig. 3-7. The negative time and distance efficiencies of larval search behaviour released at different distances (cm) from the host plant. Larger values indicate poor search efficiency and smaller values, good search efficiency.
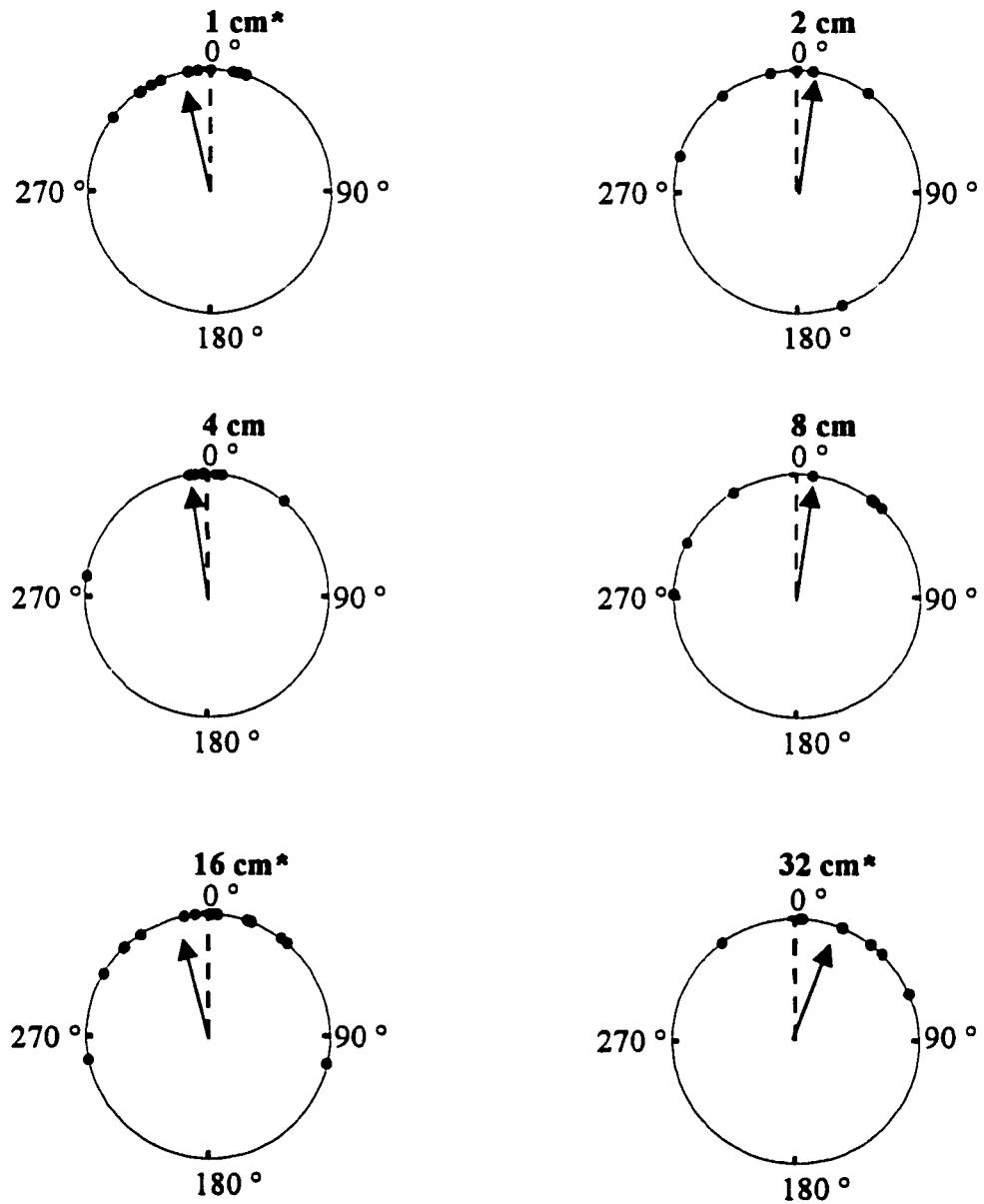
Fig. 3-8. The direction of the first move of all larvae relative to the host plant (solid circles). The median angle of larval directionality is indicated by the arrow for each release distance (1, 2, 4, 8, 16 and 32 cm). The dashed line represents the straight line between the release site and the host plant, and * indicates significant departure from straight line direction to the host plant, p<0.05.
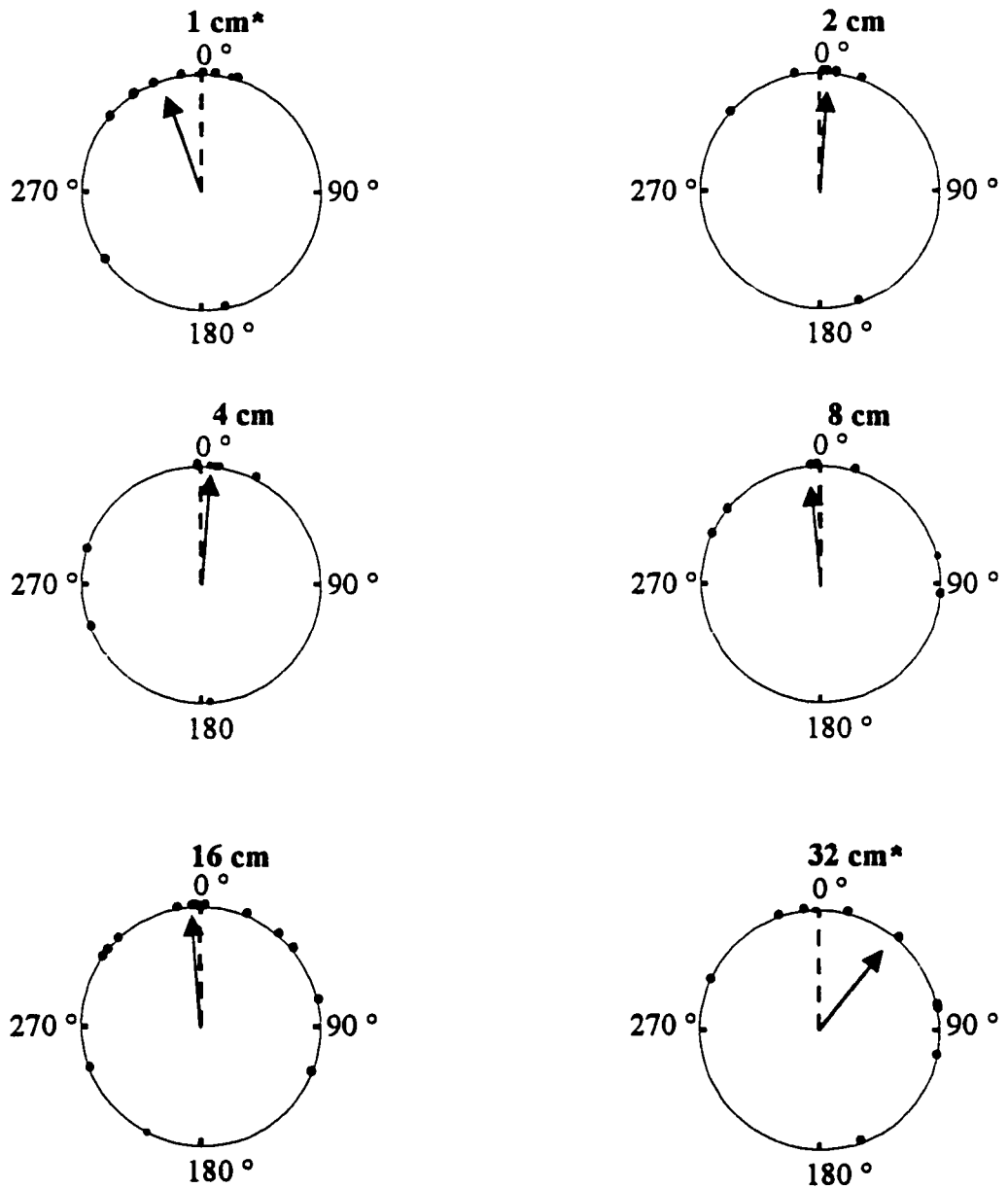
Fig. 3-9. The direction of the second move of all larvae relative to the location of the host plant (solid circles). The median angle of larval directionality is indicated by the arrow for each release distance (1, 2, 4, 8, 16 and 32 cm). The dashed line represents the straight line between the end of the first move and the host plant, and * indicates significant departure from straight line direction to the host plant, p<0.05.

DISCUSSION

Field observations of late-instar *Parnassius smintheus* larvae support earlier naturalist

accounts that they are monophagous, feeding on *S. lanceolatum* (Sperling and Kondla

1991). It is important to note, however, that no early-instar *P. smintheus* larvae were

found in the field presumably because of their small size and cryptic colouration. Cain *et*

al. (1985) reported that younger larvae of *Pieris rapae* have a harder time locating host

plants than do late-instar larvae. The relative immobility of the early-instar *P. smintheus*

larvae likely renders them the most vulnerable to starvation; therefore, knowledge of

feeding plasticity or alternative host plants at this life-cycle stage would improve our

understanding of the habitat requirements of *P. smintheus*. The mobility of late-instar

larvae was suprisingly high in the field suggesting that *P. smintheus* larvae are physically

capable of movement to or between host plant patches on Jumpingpound Ridge.

Shelter from the prevailing weather is another requirement of late-instar *P. smintheus*

larvae. The grass and rock shelter-sites identified during field observations will be

considered in the assessment of habitat suitability in Chapter 5. Larval activities of *P.*

smintheus were restricted by the weather; movement and feeding occurred mainly in cool

air, in sunny conditions. A similar pattern was also seen for *P. apollo* (Deschamps-Cottin

et al. 1997). The fact that some larvae passed directly over or in close proximity to *S.*

lanceolatum without establishing on the plant suggests that larval search abilities may be

impaired or complicated by other features of their environment. Larvae of the nymphalid

butterfly *Melitaea harrisii* have also been observed travelling within millimetres of host

plants (*Aster umbellatus*) without establishing on them (Dethier 1959). Similarly, *Pieris*

rapae larvae detect their host plant, *Brassica oleceracea*, only after physically contacting

the plant (Cain *et al.* 1985).

Larvae of *P. smintheus* reared in the laboratory had a total of five instars. Lab-reared *P.*

apollo also has five instars (Moser and Oertli 1980). Despite high levels of activity within

24 hours of hatching in the laboratory, there was substantial first-instar mortality and many

larvae would not consume the alternative host plant (*S. sexangulare*) offered to them. It is

possible that the alternative host plant did not induce feeding in many of the larvae because

it was unacceptable as a food plant. Edwards (1885) also found that laboratory reared

early-instar caterpillars of *P. smintheus* consumed wild *Sedum* (species unknown) but did

not accept cultivated *Sedum* species. Larvae which survived to their second instar all

survived to adulthood. First-instar larvae partly consumed *S. sexangulare* and *S.*

lanceolatum leaves, a fact also observed by Edwards (1885). In later instars, larval feeding

damage on *S. lanceolatum* rosettes was restricted to the internal leaves of the rosette,

which were entirely consumed. In *P. apollo* feeding occurs mainly in the area of the apical

buds of rosettes, where leaves are youngest (Deschamps-Cottin *et al.* 1997). Many

factors, including plant age (Slansky 1992) and season (McNeill and Southwood 1978,

Moser and Oertli 1980), cause tissues of host plants to vary in quality for insect herbivores.

It is possible that the young leaves of *Sedum* sp. offer the greatest nutrient reward to

Parnassius sp. larvae or that they have less chemical defenses. It is known that leaves and

flowers of *S. lanceolatum* have the highest energy content per gram of its plant tissue (Jolls

1984). Feeding damage noted in the lab and in the field was isolated to a very small

portion of the plant which suggests that larval *P. smintheus* must migrate frequently

between plants to complete development.

All mobile, first-instar larvae moved from their initial position during the five-minute study

period but only three out of fifteen exhibited a directional preference (Fig. 3-5). The

displacements observed suggest that larvae will move away from their hatching site.

Although no strong environmental effects were present in the laboratory setting, field

observations suggest that late-instar movement is restricted to sunny conditions. This

requirement for sunlight is expected because (ectothermic) caterpillars depend on the

external environment to control their body temperature (Casey 1992). I combined the

findings from the first-instar mobility study with the hours of bright sunshine data for the

Kananasksis collected at the University of Calgary Kananaskis Field Station at Barrier Lake

(51°02'N, 115°03'W, approximately 10 km northwest of Jumpingpound Ridge) for June

(the month of peak larval activity), to predict the distance traveled by individuals within the

first 24 hours following hatch. From 1990 until 1998, the hours of bright sunshine per day

in the month of June ranged between 0 and 14.1 and averaged between 4.4 and 7.7 per day.

First-instar larvae would move on average 2.55 m to 4.77 m and at most 32.6 m within 24

hours after hatching. Many unfed first-instar Lepidopteran caterpillars, including *P.*

smintheus (personal observation) can move for more than one day without food (Reavey

1992). These distances therefore can be considered conservative mobility estimates. When

applying laboratory observations to a field setting, the difference in complexity of the two

environments should be considered. Larval observations in the laboratory were conducted

in a simple, two-dimensional study arena. In contrast, larvae hatching in the field

experience a complex three-dimensional environment with abundant physical obstacles,

such as vegetation, predators and parasitoids, and large variation in microclimate. Larvae

also receive sensory information, including chemical, temperature and humidity gradients

that are absent in the laboratory setting (Wellington 1955). Despite these differences it is

clear that first-instar larvae are mobile and may be able to move to a host plant following

hatch and mitigate oviposition "errors" made by adult females.

From experiments described in Chapter 2 and Chapter 4 adult female *P. smintheus* are

known to oviposit at random locations in suitable meadows. The circular plots laid out at

random in the Jumpingpound Ridge meadows, which I used for *S. lanceolatum* mapping

(Chapter 4) thus simulate natural oviposition sites. Habitat suitability for *P. smintheus* may

depend on the particular distribution of *S. lanceolatum* within meadows, combined with the

ability of larvae to move from random oviposition sites to *S. lanceolatum* plants. In each

of the suitable meadows on Jumpingpound Ridge a *S. lanceolatum* plant was within 2.5 m

of at least 73% of randomly chosen locations. It appears that random oviposition in these

meadows would therefore place most first-instar larvae within the mobility range of a host

plant.

Differences in distances at which larvae were released from the host plant (0 to 16 cm) would not be expected to affect larval search success. This finding further demonstrates that random oviposition by adult females may not be as costly as first suspected, given the density of plants in the field. Larval search ability may be either the cause or the effect of the failure of adult females to discriminate between suitable and unsuitable oviposition sites (Chew 1977). In the presence of the host plant, late-instar larvae did not move in random directions. Rather they orientated to the host plant in a laboratory setting suggesting that their use of chemical or visual cues to find host plants. Further experimentation is necessary to identify the precise mechanisms, perhaps head waving, which lead larvae to the host plant. It is important to remember, however, that larval motivation for movement may not always be a search for food resources. Different motivation may also explains why the spatial point pattern of feeding damaged *S. lanceolatum* plants in Chapter 4 appeared random and not aggregated. Release of larvae in manipulated densities of *S. lanceolatum* and in a variety of vegetation complexities in the field may provide more realistic estimates of *P. smintheus* larval search ability than those obtained from laboratory study. It is interesting to note that larvae were more efficient, both in terms of distance traveled and time taken to reach the host plant at greater release distances. Errors associated with measurements of larval movement distances may have hindered abilities to quantify real distance search efficiencies (Fig. 3-7). If, for example, error in measurement of distances

moved is constant, the same error will have a much greater effect on the calculation of

search efficiency at a release distance of 1 cm than at a release distance if 16 cm. The same

is true for the calculations of time efficiencies. More controlled experimentation

specifically addressing search efficiencies may reveal a distance at which larvae are most

efficient at locating host plants. It is apparent from these preliminary studies that *P.*

smintheus larvae are highly mobile and capable of searching for their larval host plant, *S.*

lanceolatum. Both ability and search capability are critical for a species whose females do

not selectively oviposit on suitable host plants (Janz and Nylin 1997).

LITERATURE CITED

Bell, W.J. 1991. Searching behaviour: the behavioural ecology of finding resources.
Chapman and Hall, London, UK.

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

Cain, M.L., J. Eccelston, and P.M. Kareiva. 1985. The influence of food plant dispersion
on caterpillar searching success. Ecological Entomology 10:1-7.

Casey, T.E. 1992. Effects of temperature on foraging of caterpillars. *in* Caterpillars:
ecological and evolutionary constraints on foraging. N.E. Stamp and T.M. Casey *editors.*
Chapman and Hall, New York, pages 5 to 28.

Chew, F.S. 1974. Strategies of food plant exploitation in a complex of oligophagous
butterflies (Lepidoptera). Ph.D. dissertation. Yale University, New Haven, USA.

Chew, F.S. 1975. Coevolution of pierid butterflies and their cruciferous foodplants.

Oecologia 20:117-127.

Chew, F.S. 1977. Coevolution of pierid butterflies and their cruciferous foodplants. II. The distribution of eggs on potential foodplants. Evolution 31:568-579.

Clausen, R.T. 1975. *Sedum* of North America North of the Mexican Plateau. Cornell University Press, Ithaca, New York, USA.

Deschamps-Cottin, M., M. Roux, and H. Descimon. 1997. Larval foodplant efficiency and laying preferences in *Parnassius apollo* L. (Lepidoptera, Papilionidae). Life Sciences 320:399-406.

Dethier, V.G. 1942. The dioptric apparatus of lateral ocelli I. The corneal lens. Journal of Cellular and Comparative Physiology 19:301-313.

Dethier, V.G. 1959. Food-plant distribution and density and larval dispersal as factors affecting insect populations. The Canadian Entomologist 91: 581-596.

Edwards, W.H. 1885. Description of some of the preparatory stages of *Parnassius smintheus*, Doubl., and of *P. clodius*. The Canadian Entomologist 17:61-65.

Ehrlich, P.R. and P.H. Raven. 1964. Butterflies and plants: a study in coevolution. Evolution 18:586-608.

Fisher, M.S. 1981. Superfamily Papilionidae Latreille, 1809 (Parnassians, Swallowtails). *in* Butterflies of the Rocky Mountain States, C.D. Ferris and F.M. Brown *editors*. University of Oklahoma Press, Norman, Oklahoma, USA. pages 175-193.

Haribal, M. and J.A.A. Renwick. 1998. Differential postalightment oviposition behaviour of monarch butterflies on *Ascelpias* species. Journal of Insect Behavior 11:507-538.

Ishikawa, S. 1969. The spectral sensitivity and the components of the visual system of the stemmata of silkworm larvae, *Bombyx mori*L. (Lepidoptera: Bombycidae). Applied Entomology and Zoology 4:87-99.

Janz, N. and S. Nylin. 1997. The role of female search behaviour in determining host plant range in plant feeding insects: a test of the information processing hypothesis. Proceedings of the Royal Society of London, Series B 264:701-707.

Jolls, C.L. 1984. Contrasting resource allocation patterns in *Sedum lanceolatum* Torr.: biomass versus energy estimates. Oecologia 63:57-62.

Mayhew, P.J. 1997. Adaptive patterns of host-plant selection by phytophagous insects. Oikos 79:417-428.

McNeill, S. and T.R.E. Southwood. 1978. The role of nitrogen in the development of insect/plant relationships. *In* Biochemical aspects of plant and animal co-evolution, J.B. Harbone *editor*. Academic Press, London. pages 77-98.

Moser, H.A. and J.J. Oertli. 1980. Evidence of a biochemical interaction between insect and specific foodplant in the system *Parnassius apollo-Sedum album*. Revue Suisse de Zoologie 87:341-357.

Nishida, R. 1995. Sequestration of plant secondary compounds by butterflies and moths. Chemoecology 4:127-138.

Reavey, D. 1992. Egg size, first instar behaviour and the ecology of Lepidoptera. Journal of Zoology, London 227:277-297.

Roden, D.B., J.R. Miller and G.A. Simmons. 1992. Visual stimuli influencing orientation by larval gypsy moth, *Lymantria dispar* (L.). The Canadian Entomologist 124:287-304.

Roland, J., N. Keyghobadi, and S. Fownes. *In press*. Alpine *Parnassius* butterfly dispersal:

effects of landscape and population size. Ecology.

Saxena, K.N. and S. Goyal. 1978. Orientation of *Papilio demoleus* larvae to coloured solutions. Experientia 34:35-36.

Scott, J.A. 1986. The butterflies of North America: a natural history and field guide. Stanford University Press, Stanton, California, USA.

Singer, M.C. 1984. Butterfly-hostplant relationships: host quality, adult choice and larval success. *In*: The Biology of Butterflies: Symposium of the Royal Entomological Society of London, Series 11. R.I. Vane-Wright and P.R. Ackery *editors*. Academic Press Inc., London, UK. pages 81-90.

Singleton-Smith, J. and B.J.R. Philogène. 1981. Structure and organization of the stemmata in the larvae of five species of Lepidoptera. 40:331-341.

Slansky, F. 1992. Nutritional ecology: the fundamental quest for nutrients. *in* Caterpillars: ecological and evolutionary constraints on foraging. N.E. Stamp and T.M. Casey *editors*. Chapman and Hall, New York, USA. pages 29 to 91.

Sperling, F.A.J. and N.G. Kondla. 1991. Alberta swallowtails and parnassians: natural history, keys, and distribution. Blue Jay 49:183-192.

Weiss, H., E.E. McCoy, and W.M. Boyd. 1944. Group motor responses of adult and larval forms of insects to different wave-lengths of light. New York Entomological Society Journal 52: 27-44.

Wellington, W.G. 1955. Solar heat and plane polarized light versus the light compass reaction in the orientation of insects on the ground. Annals of the Entomological Society of America 48:67-76.

Zar, J.H. 1996. Biostatistical Analysis, *third edition*. Prentice Hall, Upper Saddle, New

Jersey, USA.

Chapter 4

PARNASSIUS SMINTHEUS ADULT FEMALE AND LARVAL BEHAVIOUR IN RESPONSE TO HOST PLANT ABUNDANCE AND SPATIAL PATTERN

"As the population of (food plants) in a given field increases, the number of larvae which will complete their development increases not because of the greater absolute food supply but because plants grow closer together," (Dethier 1959).

INTRODUCTION

Butterfly population size and distribution are constrained by the availability of suitable

habitat. A suitable habitat contains all the resources required for the survival of a

population for many years (Hanski and Thomas 1994), and may not be continuous over the

spatial extent of a population, existing instead as fragments or patches. Long-term

persistence of butterfly populations depends both on the maintenance of patches of suitable

habitat and their sustained quality (Thomas *et al.* 1992, Hanski and Thomas 1994, Dennis

and Eales 1997 and 1999, Eales and Dennis 1998 Mousson *et al.* 1999). Habitat quality, in

the context of butterflies, has traditionally been equated with the abundance of adult nectar

plants and/or larval food plants. Defining habitat suitability and quantifying habitat quality

are essential steps in the process of understanding the population dynamics of butterfly

species, and are needed to predict how changes to habitat may affect populations (Hanski

1991, Hanski *et al.* 1996, Kuussaari *et al.* 1996).

Butterflies are short lived and all life stages have explicit resource requirements. Many

butterfly larvae feed on specific host plants, and as a result have more specialized resource

requirements than do other life stages (Dempster 1983). Adult butterflies require access to

mates and nectar resources to provide them with the energy for flight, courtship and

oviposition (Wiklund 1977). In some species adult females assess landing sites for larval

suitability prior to deciding whether to oviposit or not (for detailed reviews of oviposition

site selection see Dempster 1983, Thompson & Pellmyr 1991, and Honda 1995).

Consideration of the resource requirements of both the larvae and the ovipositing females is

necessary to develop a definition of habitat suitability for butterfly species, and is critical for

establishing conservation priorities and goals for rare and threatened butterflies (for

examples of conservation recommendations for threatened butterflies based on habitat use

of adult females and larvae see Schwarzwälder *et al.* 1997 and Bergman 1999). To

simplify butterfly population models, many researchers have censussed habitat patches, and

have categorized patches as either suitable or unsuitable based on presence or absence of

the larval host plant. This type of modelling assumes that all "suitable" habitats are equal,

and overlooks the effects of habitat quality of suitable patches on the long-term persistence

of species (Singer 1972, Thomas *et al.* 1992, Baguette and Nève 1996, Hill *et al.* 1996).

Hanski (1991) called for the inclusion of a habitat quality parameter in metapopulation

models to make them more realistic. In an attempt to include habitat quality in population

models, Kuussaari *et al.* (1996) and Moilanen and Hanski (1998) demonstrated

experimentally and descriptively that at the scale of the habitat patch, habitat quality

(measured as the abundance of flowering nectar plants) determines movement of the

butterfly *Melitaea cinxia* between patches: increased habitat quality decreases emigration

and increases immigration of *M. cinxia*. Several other studies have clearly demonstrated

that resource abundance affects the quality of habitat for butterfly populations (Murphy *et*

al. 1984, Williams 1988, Harrison *et al.* 1988, Odendaal *et al.* 1989, Carey 1994, Kuusaari

et al. 1996, Sutcliffe *et al.* 1997, Bergman 1999). Few studies however, have

acknowledged or tested the potential importance of spatial pattern of a required resource as a component of habitat quality (*e.g.*, see Root and Karieva 1984, Daily *et al.* 1991).

Findings from computer models suggest that the distribution and abundance of a monophagous herbivore species is a product both of the availability and the spatial pattern of its food (Clarke *et al.* 1997 and 1998). Andersen (1992) proposes the use of spatial data analysis to study the effect of plant spacing on herbivore abundance. Determining the spatial pattern of a required resource and establishing whether it is random, or diverges from random to a clumped or clustered spatial pattern or to a more regular or over-dispersed spatial pattern, may be important in defining habitat quality for an organism. A common method for analyzing the spatial point pattern for mapped locations is Ripley's K-function (Ripley 1976; see Appendix B for a detailed explanation of Ripley's K-function). Ripley's K-function is a second-order method which considers the distances between all pairs of points to calculate the spatial point pattern and which estimates the spatial point pattern over a range of distances. It is considered an improvement from first-order methods which only use measurements from points to their nearest-neighbour to calculate spatial point patterns. Ripley's K-function has been used for a variety of plant ecological studies. Haase *et al.* (1997) studied the spatial pattern of shrubs, Larsen and Bliss (1998) studied the spatial pattern of tree seedlings, North and Greenberg (1998) studied the spatial pattern of truffles, and Harrod *et al.* (1999) studied the spatial pattern of ponderosa pine. It has been rarely used in animal ecological studies but Andersen (1992) studied the spatial

interaction between host plants with aphids and ant nests, Burke *et al.* (1998) studied

spatial pattern of turtle nests, and Powers *et al.* (1999) studied the spatial pattern of beetle-

killed trees. In this paper, both the abundance and spatial pattern of a larval host plant, will

be related to population estimates and behaviours of a monophagous butterfly species.

Larvae of the alpine butterfly *Parnassius smintheus* are monophagous, feeding only on

lance-leaved stonecrop, *Sedum lanceolatum* Torr. (Crassulaceae). The distribution of *P.*

smintheus is in effect restricted to areas that contain the larval food plant. For the most

part, the distribution of *P. smintheus* in Alberta is limited to subalpine and alpine meadows

(Sperling and Kondla 1991). During collections for an ongoing genetic study of *P.*

smintheus in the Eastern Slopes of the Canadian Rockies (Keyghobadi *in preparation*) it

was noted that some meadows with the host plant did not have *P. smintheus* populations,

indicating that the presence of the host plant does not necessarily indicate suitable habitat.

Roland *et al.* (*in press*) found that forest impedes movement of *P. smintheus* adults, that

the spatial structure of habitat affects its population dynamics, and that meadows of similar

size can support populations of very different sizes and densities. These facts suggest that

not all suitable meadows are of equal quality for *P. smintheus*. Combined with the degree

of host plant specialization of larval *P. smintheus*, the observed effects of habitat quality on

population size prompted the present study of larval host plant effects on the population

dynamics of *P. smintheus*.

Although female *P. smintheus* do not lay their eggs directly on the larval host plant, *S. lanceolatum* presence does elicit oviposition (Chapter 2). This phenomenon has also been noted in closely related species, *P. apollo* (Deschamps-Cottin *et al.* 1997), *P. clodius* (McCorkle and Hammond 1985), and *P. mnemosyne* (Meglécz 1998). Because females oviposit off the host plant, hatching first-instar larvae must locate and move to a suitable host plant. Quality of meadows therefore, depends both on the ability of ovipositing females and of larvae to orientate to host plants. Successful orientation and establishment on a host plant may be a combination of both *S. lanceolatum* availability and its spatial pattern.

The spatial arrangement of food resources can affect the search success of a herbivore by influencing its encounter rate with that resource (Stanton 1982). Because resources are typically not distributed at random (Stanton 1982) the spatial pattern of the larval host plant may affect butterfly populations through larval and/or adult search success. The effect of the host plant, *S. lanceolatum*, on adult female oviposition behaviour and larval search success was examined. The spatial arrangement and abundance of *S. lanceolatum* was related to oviposition sites and the patterns of larval feeding among available host plants was explored. It was predicted that both *S. lanceolatum* abundance and spatial pattern affect the quality of meadows for *P. smintheus* and influence population size of adult and larval *P. smintheus*.

OBJECTIVES

1. To determine if the abundance of the larval host plant, *S. lanceolatum*, explains differences in population size of *P. smintheus* among meadows on Jumpingpound Ridge, and if *P. smintheus* population size is a surrogate for meadow quality as suggested by Roland *et al. (in press)*.

2. To determine whether or not the spatial pattern of *S. lanceolatum* can explain variation in population size of *P. smintheus* in Jumpingpound Ridge meadows.

3. To determine if larval feeding damage on *S. lanceolatum* is correlated with *S. lanceolatum* abundance and/or spatial pattern and if the spatial pattern of larval feeding damage among available *S. lanceolatum* plants is aggregated, regular, or appears random.

4. To investigate whether or not adult female *P. smintheus* select oviposition sites that should improve the likelihood of larval establishment on a food plant, *S. lanceolatum*, compared to if they had oviposited at random.

METHODS

Study Site

Studies were conducted in the foothills of the Canadian Rocky Mountains on Jumpingpound Ridge, Kananaskis Country, Alberta (Fig. 4-1). Jumpingpound Ridge is a chain of nineteen subalpine meadows separated from each other by intervening forests of lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). The vegetation of the meadows is dominated by white mountain avens
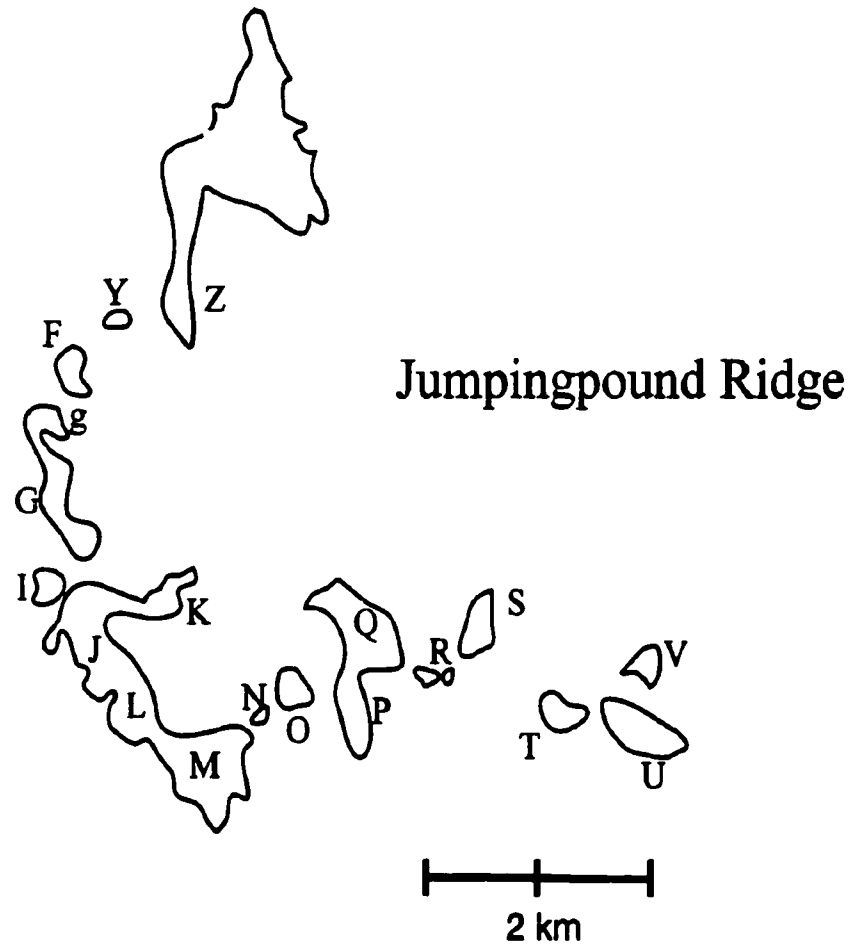
Fig. 4-1. Meadows on Jumpingpound Ridge, Alberta (50 °57'N, 114°55' W). Meadows above treeline have each been assigned a letter and are separated from one another by different distances through forest.

(*Dryas octopetala* ssp. *hookeriana*), grasses, sedges and other wildflowers and all contain

at least some of the larval host plant, *S. lanceolatum*. I subdivided large heterogeneous

meadows defined by Roland *et al.* (*in press*) into **submeadows** based on more

homogeneous plant communities and on differences in aspect (Fig. 4-2).

Parnassius smintheus **Population Indices on Jumpingpound Ridge**

Population indices for adult *Parnassius smintheus* were generated from a mark-recapture

study conducted in the summer of 1995 on Jumpingpound Ridge by Roland *et al.* (*in*

press). For analysis among the submeadows I used the number of marked *P. smintheus* as

an index of population size. For the analysis among the meadows I used Craig's method

for estimating population size (Craig 1953, Southwood 1992, Roland *et al. in press*).

Craig's method takes the number of butterflies that were recaptured once, twice, three

times and so on, and based on an assumed Poisson distribution of capture predicts the

number of butterflies never caught on that day. Summing the number seen and the number

not seen provides an estimate of butterfly population size. "Craig's estimates" for each

meadow represent the average estimate from three mark/recapture events in each meadow

(Roland *et al. in press*). For objectives one through three both submeadow- and meadow-

analyses were conducted, and the relative strength (or slope) of their relationships to *S.

lanceolatum* abundance and spatial pattern are discussed. Identifying the scale at which

resources affect populations is important for understanding population dynamics of a

species. If *P. smintheus* population indices are more correlated with resources at a smaller
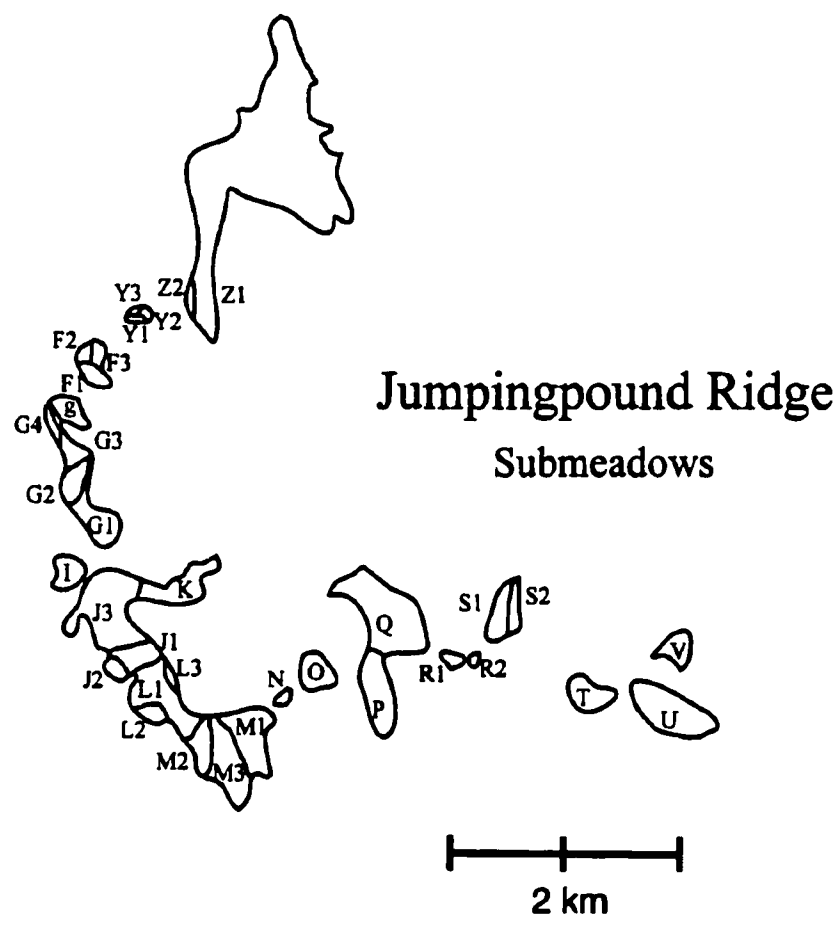
Fig. 4-2. Subdivided meadows on Jumpingpound Ridge. Divisions were determined based on aspect and general plant community.

scale (submeadow) than at a larger scale (meadow), this suggests that the distribution of

resources is heterogeneous within a meadow and that butterflies restrict themselves to only

some areas within meadows; movement within a meadow may be as important as

movement among meadows. Conversely if population indices are more strongly correlated

with resources at the larger scale than at the smaller scale, movement within meadows may

be of trivial importance.

Population indices for larval *P. smintheus* were impossible to attain from standard transect

counts or mark/recapture techniques because larvae are extremely difficult to locate in the

field. Therefore, I used evidence of larval feeding damage on the host plant as a proxy for

P. smintheus larvae.

Sedum lanceolatum mapping

S. lanceolatum is a herbaceous perennial with a broad distribution in Western North

America, occurring mostly in rocky and exposed areas (Clausen 1975). The leaves are

aggregated into rosettes and inflorescences arise from fertile rosettes. *S. lanceolatum* can

reproduce both vegetatively by rosettes and rhizomes, and sexually: it is insect pollinated.

Jolls (1980) demonstrated that *S. lanceolatum* plants invest proportionately more energy

into asexual tissues (rhizomes, leaves and stems) at higher elevations than at lower

elevations. Therefore, in alpine situations ramets may, in fact, be clonal.

Submeadows on Jumpingpound Ridge were visited in the summer of 1998. Ten, five-metre diameter circular plots were randomly placed in each of the submeadows and the locations of all (flowering and non-flowering) *S. lanceolatum* plants within the plot were mapped and assigned Cartesian coordinates (Fig. 4-3). Plants were also assessed for presence or absence of larval feeding damage and assigned a value of 1 or 0, respectively. Although some *S. lanceolatum* plants were clonal, each rosette was considered as an individual, since they would act as independent food sources and can be metabolically independent (see North and Greenberg [1998] for similar consideration of clonal food plants). The spatial pattern of *S. lanceolatum* is expected to be fairly consistent from year to year because of its perennial nature. Therefore, mapping of *S. lanceolatum* in 1998 can be related to population estimates from mark/recapture of *P. smintheus* in 1995. As well, meadows with high *P. smintheus* populations in one year tend to have high populations in the subsequent years (Roland *et al. in press*).

Female Oviposition Behaviour

Mated adult female *P. smintheus* were caught, assigned an individual mark and released. Eight individuals were followed in submeadow G4 and five were followed in submeadow J2 (Fig. 4-2). Meadow G4 had a high density of butterflies and J2 had a low density of butterflies and are therefore referred to as high- and low-density meadows, respectively. The number of *S. lanceolatum* within a 2.5-metre radius of each oviposition site was counted and each plant was mapped as in the *"Sedum lanceolatum* Mapping" section,
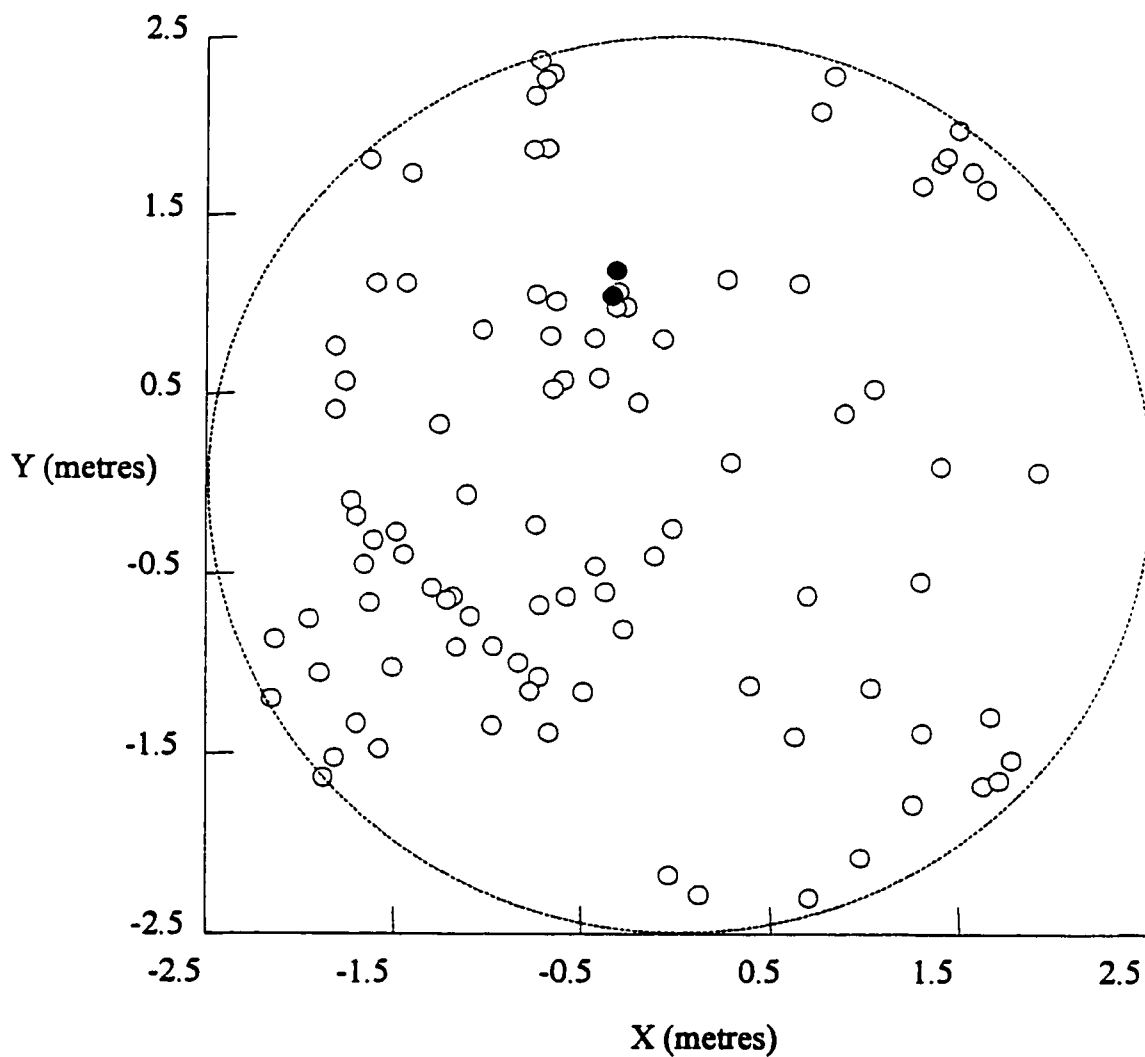
Fig. 4-3. All mapped locations of *Sedum lanceolatum* plants within a 2.5 metre radius study plot (dashed line). The open circles represent the plants without larval feeding damage and the filled circles represent plants with larval feeding damage.

above. The abundance and proximity of *S. lanceolatum* to the oviposition site and the spatial pattern of *S. lanceolatum* within 2.5 metres of the oviposition site (estimated by Ripley's Univariate K-function) were compared to the same estimates for the random plots used for objective 2. These estimates were made for both high- and low-density meadows.

ANALYSES

Objective 1. To determine if the abundance of the larval host plant, *S. lanceolatum*, explains variation in population size of *P. smintheus*.

I used linear regression to relate the mean number of *S. lanceolatum* in the circular plots for each submeadow and the number of marked *P. smintheus*. Similarly, for whole meadows, I used linear regression to relate the mean number of *S. lanceolatum* in the circular plots for each meadow to "Craig's estimates" for *P. smintheus* population size for the respective meadow.

Objective 2. To determine whether or not the spatial pattern of *S. lanceolatum* explains variation in the population size of *P. smintheus* in Jumpingpound Ridge meadows.

In plots that had more than fifteen *S. lanceolatum* plants, Ripley's Univariate K-function was calculated. Calculations of Ripley's K-function on fewer plants were difficult to interpret, and had little power to detect departures from randomness. Within each of the submeadows the results were qualitatively compared by identifying general trends in

divergence from complete spatial randomness over distances, t, ranging from 0 m to 2.50 m

at 0.10 m intervals. Submeadow estimates were pooled for the meadow-scale and trends in

departure from complete spatial randomness over the range of distances, t, were similarly

identified.

Objective 3. To determine if larval feeding damage on *S. lanceolatum* is correlated with *S. lanceolatum* abundance and/or spatial pattern and if the spatial pattern of larval feeding damage among available *S. lanceolatum* plants is aggregated, regular, or appears random.

I used logistic regression to determine whether or not feeding damage in the plots was

related to the number of *S. lanceolatum* in a plot. Plots were categorized based on the

observed spatial point pattern of *S. lanceolatum* (clustered, regular or appeared random).

The counts of plots with feeding damage in each of these categories was compared to the

same counts for plots without feeding damage using a G-test. Where a significant result

was obtained, a sub-divided G-test was conducted to determine which groups were

different from each other.

At both the meadow and submeadow-scales, the number of plots with feeding damage was

related to the abundance of *S. lanceolatum* using two regressions. First a generalized linear

model, assuming normal errors, was tested for a linear relationship between the two

variables, in S-Plus (1999). Second, a non-parametric, generalized additive model with a

spline smoother (three degrees of freedom) was fitted and compared to the linear model to

determine whether there were any additional, non-linear effects of *S. lanceolatum* abundance on the amount of larval feeding damage.

To test for association between the pattern of feeding-damaged *S. lanceolatum* and the pattern of undamaged *S. lanceolatum*, Ripley's Bivariate K-function was calculated for the plots with a sufficient number of feeding-damaged plants (more than two plants with feeding). The observed Ripley's Bivariate K-function is compared to Ripley's Bivariate K-functions generated from random shufflings of *S. lanceolatum* labels (feeding damaged or undamaged) among existing plant positions. The results indicate whether *S. lanceolatum* plants with feeding-damage appear to be arranged independently of undamaged *S. lanceolatum* plants, are positively associated (aggregated) with undamaged *S. lanceolatum* plants, or are negatively associated (segregated from) with undamaged *S. lanceolatum* plants.

Objective 4. To investigate whether or not adult female *P. smintheus* select oviposition sites to improve the likelihood of larval establishment on a food plant, *S. lanceolatum*.

The abundance of *S. lanceolatum* in the oviposition plots were compared to those for the random plots using a Mann-Whitney test among the individual meadows. The distance from the oviposition sites to the nearest host plant and the distances from the centre of randomly placed plots to the nearest host plant were compared using a Mann-Whitney test.

The direction of divergence of the spatial point pattern of *S. lanceolatum* from random was determined for each of the oviposition plots and the randomly placed plots. The number of oviposition site plots where the pattern of *S. lanceolatum* was (a) clustered over all scales (0 m to 2.5 m) or (b) clustered at small distances (less than 1 m) and regular at larger distances (greater than 1 m), were compared to the same counts for the randomly placed plots using a G-test.

Because the oviposition site selected by females is the location of interest for this objective, the Ripley's Univariate K-function was modified to estimate the spatial pattern around the egg only. In the earlier calculation of Ripley's Univariate K-function all pairs of *S. lanceolatum* plants are considered in the estimate; in my modification, only pairs of points involving the egg or the centre of the random plot are included in the estimate. Again, the direction of divergence of the spatial point pattern of *S. lanceolatum* was determined for each of the oviposition plots and the randomly placed plots. Then each plot was placed into one of four *S. lanceolatum* spatial point pattern categories: (1) clustered at most distances of *t* (0 m to 2.5 m); (2) regular at most distances of *t* (0 m to 2.5 m); (3) appeared random at all distances of *t* (0 m to 2.5 m); or, (4) clustered at small distances of *t* (0.2 m to 1 m) and regular at large distances of *t* (greater than 1 m). The counts of oviposition plots and randomly placed plots in each of the four spatial pattern categories was compared using a G-test.

RESULTS

Objective 1. To determine if the abundance of the larval host plant, *S. lanceolatum*, explains variation in population size of *P. smintheus*.

The indices of *P. smintheus* population size is predicted by the abundance of *S. lanceolatum* both at the submeadow scale (marked butterflies= 1.29 + 0.44 x sedum; R^2=0.47; p=0.0002) (Fig. 4-4a) and at the meadow-scale (Craig's estimate=-1.47+ 0.44 x sedum; R^2=0.51; p=0.0019) (Fig. 4-4b).

Objective 2. To determine whether or not the spatial pattern of *S. lanceolatum* explains variation in the population size of *P. smintheus* in Jumpingpound Ridge meadows.

The spatial point patterns observed for all submeadows and meadows are summarized in Table 4-1 and Table 4-2, respectively. Due to the absence or small number of *S. lanceolatum* plants (less than fifteen plants per plot) no second-order analyses were conducted in four of the submeadows (J1, S1, U1, and V1) nor in several plots in other submeadows (see Table 4-1 for more detail). Many of the individual plots displayed a clustered spatial point pattern of *S. lanceolatum* plants over all scales (0 m to 2.5 m) (Fig. 4-5). The remaining plots exhibited a clustered spatial pattern at small distances of *t* and a general trend towards randomness at larger spatial distances of *t* (Fig. 4-6); *i.e.*, meadows with strongly clumped host plants are no better at promoting larger butterfly populations.
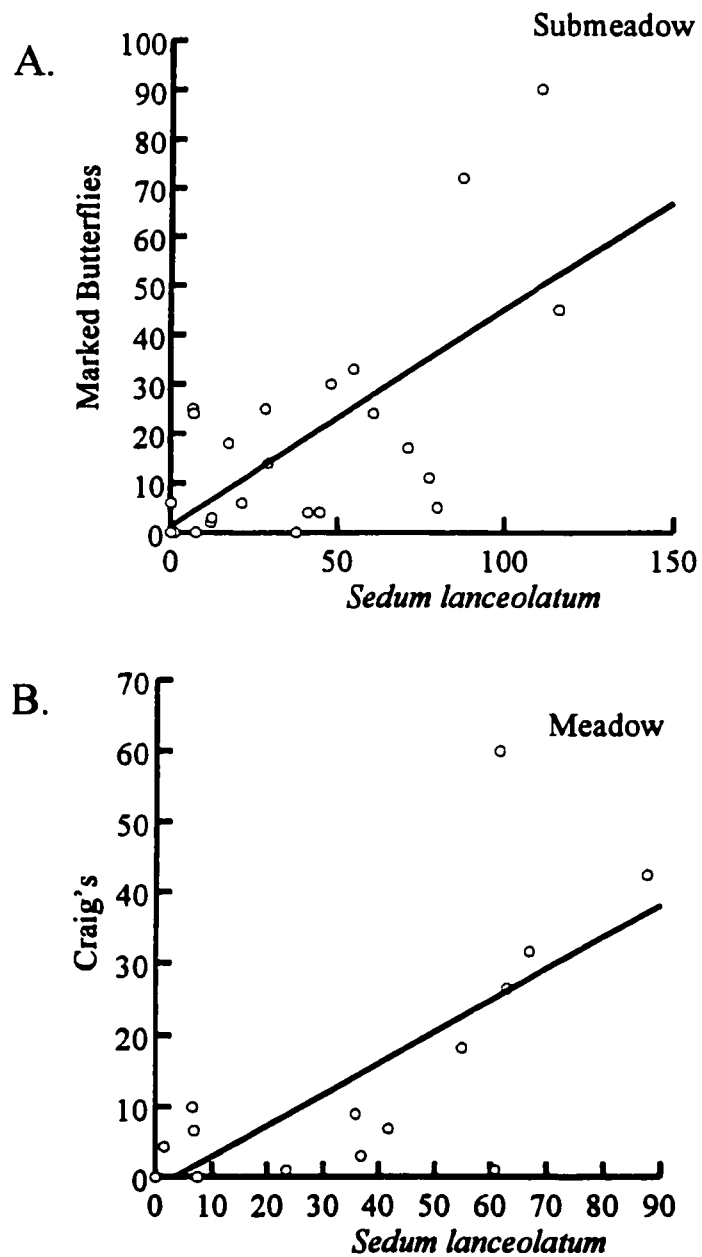
Fig. 4-4. Effect of *Sedum lanceolatum* abundance on the population indices of *Parnassius smintheus* (number of marked butterflies for the submeadows and Craig's estimate for the meadows). The linear regression line for submeadow-scale (a) and meadow-scale (b) are both significant at $p<0.005$.

Table 4-1. Summary of Ripley's Univariate K-function results for the spatial pattern of *Sedum lanceolatum* plants in Jumpingpound Ridge submeadows. Ten, five-metre diameter plots were conducted in each submeadow and plots which contained more than 15 plants were considered useable for analysis. The spatial pattern for each plot is summarized by indicating: the number of plots where clustering was detected at all distances of *t* (from 0 m to 2.5 m); the number plots where clustering was detected over some distances of *t*; and the number of total useable plots where the spatial pattern appeared random over some distances *t*.

Submeadow	Useable Plots	#Plots Clustered from *t* 0 to 2.5 m	#Plots Clustered over some *t* (m)	#Plots appearing Random over some *t* (m)
F1	5	3	4(0.1-1.4)	2(1.9-2.5)
F3	10	7	9(0-1.0)	2(1.8-1.9)
g1	9	5	9(0-1.1)	4(2.1-2.5)
G2	4	2	4(0-0.7)	highly variable
G4	10	6	10(0-0.7)	4(1.4-2.0)
I1	7	4	7(0-1.0)	3(1.7-2.5)
J1	0			
J2	8	2	8(0-0.5)	2(1.1-1.7)
J3	4	1	4(0-0.8)	3(2.3-2.5)
K1	8	3	8(0.2-1.0)	highly variable
L1	5	2	5(0-1.2)	3(1.7-1.8)
L2	6	2	6(0-0.5)	4(2.3-2.5)
L3	7	1	highly variable	6(1.2-1.3)
M1	6	1	6(0-0.8)	5(2.3-2.5)
M3	9	2	8(0.2-0.5)	highly variable
O1	4	0	4(0.2-0.9)	4(2.1-2.2)
P1	2	0	2(0-0.8)	2(2.1-2.5)
Q1	1	1	1(0-2.5)	
R1	4	1	4(0-0.9)	3(2.2-2.5)
R2	9	4	9(0-0.5)	4(2.3-2.5)
S1	0			
S2*	9	3	8(0.2-0.7)	5(2.4-2.5)
T1	2	2	2(0-2.5)	
U1	0			
V1	0			

*for this submeadow 11 plots were conducted

Table 4-2. Summary of the spatial pattern of *Sedum lanceolatum* in Jumpingpound Ridge meadows. Plants were mapped in ten$_a$, twenty$_b$, twenty-one$_c$, and thirty$_d$, five-metre diameter plots in the meadows. The number of useable plots represents the number of plots which contained more than 15 plants and therefore, could be used for Ripley's Univariate K-function analysis. The number of plots where the spatial pattern of *S. lanceolatum* was clustered at all distances of *t* (0 m to 2.5 m), the number plots where the pattern of *S. lanceolatum* was clustered over some distances of *t* and the number of plots where the spatial pattern appeared random over some distances *t* are reported.

Meadow	Useable Plots	Plots Clustered from *t* 0 to 2.5 m	Plots Clustered over some *t* (m)	Plots appearing Random over some *t* (m)
F$_b$	15	10	13(0.1-1.0)	highly variable
g$_a$	9	5	9(0-1.2)	4(2.1-2.5)
G$_b$	14	8	13(0.1-0.7)	highly variable
I$_a$	7	4	7(0-1.0)	3(1.7-2.2)
J$_d$	12	3	12(0-0.5)	highly variable
K$_a$	8	3	8(0.2-1.0)	highly variable
L$_d$	18	5	highly variable	highly variable
M$_b$	15	3	15(0.2-0.5)	highly variable
O$_a$	4	0	4(0.2-0.9)	4(2.1-2.5)
P$_a$	2	0	2(0-0.8)	2(2.1-2.5)
Q$_a$	1	1	1(0-2.5)	
R$_d$	13	5	13(0-0.5)	7(2.3-2.5)
S$_c$	9	3	8(0.2-0.7)	5(2.4-2.5)
T$_a$	2	2	2(0-2.5)	
U$_a$	0			
V$_a$	0			
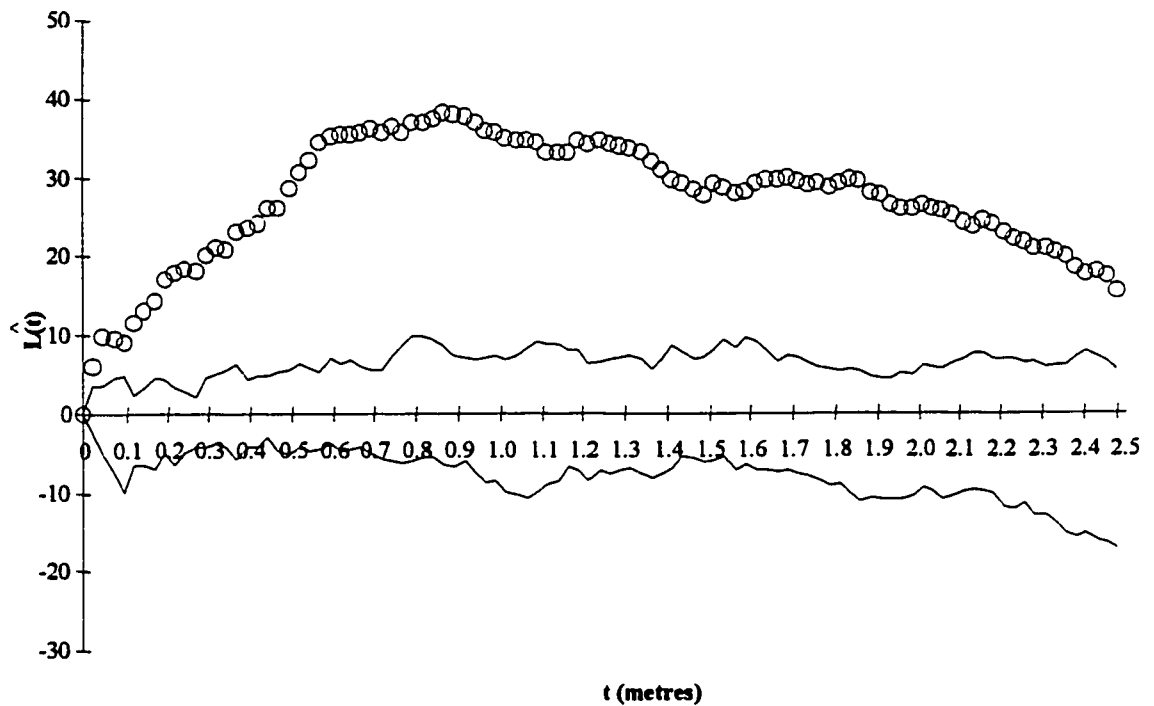
Fig. 4-5. Graphical representation of Ripley's Univariate K-function analysis demonstrating a clustered spatial point pattern at all distances of *t*, metres. The open circles represent the *L*(t) estimates for the observed spatial pattern of *Sedum lanceolatum* plants in one plot. The solid lines represent the 95% confidence envelopes from the Monte-Carlo simulations. From distance, *t*, 0 m to 2.5 m the spatial pattern of *Sedum lanceolatum* is significantly different from random in the direction of being clustered.
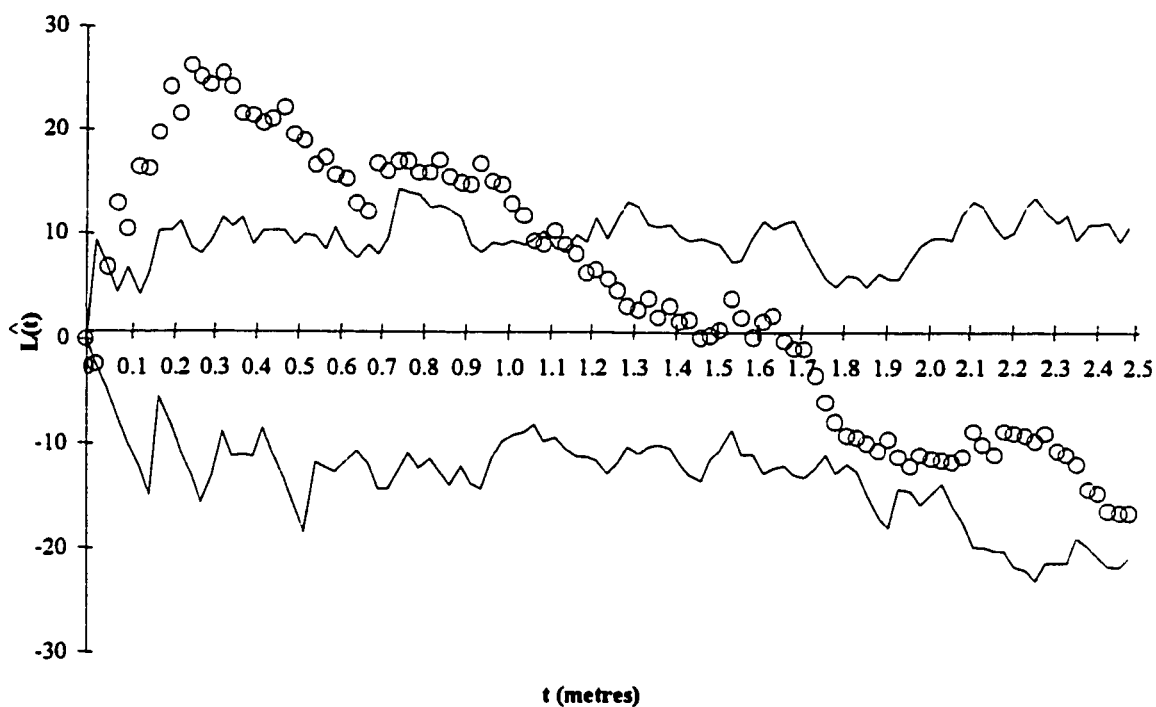
Fig. 4-6. Graphical representation of Ripley's Univariate K-function analysis demonstrating clustered spatial point patterns at small distances of *t* and seemingly random patterns at larger distances of *t*. The open circles represent the *L*(t) estimates for the observed spatial pattern of *Sedum lanceolatum* plants in one plot. The solid lines represent the 95% confidence envelopes from the Monte-Carlo simulations. From distance, *t*, 0.05 m to 1.05 m the spatial pattern of *S. lanceolatum* is significantly different from the random expectation in the direction of clustering and from distances 1.05 m to 2.5 m the spatial pattern of *S. lanceolatum* appears random.

The range of distances, t, where clustering was observed in all or most of the useable plots in submeadow-scale and meadow-scale analyses is summarized in Figure 4-7 (for more detail refer to Table 4-1 and Table 4-2). There is no clear trend in the range of distances, t, at which spatial pattern divergence from random, as a function of $P.$ *smintheus* population size indices, is evident at either the submeadow or meadow-scales of analysis.

Objective 3. To determine if larval feeding damage on *S. lanceolatum* is correlated with *S. lanceolatum* abundance and/or spatial pattern and if the spatial pattern of larval feeding damage among available *S. lanceolatum* plants is aggregated, regular, or appears random.

S. lanceolatum abundance predicted the presence or absence of feeding damage within the plots correctly 69% of the time (feeding=-2.69 + 2.29 x Sedum), and the fit of the logistic regression was good (G=112, p<0.5 x 10^{-9}, McFadden's ρ^2=0.32). There was no significant relationship between the degree of clumping of *S. lanceolatum* and the presence of feeding damage in plots (G=2.18; p=0.54).

The abundance of *S. lanceolatum* explains much of the variation in the number of larval feeding-damaged *S. lanceolatum* at the submeadow-scale and meadow-scale (Table 4-3). This is not surprising since a greater overall abundance plants might easily be associated with more plants with damage. The generalized additive model, however, detected additional non-linear effects of *S. lanceolatum* abundance on the number of *S. lanceolatum* with larval feeding-damage, but only at the meadow-scale (Table 4-4). In other words, at
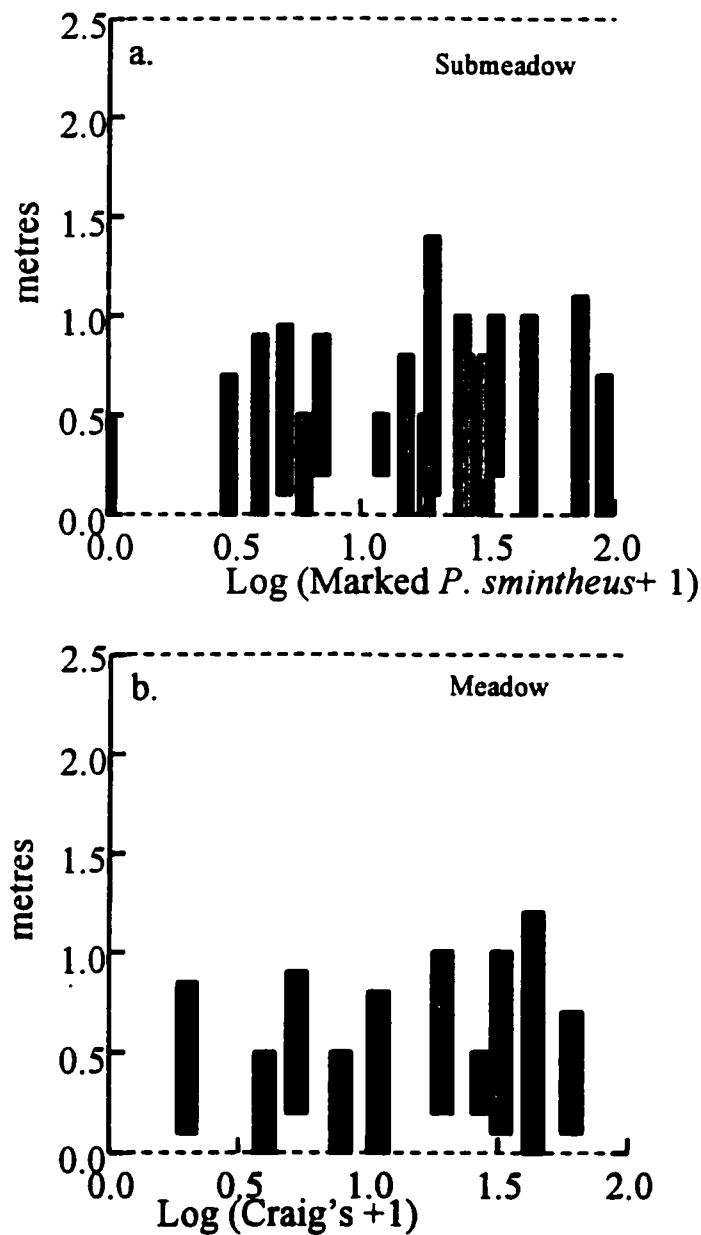
Fig. 4-7. Results from the Ripley's Univariate K-function analyses, are summarized for all plots in Jumpingpound Ridge (a) submeadows and (b) meadows with different population sizes of *P. smintheus*. The bars represent the range, in metres, over which *S. lanceolatum* plants exhibited spatial point patterns that depart significantly from complete spatial randomness in the direction of clustering. The broken lines represents distances over which Ripley's K-function was estimated. Meadows with a small number of useable plots (less than two) were not included in this summary figure.

the meadow level, the proportion of plants with feeding damage depends on the number of

available plants; with a threshold at about 20 plants per plot. Below this threshold there is

little feeding damage and no effect of plant abundance, above it there is an increase in the

effect of host plant abundance on damage (Fig.4-8).

Table 4-3. The generalized linear model results predicting the number of *S. lanceolatum* with larval feeding damage from the number of available *S. lanceolatum* at the submeadow and meadow-scales.

Scale	Coefficient (SE)	Deviance Explained	Residual df	Residual Deviance	P
Submeadow	0.14 (0.02)	582.1	23	415.3	0.9×10^{-5}
Meadow	0.14 (0.02)	228.3	14	43.2	0.6×10^{-6}

Table 4-4. Comparing the generalized linear regression model to the generalized additive model. Both models predicted the number of *S. lanceolatum* with larval feeding damage from the number of available *S. lanceolatum* at the submeadow and meadow-scales. The F-test indicates that there were significant additional non-linear effects of the number of available plants on the amount of feeding damage at the meadow but not at the submeadow-scale.

| Scale | Model | Residual df | Residual Deviance | F-test: linear vs. additive model | | | |
				df	Deviance explained	F	P
Submeadow	linear	23	415.3				
	additive	20	351.4	3	64	1.21	0.33
Meadow	linear	14	43.2				
	additive	11	22.6	3	20.6	3.35	0.1
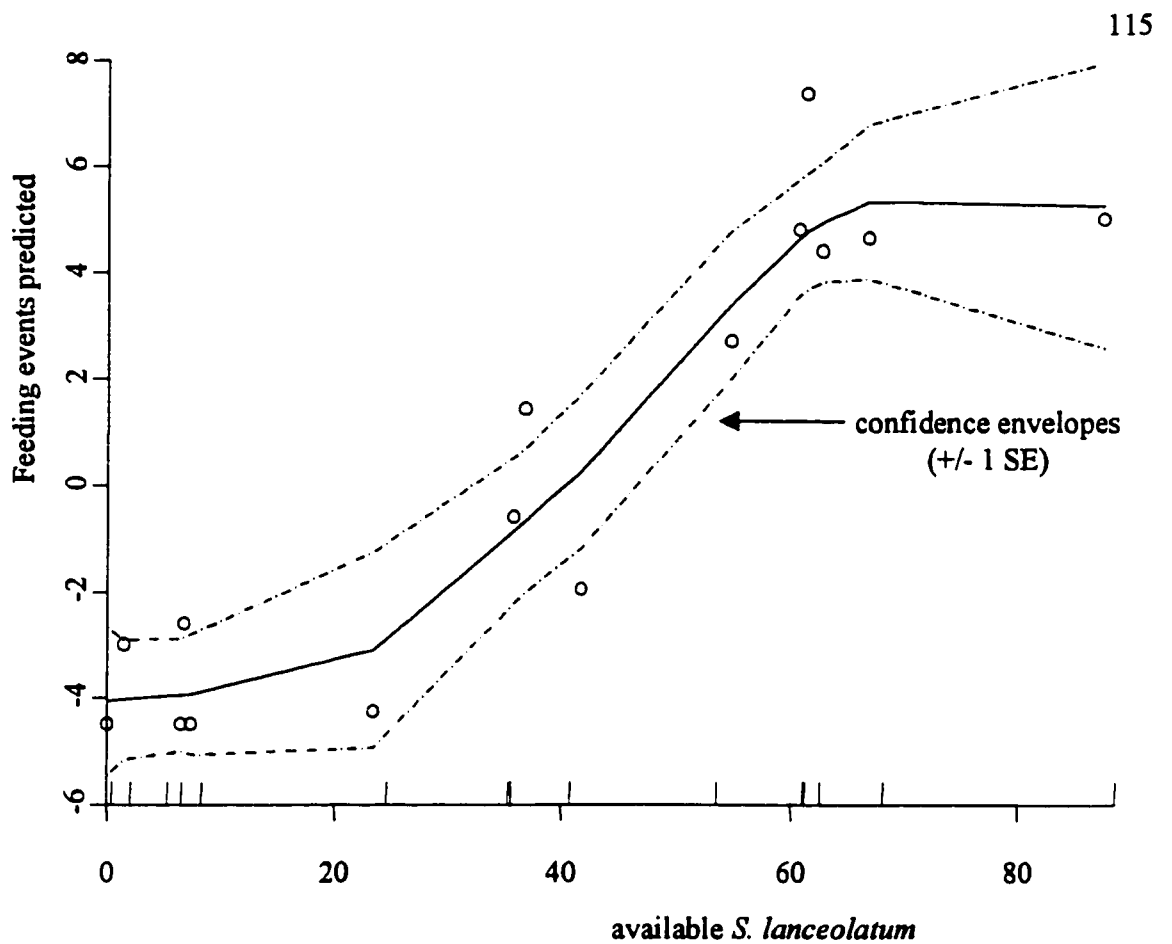
Fig. 4-8. Generalized additive model (spline-fit) predicting the amount of *S. lanceolatum* plants with feeding damage from the number of available *S. lanceolatum* plants in 5 m diameter plots, at the meadow-level. The confidence envelopes outline the estimated function (+/-) one standard error.

Because of little variation in spatial pattern of *S. lanceolatum* observed over the range of

population sizes on Jumpingpound Ridge, it was impossible to relate the presence of

feeding damage to the local *S. lanceolatum* spatial point pattern.

In most of the plots, the pattern of feeding-damaged *S. lanceolatum* plants appeared to be

arranged independently of the pattern of undamaged *S. lanceolatum* plants (Table 4-5,

Table 4-6 and Fig. 4-9). However, ignoring the confidence envelopes from the Ripley's

Bivariate K-function estimates revealed that both feeding-damaged and undamaged *S.*

lanceolatum plants were usually aggregated and rarely segregated. In a few instances, the

bivariate pattern (of feeding damaged and undamaged plants) was significantly different

from independent in the direction of positive association, but was actually under both the

maximum and minimum confidence envelopes (Fig. 4-10). This indicates that although the

bivariate spatial point pattern of undamaged and feeding damaged *S. lanceolatum* was

positively associated, it was less positively associated than expected given the existing

pattern of all plants (*i.e.*, the two types of plants are less aggregated than predicted from

the overall pattern of clumping of all *S. lanceolatum* plants).

Objective 4. To investigate whether or not adult female *P. smintheus* select oviposition sites to improve the likelihood of larval establishment on a food plant, *S. lanceolatum*.

Females did not selectively oviposit in areas of high *S. lanceolatum* abundance in either the

Table 4-5. The summary of Ripley's **Bivariate** K-function analysis of mapped locations of *Sedum lanceolatum* plants with and without larval feeding damage for Jumpingpound Ridge submeadows. The number of useable plots represents the number of plots, out of ten plots conducted in each of the submeadows, which had more than two plants with larval feeding damage and could be used for the calculation of Ripley's Bivariate K-function. The number of plots where the bivariate association between larval feeding-damaged and non-larval feeding-damaged *S. lanceolatum* plants appeared random at all distances of t (0 m to 2.5 m) and the number of plots where the bivariate association appeared random at some distances of t are reported.

Submeadow	Useable Plots	#Plots appearing **Random** from 0 to 2.5 m	#Plots appearing **Random** over some scale (m)
F1	5	5	5(0-2.5)
F3	8	3	6(0.4-1.4)
g1	7	1	highly variable
G2	3	2	3(0.8-2.5)
G4	10	6	9(1.1-2.5)
I1	6	4	5(0-2.3)
J1	0		
J2	9	6	8(0-0.9)
J3	4	2	4(0-0.7)4(2.2-2.5)
K1	9	5	8(0-1.4)
L1	5	2	5(0-0.8)
L2	1	0	1(1.4-2.5)
L3	0		
M1	9	6	9(2.1-2.5)
M3	2	0	2(1.6-1.9)
O1	3	1	3(1.6-2.5)
P1	0		
Q1	3	3	3(0-2.5)
R1	2	1	2(0-2.1)
R2	6	0	highly variable
S1	0		
S2*	1	1	1(0-2.5)
T1	0		
U1	0		
V1	0		

*for this submeadow 11 plots were conducted

Table 4-6. The summary of Ripley's **Bivariate** K-function analysis of *Sedum lanceolatum* plants with and without larval feeding damage in Jumpingpound Ridge meadows. The number of useable plots for Ripley's Bivariate K-function had more than two *S. lanceolatum* plants with feeding damage and represent the number out ten$_a$, twenty$_b$, twenty-one$_c$, and thirty$_d$ plots conducted in a meadow. The number of total useable plots where the bivariate association appeared random at all distances of t (0 m to 2.5 m) and the number of total useable plots where the bivariate association appeared random at some distances of t are reported.

| Meadow	Useable Plots	Plots appearing **Random** over 0 to 2.5 m	Plots appearing **Random** over some t (m)
F_b	13	8	11(0.4-1.4)
g_a	7	1	highly variable
G_b	13	8	12(1.1-2.5)
I_a	6	5	5(0-2.5)
J_d	13	8	13(0-0.7)
K_a	9	5	8(0-1.4)
L_d	6	2	5(0-0.8)
M_b	11	6	highly variable
O_a	3	1	3(1.6-2.5)
P_a	0		
Q_a	3	3	3(0-2.5)
R_b	8	1	highly variable
S_c	1	1	1(0-2.5)
T_a	0		
U_a	0		
V_a	0		
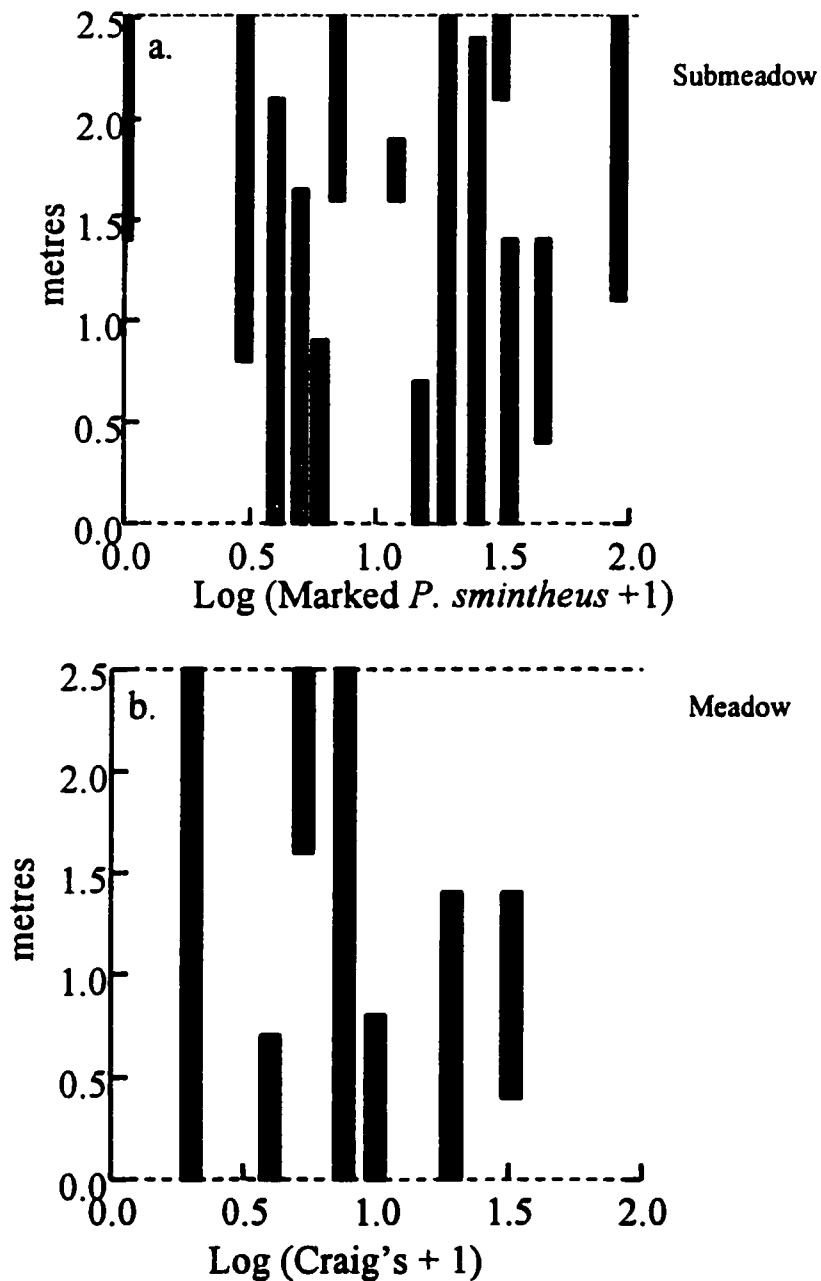
Fig. 4-9. Results from the Ripley's Bivariate K-function analyses, are summarized for all plots in Jumpingpound Ridge (a) submeadows and (b) meadows with different population sizes of *P. smintheus*. The bars represent the range, in metres, over which the spatial pattern of *Sedum lanceolatum* plants with and without feeding damage appeared independent. The broken line represents distances over which Ripley's K-function was estimated.
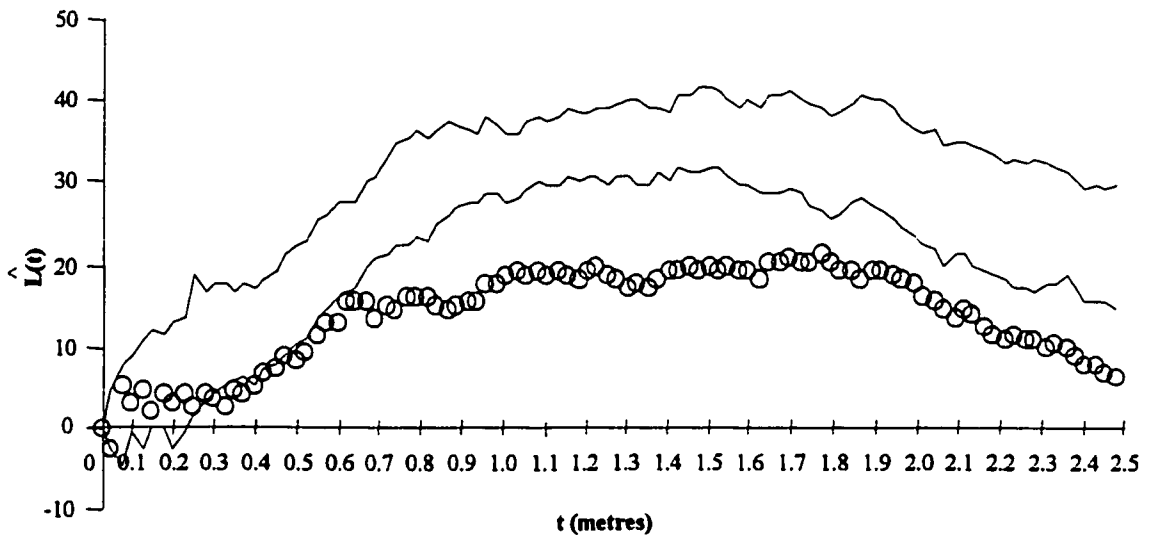
Fig. 4-10. Graphical representation of Ripley's Bivariate K-function analysis. The open circles represent the $L(t)$ estimates for the observed bivariate association between the patterns of *Sedum lanceolatum* plants with larval feeding damage and *S. lanceolatum* plants without larval feeding damage, for one plot. The solid lines represent the 95% confidence envelopes from the Monte-Carlo simulations. The overall $L(t)$ would lie within these confidence envelopes. From distance, t, 0.5 m to approximately 2.5 m the observed estimate of $L(t)$ indicates a positive association between the spatial patterns of *S. lanceolatum* plants with and without larval feeding damage. However, the observed estimates of $L(t)$ fall below the confidence envelopes, indicating that the bivariate association, although positive, is significantly less positive than expected given the underlying spatial pattern of *S. lanceolatum*.
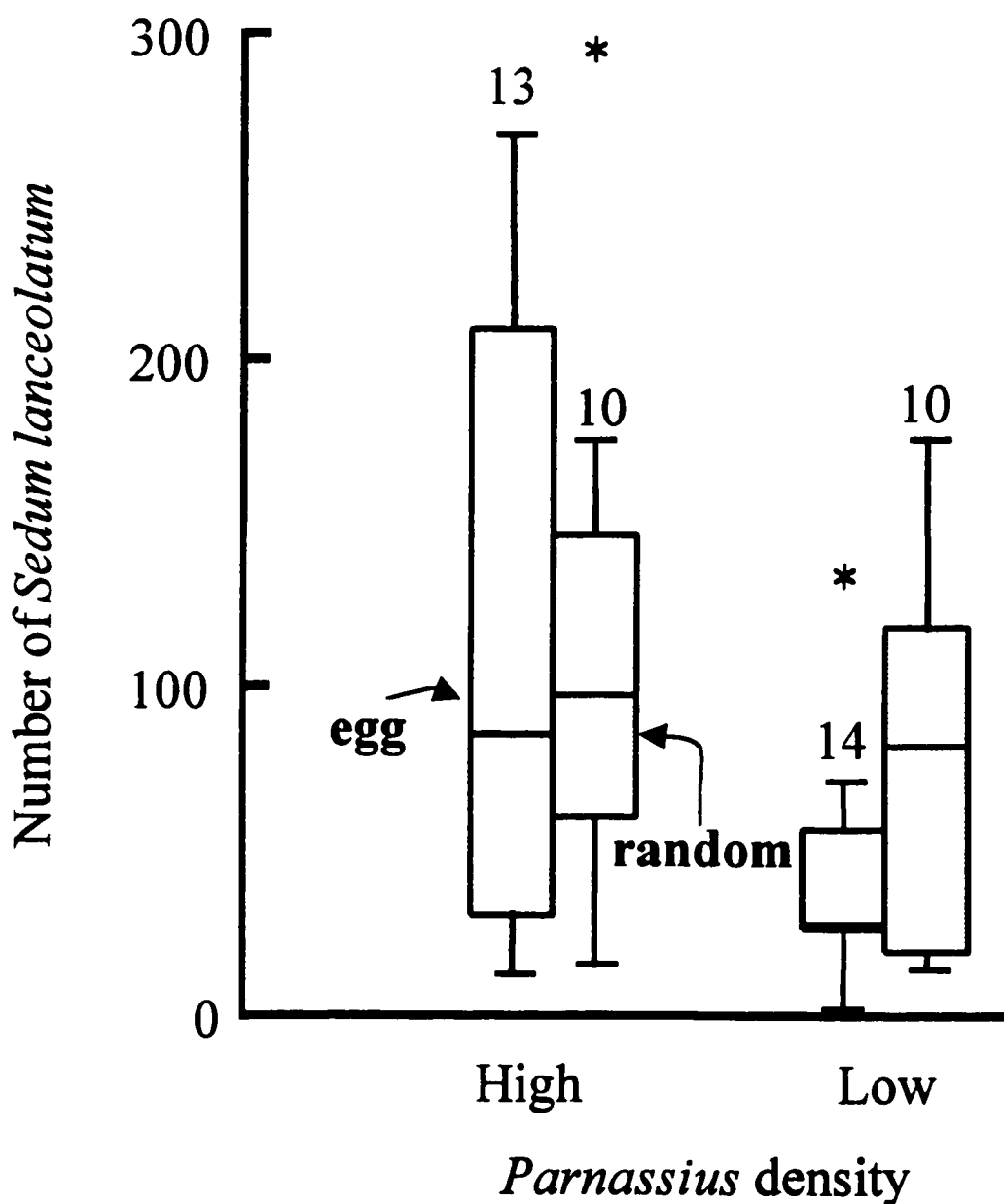
Fig. 4-11. Box and whisker plots of the number of *Sedum lanceolatum* plants within a 2.5 metre radius of oviposition sites and random sites in the high- and low-density meadows. The line in the box represents the median number of *S. lanceolatum* plants. Numbers at the tops of the boxes indicate the sample size, or the number of plots. There were no significant differences detected within meadows (p > 0.05). * represent outliers.

high-density (U=50; p=0.24) or the low-density (U=59.5; p=0.73) meadow (Fig. 4-11).

Females did not selectively oviposit near *S. lanceolatum* plants compared to if they had

oviposited at random sites in either the high-density meadow (U=75; p=0.77) or the low-

density meadow (U=70.5; p=0.73) (Fig. 4-12). Counts of the spatial patterns of *S.

lanceolatum*, from the unmodified Ripley's Univariate K-function, around oviposition sites

and random locations did not differ in the high-density meadow (G=1.18; p=0.28) nor in

the low-density meadow (G=0.52; p=0.47) (Fig. 4-13). The modified Ripley's Univariate

K-function results revealed that near the egg in the oviposition plots, and the centre of the

random plots, there are fewer *S. lanceolatum* plants than expected if plants had been

arranged randomly in the plot (Table 4-7 and Fig. 4-14). There were, however, no

significant differences in the counts of plots exhibiting each of the spatial patterns of *S.

lanceolatum* (clustered at most distances of *t*, regular at most distances of *t*, random at

most distances of *t*, and clustered at small distances of *t* (0.2 m to 1.0 m) and regular at

large distances of *t* (greater than 1 m)) between the oviposition and random plots in the

high- (G=3.73; p=0.29) and the low- (G=1.58; p=0.46) density meadows (Fig. 4-15).
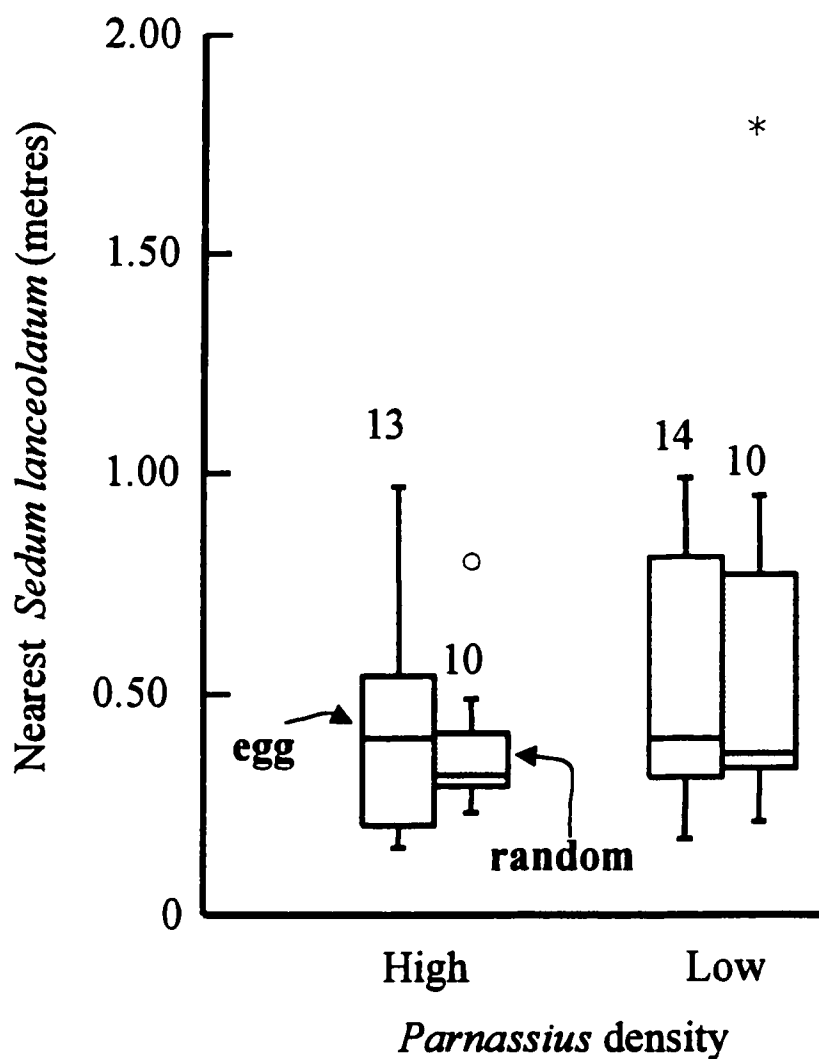
Fig. 4-12. Box and whisker plots of the distance to the nearest *Sedum lanceolatum* plant from oviposition sites and random sites in the high- and low-density meadows. Numbers at the tops of the boxes indicate the number of plots sampled. There were no significant differences detected within meadows ($p>0.05$). * and ° are outliers.
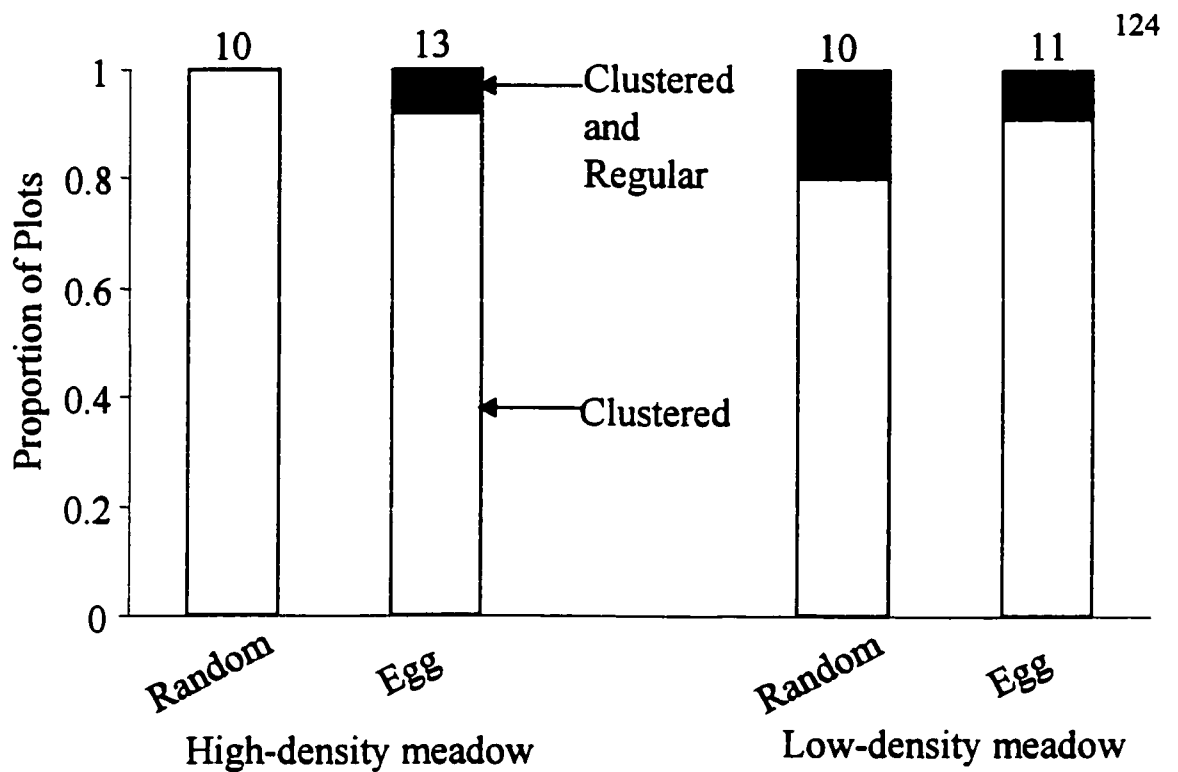
Fig. 4-13. The proportion of random and egg-laying plots where the spatial patterning of *S. lanceolatum* plants was: **clustered** at all distances (0 m to 2.5 m) or **clustered** at small distances and **regular** at larger distances in the high- and low-density quality meadows on Jumpingpound Ridge. No significant differences in the counts of spatial patterns of *Sedum lanceolatum* were detected between random and oviposition plots in either meadow (p>0.05). The numbers at the top of the bars indicate the number of plots sampled.

Table 4-7. The spatial point pattern of *Sedum lanceolatum* is in the direction of regularity or over-dispersion but is not significantly different from random, over the range of distances (metres), for the random and egg laying plots in the high- and low-density butterfly meadows. Values are from the modified Ripley's Univariate K-function.

Meadow	Plots	Range (m)
Low-density (J2):	Random	0-0.2
	Egg	0-0.3
High-density (G4):	Random	0-0.2
	Egg	0-0.1
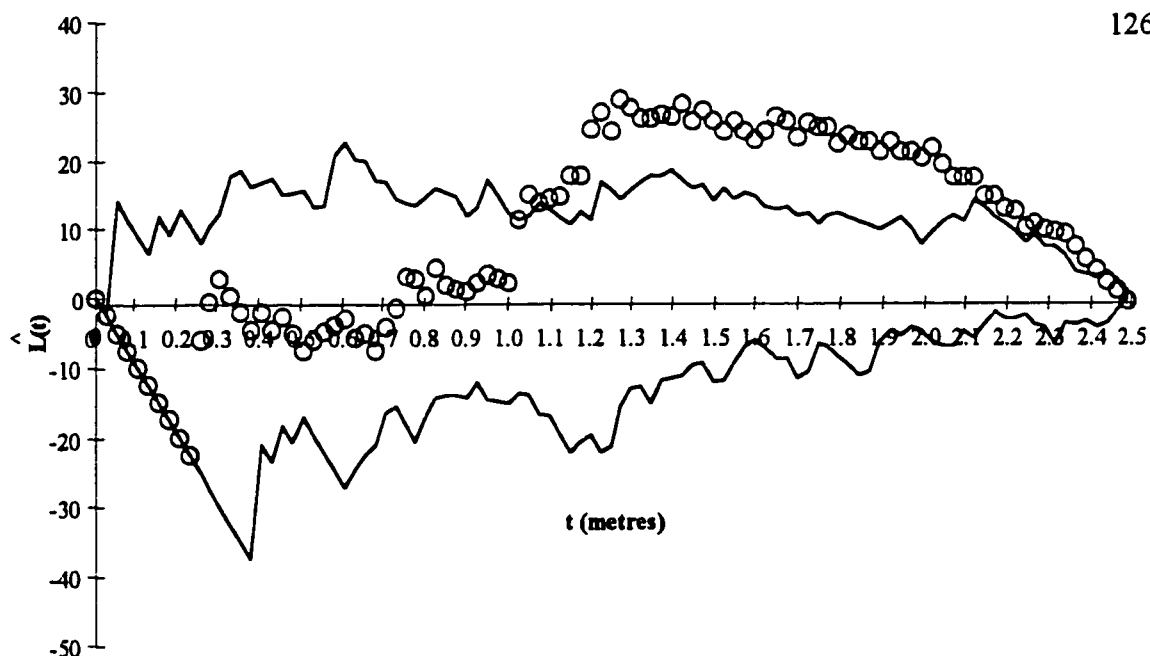
Fig. 4-14. Graphical representation of the modified version of Ripley's Univariate K-function analysis. The open circles represent the $L(t)$ estimates for the observed spatial pattern of *Sedum lanceolatum* plants from the centre, of one plot. The solid lines represent the 95% confidence envelopes from the Monte-Carlo simulations. From distance, t, 1.1 m to approximately 2.4 m the observed estimate of $L(t)$ indicates that the spatial pattern of *S. lanceolatum* is clustered. Notice how $L(t)$ from 0 m to 0.25 m follows the lower confidence envelopes from 0 m to 0.25 m. This is because the nearest *S. lanceolatum* plant from the centre of the plot is at 0.25 m, causing the abrupt increase of $L(t)$ from the lower confidence envelope to randomness.
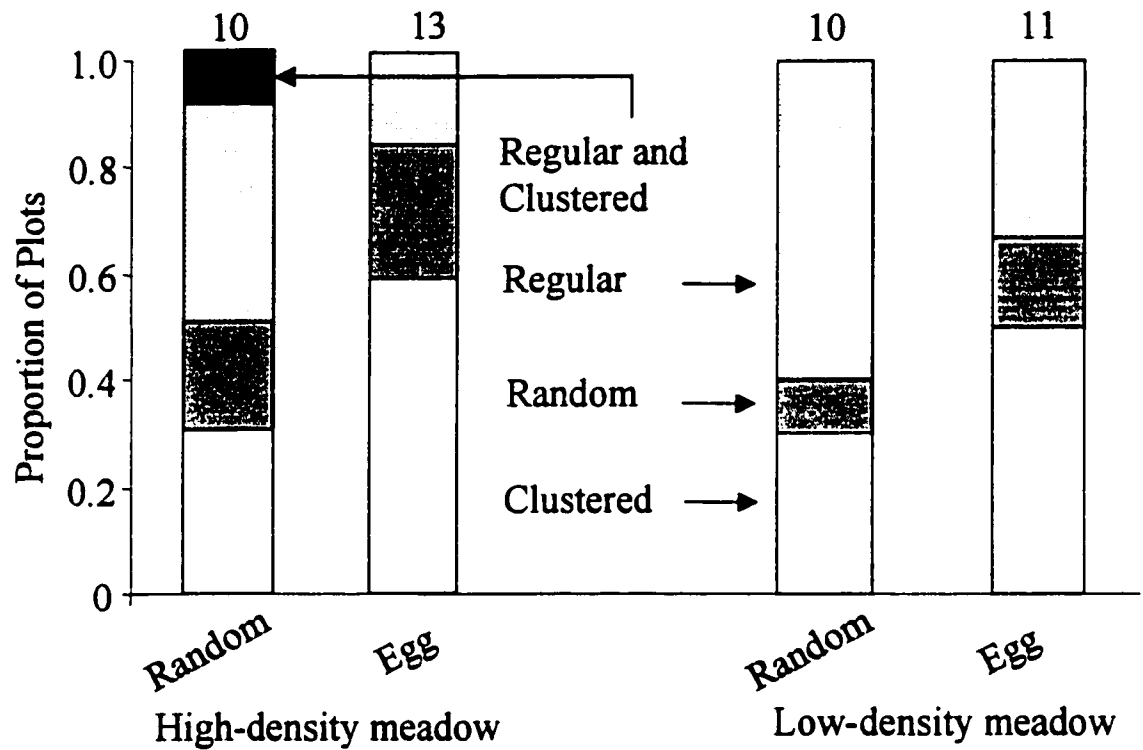
Fig. 4-15. Results from the modified Ripley's Univariate K-function. The proportion of plots where the spatial pattern of *Sedum lanceolatum*, around the centre of the random plots and the egg laying site in the oviposition plots, appears **random** or diverges from complete spatial randomness in the direction of **regularity** or **clustered**, or **both**. No significant differences in counts of the spatial patterns of *Sedum lanceolatum* were detected between random and oviposition plots in either meadow (p>0.05). The numbers at the top of the bars indicate the number of plots sampled.

DISCUSSION

Sedum lanceolatum **Abundance and Habitat Quality**

At both submeadow- and meadow-scales, much of the variation in population size of *P. smintheus* is explained by the abundance of *S. lanceolatum* plants. This relationship suggests that areas with abundant larval host plants are of high quality for *P. smintheus* and therefore, not all Jumpingpound Ridge meadows are of equal quality. Consideration of how habitat quality (host plant abundance) may influence populations can help us to understand *P. smintheus* population dynamics more generally on Jumpingpound Ridge. Some habitat patches are more important to population persistence of ringlet butterflies (*Aphantopus byperantus*) than are others (Sutcliffe *et al.* 1997). Although different factors are likely responsible for variation in the abundance of adults and larvae (Dempster 1983), *S. lanceolatum* is highly correlated with both *P. smintheus* adult and larval population indices (Fig. 4-4 and Fig. 4-8). It is clear that meadows with abundant adult butterflies also have abundant larvae. It is impossible, at this time, to assess the direct relationships between host plant and both adult and larval abundance due to the high degree of correlation with both. To understand their direct effects on one another would require an experimental manipulation of these variables.

Potential reasons for the positive correlation of *P. smintheus* adults and larvae with *S. lanceolatum* abundance on Jumpingpound follow:

1) Adults may move to and be retained in areas of high *S. lanceolatum* abundance; females

searching for *S. lanceolatum* and males searching for females. However, because of the small number of between-meadow movements detected within a generation on Jumpingpound Ridge (around eight percent of movements during the 1995 mark/recapture session, J. Roland *pers. comm.*), it is unlikely that the among-meadow correlations with *S. lanceolatum* abundance is due to movement. In addition, I have shown that adult female movement and oviposition does not differ between low and high density populations (Chapter 2).

Harrison (1989) attempted to separate the effects of habitat patch quality from existing butterfly abundance. She found that *Euphydryas editha bayensis* butterflies released into extinct patches are poor colonizers and do not move in response to habitat patch area and quality. Instead, these butterflies emigrate at low densities and have little ability to move across non-habitat. A similar study with *P. smitntheus* would help to quantify the relative importance of movement and habitat patch quality on population sizes.

2) Females remain in their natal patch, where they invest most or all of their reproductive output. This would help explain why high population meadows remain so from year to year. Occasional dispersal of gravid adult females to low-quality, non-natal meadows would result in a low probability of larval establishment on host plants, due to the smaller number of host plants available. Encounter rates of randomly searching herbivores, for example *P. smintheus* larvae, with their food plant are likely proportional to the abundance

of their food. In contrast, offspring of adult females dispersing to high quality non-natal meadows would likely be successful in reaching one of the abundant larval food plants and contribute to population increase there.

Monitoring larval search behaviour and success in experimentally manipulated densities of *S. lanceolatum* would improve our understanding of the number of larvae producing both the quantity of feeding damage observed in the plots and the pattern of feeding damage observed. It would also be of great interest to study movements of adult female butterflies throughout their life to determine the probability of dispersal out of natal meadows of different quality, because limited mark/recapture provide only poor estimates of this (Roland *et al. in press*). Improvements to harmonic radar (Roland *et al.* 1996) and/or more intensive mark/recapture would enable researchers to continue following the same individual throughout their adult life.

Submeadow-scale versus Meadow-scale Analysis

Despite obvious differences in plant community structure within meadows, the meadow-scale analysis had stronger correlations between population indices and *S. lanceolatum* abundance compared to the submeadow-scale analysis. Submeadow-scale analysis was expected to yield stronger relationships with *S. lanceolatum* abundance than the meadow-scale analysis because larval movement is restricted to small distances; larvae are likely confined to an area smaller than a submeadow during their development, even though adult

movement is not. The differences in strength of correlations at the meadow-scale and at the submeadow-scale may be caused, in part, by the method used to estimate adult population in each case. "Craig's estimates" of adult density, used for the meadow-scale analysis, control somewhat for marking effort in each mark-recapture session and the total number of marked butterflies in each submeadow during all 1995 mark-recapture sessions do not. At first, the lack of control for "effort" in the population indices at the submeadow-scale, seemed the best explanation for the differences between submeadow and meadow-scales of analysis. However, the correlations between larval feeding damage and *S. lanceolatum* abundances are also strongest at the meadow-scale and do not require a control for "effort". These findings suggest that habitat quality for *P. smintheus* generally is better approximated at the meadow-scale on Jumpingpound Ridge, than at the submeadow-scale and supports the hypothesis that adult females move freely within meadows and do not restrict themselves to areas of higher-quality within meadows. The movement of females among meadows however, is much more restricted (Roland *et al. in press*).

Spatial pattern of *Sedum lanceolatum* and Habitat Quality

Although there are clear differences in *S. lanceolatum* abundance among meadows along Jumpingpound Ridge, the general growth pattern of *S. lanceolatum* does not differ significantly among them. *S. lanceolatum* is clustered, but only at distances of less than one metre. This value can be interpreted as the approximate size of *S. lanceolatum* clumps.

This clumped pattern is not surprising given that *S. lanceolatum* can reproduce asexually

by means of rhizomes and rosettes (Clausen 1975) or if seed dispersal is spatially limited.

In several plots, the spatial pattern is more random at distances greater than two metres,

suggesting that within these plots the size of the entire *S. lanceolatum* clump was captured.

In plots where the spatial point pattern of *S. lanceolatum* is clumped at all distances, this

suggests that the entire clump may not have been captured in the five-metre diameter

circular plots used in this study.

Other attributes of the *S. lanceolatum* plants, such as their size, age, nutritional quality, and

concentration of secondary plant compounds, as well as the structural complexity of

surrounding vegetation may also determine the effect which *S. lanceolatum* has on *P.*

smintheus populations (see review for Lepidoptera generally by Dempster 1983 and

Stanton 1983). Longer term studies of individual *S. lanceolatum* plants over the field

season may reveal differences in growth and phenology among meadows. Timing of larval

hatch synchronized with availability of new *S. lanceolatum* rosettes may be critical to early

survival, and the availability of abundant nectar for adults during the flight season would

provide important energetic resources to adults and possibly oviposition cues for females.

Weiss *et al.* (1988), for example, demonstrated that the phenology of nectar plants and

larval host plants and adult eclosion affected quality of grasslands for populations of the

butterfly *Euphydryas editha bayensis*.

Larval and Adult Behavioural Responses to *Sedum lanceolatum* Abundance and Spatial Pattern

The results indicate that larvae of *P. smintheus* are more successful at establishing on host plants, as evidenced by more feeding damage, when the host plant is abundant. However, the spatial point pattern of *S. lanceolatum* in each meadow appears to be unrelated to the presence of feeding damage. The findings from larval feeding damage analyses therefore suggest that larvae of *P. smintheus* forage and/or encounter *S. lanceolatum* plants randomly. The total number of plants encountered by a randomly moving herbivore depends only on the density of host plants and is unaffected by their distribution (Stanton 1983).

The spatial pattern of feeding-damaged *S. lanceolatum* plants and undamaged *S. lanceolatum* plants appear to be independent of each other; feeding-damaged plants are not isolated in any one section of the circular plots, rather, they occur randomly among undamaged *S. lanceolatum*. This pattern suggests that larvae move randomly among plants, that larvae do not necessarily move to the next-nearest plant to continue feeding and/or that several larvae are producing the feeding damage within one plot. The ability of larvae to detect and move to hosts may also be complicated by the structure of the surrounding vegetation (Stanton 1984); larvae may be searching for other resources, such as resting sites with suitable microclimates between feedings (*e.g.*, locations with preferred moisture level or temperature). Findings from a study of the search behaviour of larvae

suggest that *P. smintheus* larvae can orientate to the host plant and potentially mitigate "errors" in adult female oviposition site selection (Chapter 3).

Females do not selectively oviposit in high density patches of host plant nor do they oviposit closer to host plants than would be expected if they oviposited at random in both the high- and low-density meadows. There was also no difference between the spatial pattern of *S. lanceolatum* around oviposition sites and random sites within a meadow. It is of interest to note that at two oviposition sites in the low-density meadow, the spatial pattern of *S. lanceolatum* could not be estimated because only a single plant was within 2.5 m of the egg, suggesting regularity of the spatial point pattern of *S. lanceolatum* at a scale larger than the study plot radius. Within this meadow the abundance of *S. lanceolatum* in random plots was 13 to 176 plants, within 2.5 m. These results may be produced by random female oviposition provided that habitat is generally "suitable". Oviposition in other butterfly species is affected by additional factors, not considered in this study.

Examples of female butterflies whose larval development and oviposition behaviour is affected by microclimate include the following: *Papilio glaucus*: females preferentially oviposit on branch tips exposed to sunlight (Grossmueller and Lederhouse 1985); *Euphydryas gilletti*: females oviposit on the highest large leaves of their host plant that have exposure to early-morning sunshine (Williams 1981); and *Pararge aegeria*: females oviposit on parts of certain plant species with a temperature between 24 to 30°C (Shreeve

1986). Oviposition by *Euphydryas chalcedona* (Murphy *et al.* 1984) and *Papilio glaucus*

(Grossmueller and Lederhouse 1987) is in areas with host plants that are also rich in nectar

plants. Male harassment increases movement of female *Euphydryas anicia* (Odendaal *et*

al. 1989) and *Proclossiana eunomia* (Baguette *et al.* 1996). Increased movement rates of

these species reduces the time females spend searching for oviposition sites and decreases

the frequency of oviposition events. Oshaki and Sato (1994) demonstrated that *Pieris*

rapae and *P. napi* females select low quality oviposition sites so that their offspring are at

lower risk of parasitism. Similarly, Mappes and Kaitala (1995) found that female bugs

(*Elasmucha grisea*) selected oviposition sites to avoid ant predation and increase nymph

survivorship. In a review of 151 butterfly species in Sweden, Wiklund (1984)

demonstrated that butterflies with conspicuous hosts are more likely to oviposit on them

because they seldom alight on non-hosts. Because of the apparently "haphazard"

oviposition style of *P. smintheus* females, a high-density of host plants is required to ensure

larval establishment. Species where larvae crawl between plants and are highly mobile

during their development, have been suggested to undergo less selection for oviposition

site selection (Janz and Nylin 1997, Mayhew 1997). *P. smintheus* larvae readily move

between plants, therefore, adult female oviposition site selection may be of minor

importance.

CONCLUSION

The findings from this descriptive study demonstrate that the abundance of the larval host

plant, *S. lanceolatum*, is correlated with the population indices of both *P. smintheus* adults

and larvae. Therefore, *S. lanceolatum* abundance will be incorporated, as an index of

meadow quality, into a current population model for *P. smintheus* on Jumpingpound Ridge

(Roland *et al. in press*). The spatial pattern of *S. lanceolatum* in meadows does not change

systematically with its abundance, nor is it correlated with *P. smintheus* population size.

LITERATURE CITED

Andersen, M. 1992. Spatial analysis of two-species interactions. Oecologia 91:134-140.

Baguette, M., I. Convié and G. Nève. 1996. Male density affects female spatial behaviour in the butterfly *Proclossiana eunomia*. Acta Œcologica. 17:225-232.

Bergman, K. 1999. Habitat utilization by *Lopinga achine* (Nymphalidae: Satyrinae) larvae and ovipositing females: implications for conservation. Biological Conservation 88:69-74.

Burke, V.J., S.L. Rathbun, J.R. Bodie and J.W. Gibbons. 1998. Effect of density on predation rate for turtle nests in a complex landscape. Oikos 83:3-11.

Carey, D.B. 1994. Patch dynamics of *Glaucopsyche lygdamus* (Lycaenidae): correlations between butterfly density and host species diversity. Oecologia 99:337-342.

Clarke, R.T., J.A. Thomas, G.W. Elmes and M.E. Hochberg. 1997. The effects of spatial patterns in habitat quality on community dynamics within a site. Proceedings of the Royal Society of London, Series B 264:347-354.

Clarke, R.T., J.A. Thomas, G.W. Elmes, J.C. Wardlaw, M.L. Munguira and M.E. Hochberg. 1998. Population modelling of the spatial interactions between *Maculinea rebeli*, their initial foodplant *Gentiana cruciata* and myrmica ants within a site. Journal of Insect Conservation 2:29-37.

Clausen, R.T. 1975. *Sedum* of North America North of the Mexican Plateau. Cornell University Press, Ithaca, New York, USA.

Craig, C.C. 1953. On the utilisation of marked specimens in estimating populations of flying insects. Biometrika 40:170-176.

Daily, G.C., P.R. Ehrlich, and D. Wheye. 1991. Determinants of the spatial distribution in a population of the subalpine butterfly *Oeneis chryxus*. Oecologia 88:587-596.

Dempster, J.P. 1983. The natural control of populations of butterflies and moths. Biological Review 58:461-481.

Dennis, R.L.H. and H.T. Eales. 1997. Patch occupancy in *Coenonympha tullia* (Müller, 1764) (Lepidoptera: Satyrinae): habitat quality matters as much as patch size and isolation. Journal of Insect Conservation 1:167-176.

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

Deschamps-Cottin, M., M. Roux, and H. Descimon. 1997. Larval food plant efficiency and laying preferences in *Parnassius apollo* L. (Lepidoptera, Papilionidae). Life Sciences 320:399-406.

Dethier, V.G. 1959. Egg laying habits of Lepidoptera in relation to available food. Canadian Entomologist 91:554-561.

Eales, H.T. and R.L.H. Dennis. 1998. Predicting site occupancy for *Coenonympha tullia* (Müller, 1764) (Lepidoptera: Nymphalidae, Satyrinae) using habitat parameters. Entomologist's Gazette 49:3-16.

Grossmueller, D.W., and R.C. Lederhouse. 1985. Oviposition site selection : an aid to rapid growth and development in the tiger swallowtail butterfly, *Papilio glaucus*.

Oecologia 66:68-73.

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

Haase, P., F.I. Pugnaire, S.C. Clark, and L.D. Incoll. 1997. Spatial pattern in *Anthyllis cytisoides* shrubland on abandoned land in southeastern Spain. Journal of Vegetation Science 8:635-642.

Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models and observations. Biological Journal of the Linnean Society 42:17-38.

Hanski, I., A. Moilanen and M. Gyllenberg. 1996. Minimum viable metapopulation size. The American Naturalist 147:527-541.

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

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

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

Harrod, R.J., B.H. McRae, and W.E. Hartl. 1999. Historical stand reconstruction in ponderosa pine forests to guide silvicultural prescriptions. Forest Ecology and Management 114:433-446.

Hill, J.K., C.D. Thomas, and O.T. Lewis. 1996. Effects of habitat patch size and isolation on dispersal by *Hesperia comma* butterflies: implications for metapopulation structure.

Journal of Animal Ecology 65:725-735.

Honda, K. 1995. Chemical basis of differential oviposition by Lepidopterous insects. Archives of Insect Biochemistry and Physiology 30:1-23.

Janz, N. and S. Nylin. 1997. The role of female search behaviour in determining host plant range in plant feeding insects: a test of the information processing hypothesis. Proceedings of the Royal Society of London, Series B 264:701-707.

Jolls, C.L. 1980. Phenotypic patterns of variation in biomass allocation in *Sedum lanceolatum* Torr. at four elevational sites in the Front Range, Rocky Mountains, Colorado. Bulletin of the Torrey Botanical Club 107:65-70.

Keyghobadi, N. *In preparation*. PhD thesis. University of Alberta, Edmonton, Alberta, Canada.

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

Larsen, D.R. and L.C. Bliss. 1998. Analysis of structure of tree seedling populations on a Lahar. Landscape Ecology 13:307-322.

Mappes, J. and A. Kaitala. 1995. Host-plant selection and predation risk for offspring of the parent bug. Ecology 76:2668-2670.

Mayhew, P.J. 1997. Adaptive patterns of host-plant selection by phytophagous insects. Oikos 79:417-428.

McCorkle, D.V. and P.C. Hammond. 1985. Observations on the biology of *Parnassius clodius* (Papilionidae) in the Pacific Northwest. Journal of the Lepidopterists' Society 39:156-162.

Meglécz, E, K. 1998. Population structure and variability of *Parnassius mnemosyne* (L.) (Lepidoptera) populations in the Carpathian basin. PhD Thesis. Department of Evolutionary Zoology and Humanbiology, Kossuth Lajos University, Debrecen, Hungary.

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

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

Murphy, D.D., M.S. Menninger, and P.R. Ehrlich. 1984. Nectar source distribution as a determinant of oviposition host species in *Euphydryas chalcedona*. Oecologia 62:269-271.

North, M. and J. Greenberg. 1998. Stand conditions associated with truffle abundance in western hemlock/douglas-fir forests. Forest Ecology and Management 112:55-66.

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

Oshaki, N. And Y. Sato. 1994. Food plant choice of *Pieris* butterflies as a trade-off between parasitoid avoidance and quality of plants. Ecology 75: 59-68.

Powers, J.S., P. Sollins, M.E. Harmon and J.A. Jones. 1999. Plant-pest interactions in time and space: a douglas-fir bark beetle outbreak as a case study. Landscape Ecology 14:105-120.

Ripley, B.D. 1976. The second-order analysis of stationary point processes. Journal of Applied Probabilities 13:255-266.

Roland, J., N. Keyghobadi, and S. Fownes. *In press*. Alpine *Parnassius* butterfly dispersal:

effect of landscape and population size. Ecology.

Roland, J., G. McKinnon, C. Backhouse, and P.D. Taylor. 1996. Even smaller radar tags on insects. Nature 381:120.

Root, R.B. and M. Kareiva. 1984. The search for resources by cabbage butterflies (*Pieris rapae*): ecological significance of markovian movements in a patchy environment. Ecology 65:147-165.

Schwarzwälder, B., M. Lörtscher, A. Erhardt and J. Zettel. 1997. Habitat utilization by the heath fritillary butterfly, *Mellicta athalia* ssp. *celadussa* (Rott.)(Lepidoptera: Nymphalidae) in montane grasslands of different management. Biological Conservation 82:157-165.

Scott, J.A. 1986. Butterflies of North America: a natural history and field guide. Stanford University Press, Stanford, California, USA.

Shreeve, T.G. 1986. Egg-laying by the speckled wood butterfly (*Pararge aegeria*): the role of female behaviour, host plant abundance and temperature. Ecological Entomology 11:229-236.

Singer, M.C. 1972. Complex components of habitat suitability within a butterfly colony. Science 176:75-77.

Sperling, F.A.J. and N.G. Kondla. 1991. Alberta swallowtails and parnassians: natural history, keys, and distribution. Blue Jay 49:183-192.

S-Plus. 1999. Modern Statistics and Advanced Graphics. Data Analysis Products Division, MathSoft, Seattle, USA.

Southwood, T.R.E. 1992. Ecological Methods, second edition. Chapman and Hall, Cambridge, USA.

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

Stanton, M.L. 1983. Spatial patterns in the plant community and their effects upon insect search. *In:* Herbivorous Insects. Sami Ahmad *ed.* Academic Press, Inc., New York, USA. pages 125-157.

Stanton, M.L. 1984. Short-term learning and the searching accuracy of egg-laying butterflies. Animal Behaviour 32:33-40.

Sutcliffe, O.L., C.D. Thomas, T.J. Yates and J.N. Greatorex-Davies. 1997. Correlated extinctions, colonizations and population fluctuations in a highly connected ringlet butterfly metapopulation. Oecologia 109:235-241.

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

Thompson, J.N. and O. Pellmyr. 1991. Evolution of oviposition behaviour and host preference in Lepidoptera. Annual Review of Entomology 36:65-89.

Weiss, S.B., K.K. Murphy, and R.R. White. 1988. Sun, slope, and butterflies: topographic determinants of habitat quality for *Euphydryas editha*. Ecology 69:1486-1496.

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

Wiklund, C. 1984. Egg-laying patterns in butterflies in relation to their phenology and the visual apparency and abundance of their host plants. Oecologia 63:23-29.

Williams, E.H. 1981. Thermal influences on oviposition in the montane butterfly *Euxphydryas gillettii*. Oecologia 50:342-346.

Williams, E.H. 1988. Habitat and range of *Euphydryas gillettii* (Nymphalidae). Journal of the Lepidopterists' Society 42:37-45.

Chapter 5

Topographical and Ecological Factors Determining Alpine and Subalpine Meadow Suitability and Quality for the Butterfly *Parnassius smintheus*

"In areas...where large vertebrates are but distant memories, small mammals, small cold-blooded vertebrates, invertebrates, and many plants are now the subjects of conservation efforts," (Murphy *et al.* 1990).

INTRODUCTION

"Suitable habitat" has been defined as containing all the resources required for the survival

of an animal population for many years (Hanski and Thomas 1994), and its availability

constrains both the abundance and distribution of populations. Strategies for conservation

and management of natural areas often consider the availability of suitable habitat for

vertebrate species that are rare, threatened, endangered, endemic, or of economic interest,

but which tend to respond to habitat at relatively large-scales. Typically habitat models are

developed for these species and used as tools to identify areas of greatest conservation

concern (Murphy *et al.* 1990, Bender *et al.* 1996). Identification of these required

resources and sampling for their estimation is needed to create models of habitat suitability,

such as habitat suitability index (HSI) models (Brooks 1997). This step is often time-

consuming and difficult for long-lived vertebrate species, where assessment of habitat

suitability involves consideration of seasonal and annual changes in forage availability and

preference (Merrill *et al.* 1999). Invertebrates, including butterflies, in contrast, are

relatively short-lived and all life stages typically have very specific resource requirements.

These facts make habitat suitability models for animals such as butterflies easier to develop

than for long-lived vertebrates. Many butterfly larvae feed on a single host plant species. In

addition, adult butterflies require access to mates, suitable microclimates for

thermoregulation and nectar to successfully reproduce (Wiklund 1977). Consideration of

the resource requirements of all life stages is, of course, necessary to develop a definition

of habitat suitability for butterfly species and is critical for establishing conservation goals

and priorities for rare and threatened butterflies (Schwarzwälder *et al.* 1997, Bergman

1999). Development of habitat suitability models for non-vertebrate species will

complement those of vertebrate species to better preserve the ecological integrity of natural

areas over a broader range of scales (Murphy and Wilcox 1986, Murphy *et al.* 1990).

Butterflies, because of their relatively narrow resource requirements and relatively limited

dispersal abilities, likely interact with the landscape at a much smaller scale than do large

vertebrates. Protecting and managing areas based solely on the habitat requirements of

large vertebrates is probably too coarse for smaller animals. As acknowledged by

Oostermeijer and van Swaay (1998), species such as butterflies, with very narrow

tolerances will be particularly sensitive to environmental changes.

During collections of the alpine butterfly, *Parnassius smintheus*, for a genetic study in

Banff National Park and Kananaskis Country, Alberta (Keyghobadi *in preparation*), it was

discovered that some alpine meadows where the larval host plant, *Sedum lanceolatum*, is

present did not support *P. smintheus* populations (personal observation). Although the

availability of the larval host plant is a critical component of habitat suitability for *P.*

smintheus, its presence does not guarantee that the meadow is suitable. Habitat

characteristics in addition to the presence of the larval host plant, such as nectar plants,

suitable microclimates, and enemy-free space, constrain the distribution of other species of

insects (Förare and Solbreck 1997, Quinn *et al.* 1998). Such effects may explain patterns

in occurrence of *P. smintheus* not accounted for by the distribution of the larval host plant.

Other known resource requirements of *P. smintheus* larvae include shelter sites,

microclimates which facilitate feeding and movement and suitable pupation sites (Chapter

3). *P. smintheus* larvae relocate to spaces under rocks and grass to rest or conceal

themselves. They are mobile only when it is sunny and warm, and larvae pupate on the soil

surface (Chapter 3). Adult *P. smintheus* nectar-feed on a variety of flowering plant species

including the larval host plant, and members of the rose family (Rosaceae) and the daisy

family (Asteraceae). They also require access to mates, and adult females need the

presence of the host plant to oviposit (Chapter 2). The goal of the first part of this chapter

was to identify the relative importance of meadow characteristics that explain patterns of *P.

smintheus* occurrence. Identification of these characteristics is essential for designing

management plans for species of concern (for an example of recovery plans based on patch

attributes that explain occurrence of an endangered vertebrate see Forys and Humphrey

[1999]).

Two statistical models explaining *P. smintheus* occurrence (presence/absence) were

generated: a coarse topographic model and a detailed ecological model. Data for the

ecological model are time-consuming and expensive to acquire and the intent of the coarse

model was to develop a workable model that would predict *P. smintheus* occurrence

without the need for detailed field sampling of vegetation and soil.

Many butterfly population models overlook the effects of habitat quality by assuming that

all "suitable" patches are of equal quality(Singer 1972, Thomas *et al.* 1992, Baguette and

Nève 1994, Hill *et al.* 1996) despite evidence that habitat quality affects the long-term

persistence of populations (Thomas *et al.* 1992, Hanski and Thomas 1994, Dennis and

Eales 1997 and 1999, Eales and Dennis 1998, Mousson *et al.* 1999). Quantifying habitat

quality will improve our understanding of butterfly population dynamics, and is needed to

predict how changes in habitat amount and structure will affect populations (Hanski 1991,

Hanski *et al.* 1996, Kuussaari *et al.* 1996, Sutcliffe *et al.* 1997). Habitat quality for

butterflies has traditionally been equated with the abundance of nectar plants and larval

host plants (Odendaal *et al.* 1989), and several studies have clearly demonstrated that

resource abundance is positively correlated with butterfly population size (Murphy *et al.*

1984, Williams 1988, Harrison *et al.* 1988, Odendaal *et al.* 1989, Carey 1994, Kuusaari *et*

al. 1996, Sutcliffe *et al.* 1997, Bergman 1999).

Roland *et al.* (*in press*) discovered that individual meadows on the same ridge- top support

different sized populations and densities of *P. smintheus*. Although all of these meadows

were capable of supporting *P. smintheus* populations, they are not of equal quality. In the

second part of this chapter, I determined which habitat characteristics are best related to *P.*

smintheus abundance, at a small-scale, on this ridge top. Again two statistical models were

made: a coarse topographical model and a detailed ecological model.

OBJECTIVES

1. To develop statistical models using coarse topographical variables that are easily extracted from topographic maps and Geological Survey of Canada maps, of: (a) *P. smintheus* occurrence, at a large-scale, in Banff National Park and Kananaskis Country; and, (b) *P. smintheus* abundance, at a small-scale among Jumpingpound Ridge submeadows.

2. To develop statistical models that incorporate additional detailed ecological variables to improve our ability to predict: (a) *P. smintheus* occurrence, at a large-scale, in Banff National Park and Kananaskis Country; and, (b) *P. smintheus* abundance, at a small-scale among Jumpingpound Ridge submeadows.

METHODS

Coarse topographical models

These models included: latitude, longitude, elevation, slope, aspect, and bedrock geology, as independent (predictor) variables. Bedrock geology is well known for these areas and Geological Survey of Canada (GSC) maps can be overlain on topographical maps.

Detailed ecological models

These models included: the above variables plus fine scale information — soil texture, soil depth to bedrock, presence or absence of the larval host plant (*S. lanceolatum*), and the plant community (as described by Detrended Correspondance Analysis, see below).

Because *P. smintheus* spend both the larval and pupal life-stages in contact with the soil,

surface soil attributes are likely important to these stages of the life-cycle. Presence of the

host plant is required for growth and survival of *P. smintheus* larvae, and adult butterflies

require nectar sources, providing energy for flight, mating and oviposition (Wiklund and

Åhrberg 1978).

Large-scale study of meadow suitability

Data were collected for subalpine and alpine meadows in Banff National Park and

Kananaskis Country, Alberta (Fig. 5-1) in the summers of 1997 and 1998. Sites were

selected based on known *P. smintheus* locations from collections for a study of the genetic

structure of populations (Keyghobadi *in preparation*). I sampled additional subalpine and

alpine meadows on sunny days during the peak of the butterfly flight season. Meadows

had no evidence of recent disturbances and were relatively pristine, although most

contained hiking trails that host small parties of hikers and mountain bikers. Meadows

were grouped into two categories: *P. smintheus* present or *P. smintheus* not found

(assumed absent). Site variables estimated at each site were: latitude, longitude, elevation,

slope, aspect, bedrock geology, soil depth to bedrock, soil texture, plant community and

larval host plant (*S. lanceolatum*) presence.

Coarse Topographical Model

Longitude and latitude were measured at a representative location within each site using
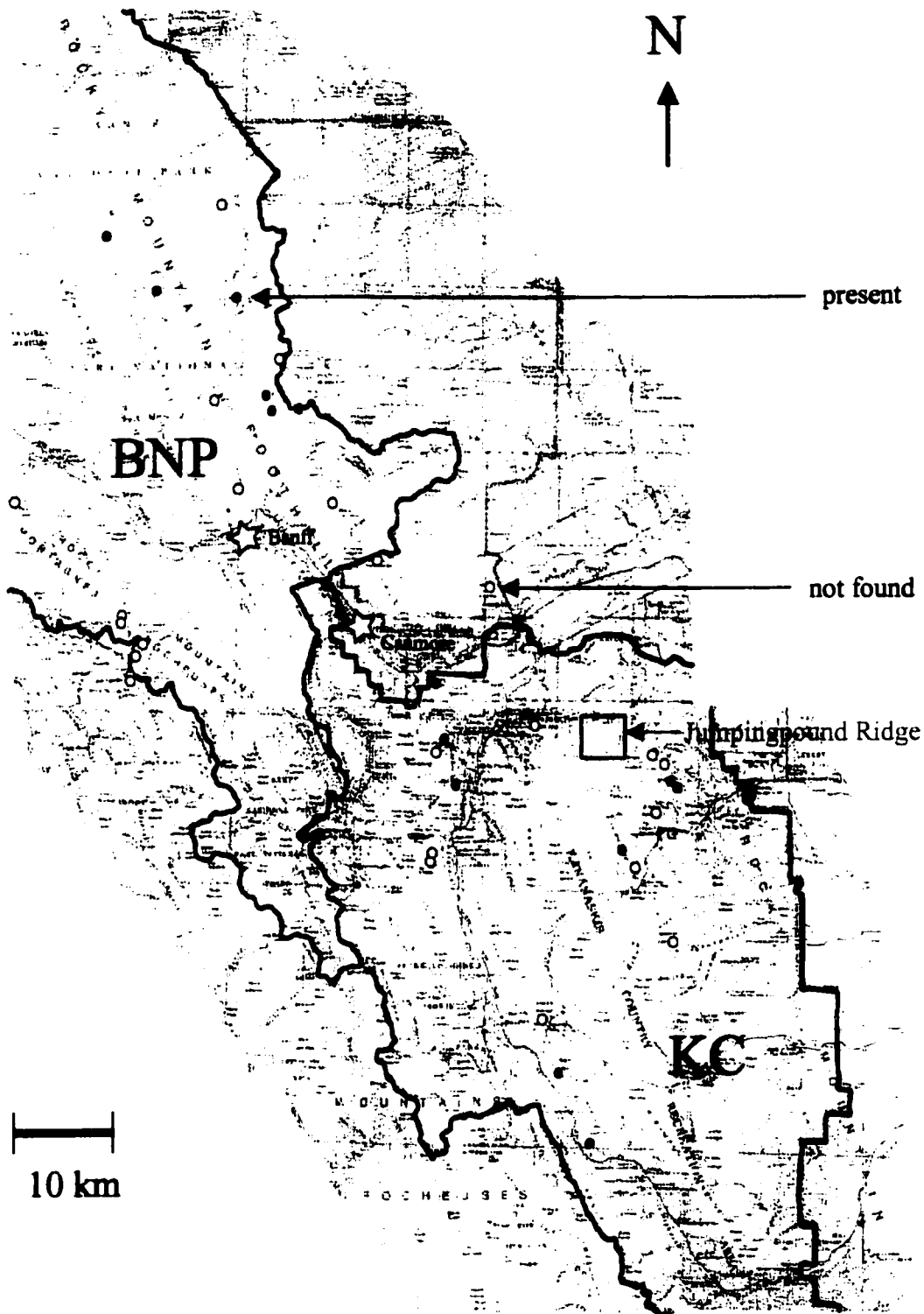
Fig. 5-1. Large-scale study sites in Banff National Park (BNP) and Kananaskis Country (KC), Alberta, where *P. smintheus* were present or not found. The perimeters of the park boundary and recreation area are outlined in black. Jumpingpound Ridge (red square) is the location of the small-scale study.

both GPS (Garmin 45 XL) coordinates and topographical map coordinates. GPS

coordinates were used in later analyses after verifying with the topographical map

coordinates. Longitude and latitude were measured in degrees and minutes and were

converted into minutes for analysis. Elevation was measured in metres using a Thommen,

Altitrek altimeter and was calibrated each morning at the University of Calgary Kananaskis

Field Station at Barrier Lake (51°02'N, 115°03'W; elevation 1210 metres) for daily

differences in barometric pressure. Slope was estimated using a clinometer. The angle was

estimated between the observer and a second person standing 25 metres downslope.

Aspect was determined at the same location, using a compass, adjusted for declination

from true north. Aspect was converted into four categories each 90 degrees wide (1 to 90,

91 to 180, 181 to 270, and 271 to 360) for inclusion in regression analyses. Bedrock

geology was determined from GSC maps for Banff National Park (1:50,000) and for

Kananaskis Country (1:100,000). Sites were classified into one of two bedrock geology

categories: limestone present or limestone absent. These categories were used because

limestone and other calcareous substrata are known to affect alpine plant distribution and

communities (Bamberg and Major 1968, Billings 1988).

Detailed Ecological Model

Finer-scale abiotic data gathered in the meadows include soil depth and soil texture. One

hole was dug perpendicular to the soil surface until bedrock was reached. The distance

from the soil surface to the bedrock was measured in centimetres. Most soils did not

display any vertical horizon development. The texture of the soil was classified using texture field tests (Corns and Annas 1986). If more than one soil horizon was present, only the soil texture of the uppermost horizon was considered in the analysis because it is likely to be the most relevant to the larval and pupal life-stages of *P. smintheus*. Larvae crawl on the soil and use rocks and soil as shelter sites during climatic extremes. Larvae also pupate on the soil surface. The soil texture classes were converted to percent sand and percent clay based on the soil textural triangle (Corns and Annas 1986). These percentages were then converted to binary variables for analyses. Soils with greater than 49% and less than 50% sand were classified as 1 and 0, respectively. Soils with greater than 14% clay and less than 15% clay were classified as 1 and 0, respectively. These categories were determined from natural breaks in the percent sand and percent clay histograms.

Meadows were searched for *S. lanceolatum*, and plant community data were estimated for each meadow. Two transects, 20 metres in length and perpendicular to each other, were placed in each meadow. The percent cover of individual plant species, including *S. lanceolatum*, was estimated in ten random, rectangular quadrats (10 cm by 20 cm) along each of the transects, for a total of 20 quadrats per meadow. Percent cover estimates for each species were summed for each meadow. Of all species sampled only those considered to be a potential nectar source for adults (members of the families Asteraceae, Rosaceae and Crassulaceae), a larval host plant (*S. lanceolatum*), or a shelter site (rocks, sedges, grasses, and leaf-litter) were included in later analyses. Data reduction of percent cover

estimates for the above species, was accomplished using a Detrended Correspondance

Analysis (DCA) in CANOCO. Only the first three axes calculated by the DCA (DCA1,

DCA 2 and DCA3) were used in the regression analyses predicting *P. smintheus*

occurrence.

Small-scale study of meadow quality

Site variables were measured at the centre of each Jumpingpound Ridge submeadow (Fig.

5-1 and Fig. 5-2). All topographical and finer-scale abiotic and plant community data

except bedrock type were gathered as described above for the large-scale study. Only 3

out of 25 sites had no limestone component of their bedrock geology. Therefore, the

effects of geology are not discussed in depth. Estimates of percent sand and clay in the soil

were not converted to binary variables. *S. lanceolatum* abundance was estimated in the

summer of 1998 using ten, five-metre diameter circular plots randomly placed in

submeadow. All flowering and non-flowering *S. lanceolatum* plants within the plot were

counted. Although some *S. lanceolatum* plants are clonal, all rosettes were treated as

individuals in the analyses because they were considered as separate food sources (see

North and Greenberg (1998) for similar consideration of clonal food plants). Subsequent

analysis used the mean of the log-transformed *S. lanceolatum* abundances from the circular

plots in each submeadows.

Indices of butterfly abundance were based on mark/recapture data collected by Roland *et*
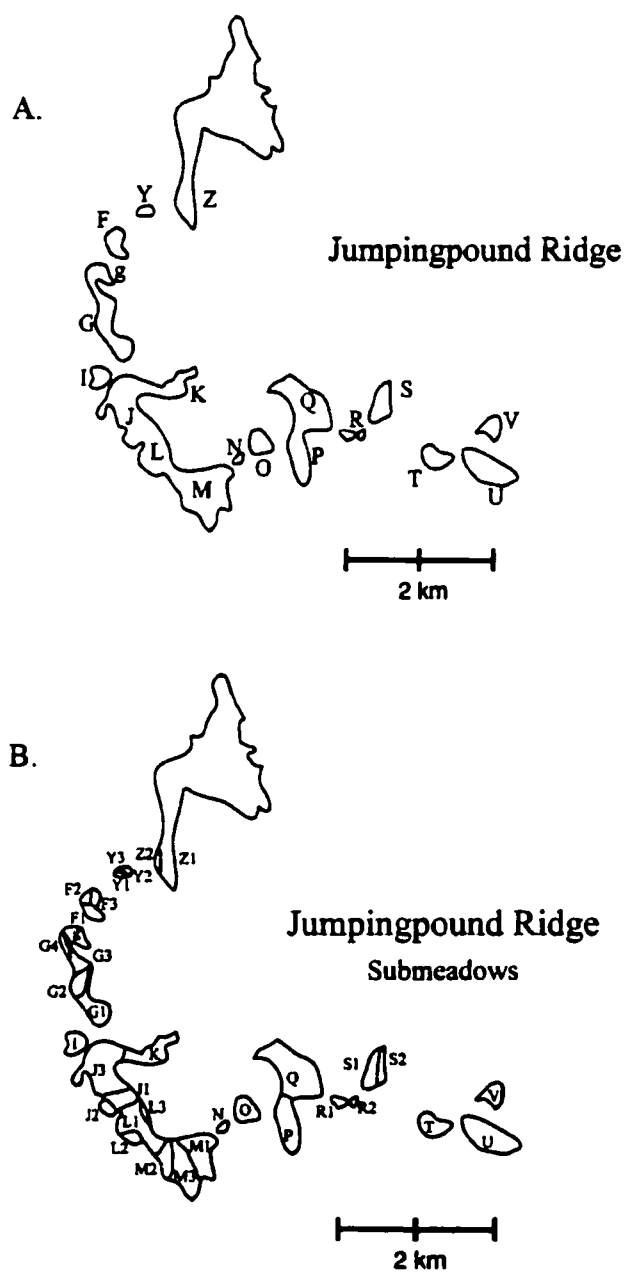
Fig. 5-2. Meadows (a) and submeadows (b) on Jumpingpound Ridge, Kananaskis Country, Alberta (50 °57'N, 114°55' W).

al. (*in press*) during the summer of 1995. The number of marked butterflies in each submeadow was determined using the coordinates of the location of initial capture of each butterfly. It is possible to combine butterfly population indices from 1995 with site variables from 1997 and 1998 because although absolute numbers of butterflies vary from year to year, high population meadows tend to remain so (Roland *unpublished results*), and *S. lanceolatum* abundance changes little from year to year.

ANALYSES

Large-scale study of meadow suitability

Coarse Topographical Model

Variables included in the final model were determined based on a forward step-wise selection procedure with a cut-off of p<0.15 in SYSTAT® (1998). A cut-off of p<0.15 was selected because the traditional cut-off of p<0.05 is often too statistically rigorous for descriptive-biological studies using logistic regression analysis (Hosmer and Lemshow 1989). Additionally, those variables included in the final model were tested for interaction with each other. The log-likelihood ratio test was done to assess the significance of the final model.

To assess the fit of the regression model and identify sites which may be poorly fit by it, a Hosmer-Lemeshow (goodness-of-fit) test was conducted and regression diagnostics were assessed. The Hosmer-Lemeshow test compares the observed frequency of subjects (*e.g.*,

sites) among the estimated logistic probability categories (g) from the model to those expected from the model. The resulting test-statistic ( ) can be compared to the chi-square distribution to assess its significance. The degrees of freedom are calculated by subtracting 2 from the number of categories (g-2) used in the calculation of . A significant result (p<0.05) for the Hosmer-Lemeshow test indicates that the model is not a good fit to the data and a non-significant result (p>0.05) suggests that the model is a good fit to the data. As suggested by Hosmer and Lemeshow (1989) the estimated logistic probability was plotted against: (a) the change in deviance resulting from the removal of individual sites; (b) the change in Pearson's χ^2 resulting from removal of individual sites; and, (c) the change in influence of each site on the value of estimated parameters when individual sites were removed. These plots were visually examined to identify sites poorly fit by the model parameters and those that have a great deal of influence on the values of the estimated parameters.

A forward-stepwise discriminant function analysis (DFA) with a cut-off of p<0.15 (SYSTAT® 1998) was performed using the same predictor variables, in order to determine which variables best discriminate between sites with and without *P. smintheus*. The analysis included an estimate of the discriminatory power and percentage correct classification of the sites.

Detailed Ecological Model

For this model, the first and second plant community axes from the DCA analyses, *S. lanceolatum* presence/absence, soil depth to bedrock, and soil texture were added to those variables found to be significant in the coarse topographical model. Independent variables included in the detailed ecological model were identified using a forward step-wise selection procedure with a cut-off of $p<0.15$, in SYSTAT®(1998). The variables included in the final model were tested for interaction with each other. Assessment-of-fit of the model was achieved using the same methods as were used for the topographical model. Another DFA of these predictor variables was conducted to determine the discriminatory power and the percentage correct classification of the sites.

Small-scale study of meadow quality

Coarse Topographical Model

Latitude, longitude, elevation, slope and aspect were assessed in their effect on the number of marked butterflies (log_{10} transformed) in each meadow using a multiple linear regression. Variables included in the final model were determined based on forward step-wise selection procedure with a cut-off of $p<0.05$, in SYSTAT®(1998). Variables were tested for multicollinearity with an adjustment for experimentwise error (Sokal and Rohlf 1998).

Detailed Ecological Model

Plant community factors, *S. lanceolatum* abundance, depth to bedrock, and soil texture

were added to those variables included in the final coarse topographical model, and were

selected based on forward step-wise selection procedure with a cut-off of p<0.05, in

SYSTAT®(1998). Variables were tested for multicollinearity with adjustment for

experimentwise error.

Because I had data on *S. lanceolatum* abundance for these meadows, a similar series of

multiple-linear regressions were conducted, using the coarse topographical variables and

detailed ecological variables to predict *S. lanceolatum* abundance. The *S. lanceolatum*

analysis was performed to interpret regression findings and to determine if the same

variables are influencing both *S. lanceolatum* and *P. smintheus* abundance, or possibly if

the effects on *P. smintheus* abundance simply reflect those effects on host plant abundance.

RESULTS

Large-scale study of meadow suitability

Coarse Topographical Model

Only slope and elevation were significant predictor variables for the coarse topographical

model predicting *P. smintheus* occurrence (presence/absence) (Table 5-1). The model

predicted that sites with steeper slopes and in the middle range of elevations sampled were

more likely to have *P. smintheus*. The model fit the data well for all sites ($_{1,6}$=6.46,

p=0.59) except for Highwood meadow, which supported *P. smintheus* populations (Fig.

5-3), despite being predicted to not have butterflies. The failure of the model to classify

this site correctly is likely because the meadow had a small slope and relatively high

elevation. Regression diagnositics suggested that the model was a good fit to the data and

that no individual site was exerting too much influence on the model parameters.

Table 5-1. The large-scale regression statistics for the **coarse topographical** multiple logistic regression model predicting *P. smintheus* occurrence in Banff National Park and Kananaskis Country, Alberta (N=37). The log-likelihood of the overall model (LL) is presented at the bottom of the table. The significance of the model is represented by both the log-likelihood ratio test statistic (G), which compares the log-likelihood of the constants-only model to that of the model including the significant variables, and McFadden's ρ^2, which is an expression of the likelihood ratio test and is analogous to the R^2 from linear regression, however unlike values for R^2, ρ^2 values lying between 0.2 and 0.4 indicate that the model is good.

	Estimate (SE)	t	p	Odds Ratio	95% CI
Constant	5.99(5.0512)	1.1854	0.236		
Slope	0.0547(0.0276)	1.9806	0.05	0.9468	0.897-0.999
Elevation	-0.0038(0.0024)	-1.561	0.119	1.0038	0.999-0.101

LL=-20.32; G=7.53, df=2, p=0.026; McFadden's ρ^2=0.16

The DFA using topographical data, also identified slope and elevation as the variables that

maximally discriminate among the 37 sites for *P. smintheus* occurrence (presence/absence).

The Wilk's lambda estimate (0.81) indicates that the discriminatory power of the

topographical DFA is poor, despite the model successfully classifying 70% of the sites.

Misclassified sites included both sites with *P. smintheus* and those without.

Fig. 5-3. A scatterplot of *P. smintheus*-present and *P. smintheus*-not found sites for the two significant topographical predictor variables of *P. smintheus* occurrence, slope (degrees) and elevation (metres).

Detailed Ecological Model

Summary information for data reduction of plant community are presented in Table 5-2.

Two sites that were missing soil texture data were removed from the analyses. The

inclusion of fine-scale variables improved the topographical model, reducing the residual

deviance of the topographical model. The binary variable for proportion of sand in the soil

and scores from the first and third DCA axes of the plant community data were significant

variables in the detailed ecological model (Table 5-3 and Fig. 5-4). Inclusion of these

variables rendered the topographical variables non-significant (Table 5-1). Diagnostic plots

and statistical tests ($_{1,2}$=2.82, p=0.59) indicated that the model fit the data well. In order

to get sufficiently high observed counts of sites in the groupings for the Hosmer-Lemeshow

test, the number of groupings was small (g=4). The Hosmer-Lemeshow test statistic

therefore, should be interpreted with caution, when data are divided into less than six

groups because the test becomes less powerful (Hosmer-Lemeshow 1989). Visual

assessment of regression diagnostics, however supported the Hosmer-Lemeshow test result

and suggested that the model was a good fit. Regression diagnostics further indicated that

no single site exerted too much influence on the model parameters.

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Table 5-2. Results from the reduction of plant community data collected for the large-scale model of *Parnassius smintheus* occurrence, using detrended correspondance analysis (DCA). The eigenvalue for each DCA axis is the measure of importance of that axis in the ordination of sites, and ranges between 0 and 1. Larger values mean greater importance.

	Axis 1	Axis 2	Axis 3	Axis 4
eigenvalue	0.596	0.285	0.176	0.124
cumulative % of variance explained	18.7	27.6	33.2	37

Table 5-3. Regression statistics for the large-scale **detailed ecological** logistic regression predicting *P. smintheus* occurrence in Banff National Park and Kananaskis Country, Alberta (N=35). The log-likelihood of the model (LL) and the significance of the overall model (G and McFadden's ρ^2) are presented below the table.

	Estimate (SE)	t	p	Odds Ratio	95% CI
Constant	-0.034 (2.86)	-0.12	0.91		
Catsand_0	-1.839 (0.936)	-1.96	0.1	0.159	0.025-0.996
DCA(1)	2.035 (1.129)	1.8	0.1	0.765	0.837-69.93
DCA(3)	-2.888 (1.944)	-1.49	0.14	0.056	0.0012-2.512

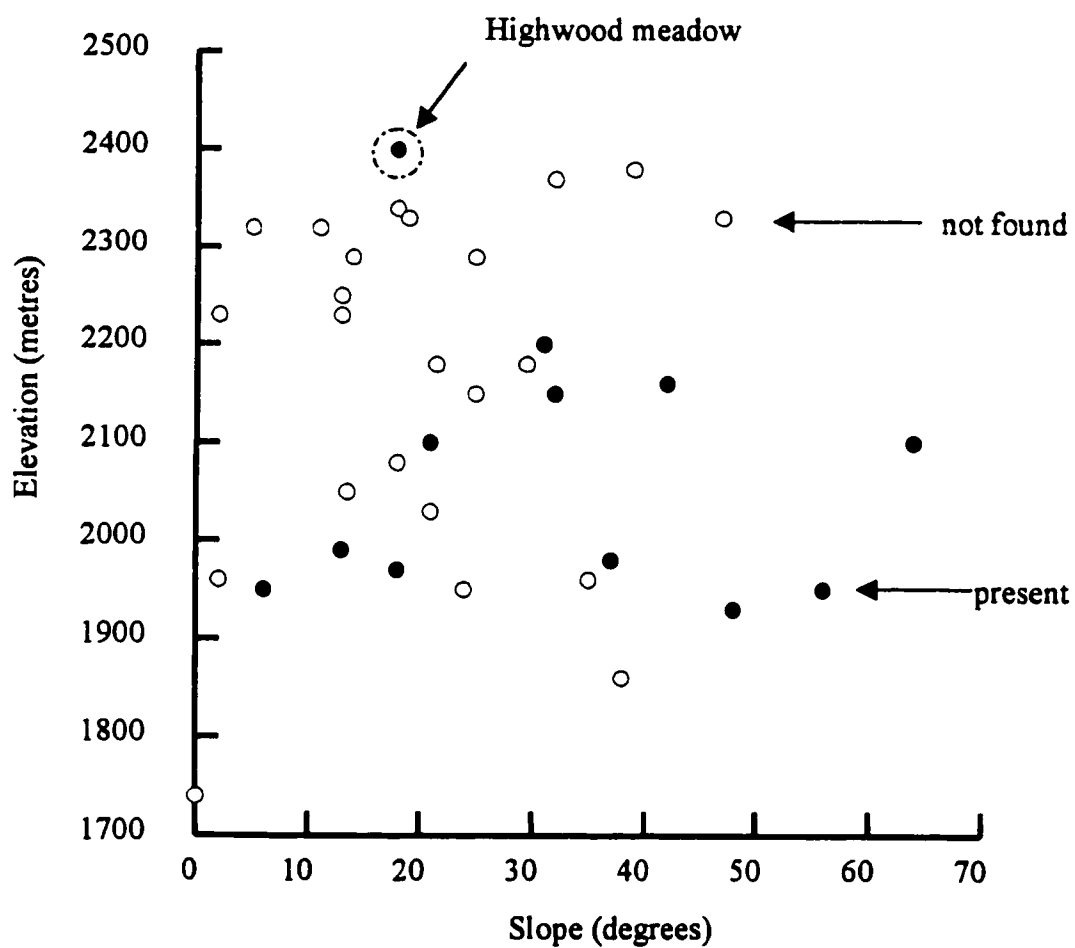LL=-17.14; G=10.72, df=3, p=0.013; McFadden's ρ^2=0.24

o
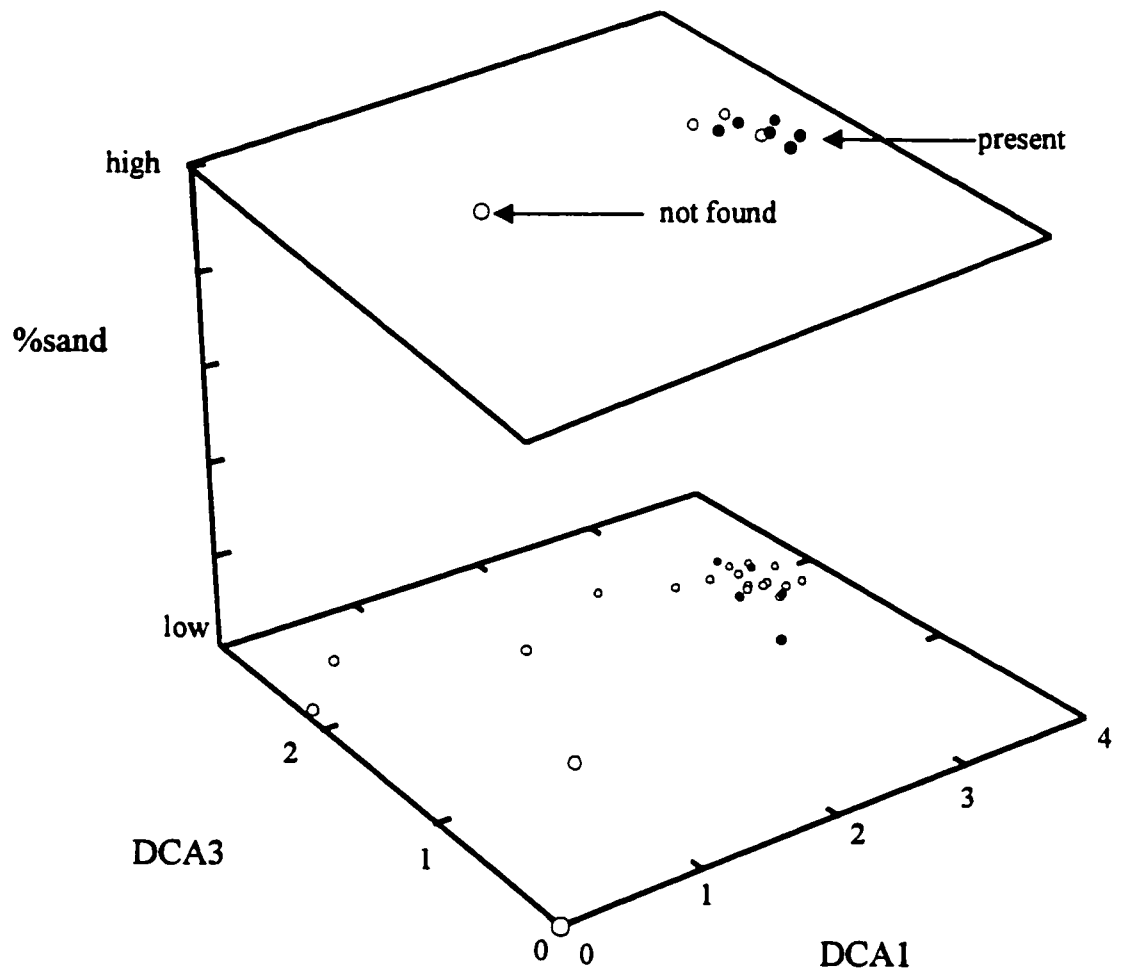
Fig. 5-4. Scatterplot of *P. smintheus*-present and *P. smintheus*-not found sites for the three significant ecological predictor variables of *P. smintheus* occurrence: two plant community axes (DCA1 and DCA3), and the binary variable for percent sand in the soil.

The DFA including finer-scale variables identified the percent of sand in the soil, the first

DCA axis, and the soil depth to bedrock as variables that maximally discriminate among the

35 sites for *P. smintheus* occurrence. A Wilk's lambda estimate

of 0.74 suggests that the discriminatory power of the detailed ecological DFA is poor, but

an improvement over the coarse topographical DFA. The detailed ecological DFA

successfully classified 74% of sites. Misclassified sites include sites which have populations

of *P. smintheus* and sites which do not.

Small-scale study of meadow quality

Coarse Topographical Model

There were significant correlations between some of the predictor variables (Table 5-4). In

cases of multicollinearity, Zar (1996) advises deletion of one or more of the intercorrelated

independent variables followed by re-analysis. Only the most significant of the correlated

predictor variables was included in the model. The topographical model included latitude

and slope as significant predictor variables (Table 5-5). Bedrock geology was similar for

most meadows, due to the small scale of the study area. Only three meadows (S, U and V

in Fig. 5-2) had a limestone component. Neither U nor V support *P. smintheus*

populations nor do they contain abundant *S. lanceolatum*. Only part of meadow S (S2)

supports populations of *P. smintheus* and contains abundant *S. lanceolatum*. S1 had few

butterflies and no *S. lanceolatum* plants.

Table 5-4. Significant correlations between independent predictor variables in the coarse topographical model of *P. smintheus* population abundance on Jumpingpound Ridge (N=25).

Correlation	Pearson's r	p-value
Latitude vs. Longitude	0.57	0.02
Longitude vs. Elevation	0.48	0.09

Table 5-5. The Jumpingpound Ridge submeadow regression statistics from multiple linear regression of the effect of **coarse topographical** site variables on the abundance of *P. smintheus* butterflies (log_{10} transformed).

Variable	Coefficient (SE)	Standardized Coefficient	t	significance *p*
Latitude (minutes)	0.49 (0.20)	0.399	2	0.021
Slope (degrees)	0.075 (0.0059)	0.4738	3	0.0072

R^2 for the full model is 0.46; N=25

Detailed Ecological Model

The results of the plant community data reduction are presented in Table 5-6. Significant correlations were detected between some of the independent variables (Table 5-7). Only the most biologically relevant of the correlated predictor variables was considered in the model (see similar treatment of correlated independent variables by Forys and Humphrey [1998]); the ecological variable was retained in favour of its correlated topographical variable. Only one fine-scale variable was significant, *S. lanceolatum* abundance (Table 5-8), and increased the amount of variation in butterfly abundance explained by the coarse topographical model by 10% (Table 5-5); the DCA axes describing plant community

(DCA1, DCA2 and DCA3) and soil depth and texture were not significant.

Table 5-6. Results from the reduction of plant community data collected for the small-scale model of *Parnassius smintheus* abundance, using detrended correspondance analysis (DCA).

	Axis 1	Axis 2	Axis 3	Axis 4
eigenvalue	0.652	0.329	0.189	0.086
cumulative % of variance explained	28.8	43.4	51.7	55.5

Table 5-7. Significant correlations between independent predictor variables in the detailed ecological model of *P. smintheus* population abundance on Jumpingpound Ridge (N=25).

Correlation	Pearson's r	p-value
$\log_{10}$ *Sedum lanceolatum* vs. Longitude	0.58	0.1
Slope (degrees) vs. Percent Sand In Soil	0.69	0

Table 5-8. The Jumpingpound Ridge submeadow regression statistics from multiple linear regression of the effect of detailed ecological variables on the abundance of *Parnassius smintheus* butterflies ($\log_{10}$ transformed).

Variable	Coefficient (SE)	Standardized Coefficient	t	significance p
$\log_{10}$ *Sedum lanceolatum*	0.531 (0.15)	0.55	12.6	0.002
Slope (degrees)	0.012 (0.006)	0.33	4.6	0.042

R^2 for the full model is 0.56; N=25

Variables that best explain butterfly abundance at Jumpingpound Ridge similarly are the

best predictors of the abundances of the host plant, *S. lanceolatum* (Table 5-9). There

were significant correlations between some of the predictor variables in the model for host

plant abundance (Table 5-10).

Table 5-9. The Jumpingpound Ridge submeadow regression statistics from multiple linear regression of the effect of **coarse topographical** and **detailed ecological** variables on the abundance of *Sedum lanceolatum* ($\log_{10}$ transformed).

Variable	Coefficient (SE)	Standardized Coefficient	t	significance *p*
latitude (minutes)	0.24 (0.067)	0.565	13	0.0014
Slope (degrees)	0.014 (0.0059)	0.371	5.8	0.025

R^2 for the full model is 0.48; N=25

Table 5-10. Significant correlations between independent predictor variables in the **coarse topographical** and **detailed ecological** of *S. lanceolatum* abundance on Jumpingpound Ridge (N=25).

Correlation	Pearson's r	p-value
Latitude vs. Longitude	0.57	0.02
Elevation vs. Longitude	0.28	0.09

DISCUSSION

Murphy and Wilcox (1986) warn that critical resource requirements for butterfly species

are often missed during studies of vertebrate habitat suitability, and that butterflies may be

more sensitive than vertebrates to intensive local fragmentation of habitat. In their review

of butterfly conservation New *et al.* (1995) also point out that insects have experienced

extinctions in ecosystems that managed to conserve rare vertebrates and plants. My study

attempts to address these concerns. I assessed large-scale habitat suitability of patches for

a native butterfly using two levels of information: coarse topographical information and

detailed ecological information. At a much smaller spatial scale, the quality of suitable

habitat patches was also investigated using the same levels of information. The relative

success of these two scales of habitat evaluation is discussed in the context of butterfly

population dynamics and conservation of invertebrates.

In Alberta *P. smintheus* inhabits subalpine and alpine meadows where its larval host plant,

S. lanceolatum grows. Although distribution of this butterfly is of necessity constrained by

the distribution of its host plant, not all meadows containing the host plant support

populations of butterflies. This is not unusual because host plant ranges are often greater

than those of the butterflies dependent on them (Quinn *et al.* 1998). This study attempted

to identify those topographic and ecological variables, in addition to host plant occurrence,

which describe suitability and quality of these meadows for populations of *P. smintheus* at

both the large and smaller scales. Modelling of both *P. smintheus* distribution in the

province of Alberta and *P. smintheus* abundance in a chain of subalpine meadows was

conducted.

Slope and elevation were the best large-scale predictors of *P. smintheus* occurrence.

Within the range of meadows sampled, butterflies were most likely to occur on slopes

greater than 30°, with poorly developed soils that are well drained. Drainage of soils likely

affects the chances of successful pupation and emergence of adult butterflies – all of which

takes place on the soil surface. As well, these well-drained soils are also preferred by the

larval host plant *S. lanceolatum* (Clausen 1975). Although sites ranged in elevation from

1740 m to 2400 m, most butterfly meadows were between 1900 m and 2000 m. In the

Kananaskis Valley the average treeline is approximately 2200 m but may be as high as 2450

m (Williams 1990) and in Banff National Park, treeline is generally at 1950 m on north-

facing slopes and 2250 m on south-facing slopes (Achuff 1982). *P. smintheus* were less

likely to occur in meadows lying far above treeline and was found more often at sites

sampled at, or just below these elevations.

If the global warming trend continues, treeline in alpine areas will likely rise (Grabherr *et*

al. 1994). Suitable habitat for the host plant *S. lanceolatum* and *P. smintheus* may

decrease in size and become more isolated from other suitable habitat patches. Although

some butterflies have been able to track shifts in habitat poleward (Parmesan *et al.* 1999) it

is clear that these changes in the configuration of suitable habitat may have implications for

P. smintheus persistence. Increasing habitat patch area and decreasing isolation of habitat

patches from each other in the landscape have been suggested as management strategies to

preserve the endangered *Parnassius mneomosyne*, which occupies naturally fragmented

habitat patches in mountains of north-east Hungary (Meglécz *et al.* 1999).

Meadows with sandy soils (greater than 49% sand) were more likely to have butterfly

populations. This again, may be due to the effect of soil texture on the host plant. Sites

with high values for DCA1 and low values for DCA3 were more likely to have butterfly

populations. It was expected that plant community would be important in describing

suitability of sites for *P. smintheus* due to the tight link between butterflies and larval host

plants as well as their need for nectar resources. Models containing detailed site

information explained more of the variability in *P. smintheus* occurrence than models which

considered only topographical information (McFadden's ρ^2 < 0.2 for the coarse

topographcial model and McFadden's ρ^2 > 0.2 for the detailed ecological model). Neither

model explained a large amount of the variation in butterfly occurrence and this is likely

attributable to the small sample size (37 sites) and the structural complexity of alpine

environments. Haslett (1997) reports that mountain landscapes are spatially

heterogeneous. Sampling at a random location within a subalpine or alpine meadow may

not be appropriate for measuring habitat suitability for insect species. An increased sample

size, estimates of nectar plant abundance during the flight season, and host plant abundance

as additional predictor variables, may improve the model's ability to explain occurrence of

P. smintheus in this region. Host plant abundance was measured for the small-scale model

predicting *P. smintheus* abundance and is positively correlated with *P. smintheus*

abundance (Chapter 4), and therefore may be an important factor in determining butterfly

distribution in general.

At the small-scale, on Jumpingpound Ridge, the coarse topographical model, analogous to the coarse topographical model for *P. smintheus* occurrence, identified slope and latitude as important predictor variables for *P. smintheus* abundance. Butterfly abundance was positively correlated with slope and increased towards the north-west end of the ridge. Jumpingpound Ridge runs from south-east to north-west (Fig. 5-2) and there is an obvious gradient in habitat quality from poor to good running in this direction. The coarse topographical model explained 46% of the variation in population size along Jumpingpound Ridge. In the model containing detailed ecological information, slope continued to contribute significantly to the regression (Table 5-8); however, the abundance of the larval host plant, *S. lanceolatum*, best explained the variation in abundance of *P. smintheus* and replaced location (x,y) in the regression equation. Location on the ridge itself was correlated with *S. lanceolatum* abundance (r=0.58, p=0.098). The gradient in host plant abundance explains biologically why the topographical model explained so much of the variation in population size of *P. smintheus*. Slope was positively correlated with percent sand in the soil and its presence in the regression likely represents soil drainage. The detailed ecological model explained 56% of the variation in *P.smintheus* abundance on Jumpingpound Ridge.

To explore whether the significant predictor variables for *P. smintheus* abundance are also influencing *S. lanceolatum* abundance (and hence *P. smintheus* indirectly) I used a series of similar multiple linear regression models. Forty-eight percent of the variation in *S.*

lanceolatum abundance is explained by slope of the meadows and by their longitude on the

ridge-top, as was the case for *P. smintheus* abundance. Therefore, when *S. lanceolatum* is

included as the predictor variable in the *P. smintheus* detailed ecological model, it is already

accounting for some of the effects seen for other meadow characteristics. There are

however, additional effects of slope on *P. smintheus* abundance because slope is significant

in addition to the variable for *S. lanceolatum* (see both Table 5-8 and Table 5-9).

Two studies of other butterfly species identify microclimate diversity within habitat patches

as an important descriptor of habitat quality. For the Karner blue butterfly (*Lycaeides*

melissa samuelis) the abundance of the larval host plant, lupine (*Lupimus perennis*), and the

availability of a mixture of sun and shade contributed to habitat quality of grasslands

(Grundel *et al.* 1998). Weiss *et al.* (1988) found that each larval instar of the checkerspot

butterfly, *Euphydryas editha*, has different microclimate preferences which are influenced

by the prevailing weather. As a result, the quality of suitable grassland habitats for this

butterfly is related to measurements of extremely fine-scale topographic diversity, on the

order of less than 10 cm. Measures of within-habitat were not considered in the present

study of *P. smintheus* but may be worth considering for future studies of its habitat quality.

Such fine-scale models may identify additional meadow characteristics contributing to

quality not detected by the present study, such as aspect.

Slope was identified as an important predictor variable in both occurrence and abundance

models of *P. smintheus*. Soil texture and slope likely combine to describe soil drainage and are obviously important predictor variables for both habitat suitability and quality of meadows for *P. smintheus*. Again, these may be correlates for *S. lanceolatum* abundance. To tease apart soil drainage effects on *P. smintheus* larval and pupal life-stages directly, experimental studies quantifying *P. smintheus* survival success in meadows of different drainage classes (hydric, mesic, and xeric meadows) should be conducted.

The weakness of both the logistic regression model and the DFA for *P. smintheus* occurrence suggests that using the present large-scale habitat suitability model to predict distributions of *P. smintheus* in this region is likely premature. Although the comparison is not directly quantified, the model of *P. smintheus* abundance at the small-scale on Jumpingpound Ridge was relatively more successful than the model of *P. smintheus* occurrence. It seems that modelling occurrence of *P. smintheus* on a large scale may be more difficult than understanding smaller scale variations in their abundance. *P. smintheus* populations are best described by small-scale description of habitat, which is likely the case for many invertebrates (Murphy and Wilcox 1986). This finding should concern managers of natural areas who depend on coarse landscape classifications to identify hot-spots of conservation interest by simply categorizing the landscape into areas of suitable and unsuitable habitat.

The small-scale habitat quality model is strong and should be combined with the *P.*

smintheus population-movement models from Roland *et al.* (*in press*) and Keyghobadi *et*

al. (*in press*) to identify the relative importance of habitat configuration (their studies) and

habitat quality (this study) in determining abundance of *P. smintheus* and in determining

movement of adults between meadows. The preliminary models from this study should be

used to develop stronger models for predicting *P. smintheus* occurrence and abundance.

These models may one day provide a much-needed smaller-scale perspective of subalpine

and alpine meadow integrity to managers of these areas in the Canadian Rockies.

LITERATURE CITED

Achuff, P.L. 1982. Vegetation: introduction and methods. *In* Ecological (Biophysical) Land Classification of Banff and Jasper National Parks. Volume II. W.D. Holland and G.M. Coen *editors*. Alberta Institute of Pedology, Environment Canada, Edmonton, Canada.

Baguette, M. and G. Nève. 1994. Adult movements between populations in the specialist butterfly *Proclossiana eunomia* (Lepidoptera, Nymphalidae). Ecological Entomology 19:1-5.

Bamberg, S.A. and J. Major. 1968. Ecology of the vegetation and soils associated with calcareous parent materials in three alpine regions of Montana. Ecological Monographs 38:127-167.

Bender, L.C., G.J. Roloff, and J.B. Haufler. 1996. Evaluating confidence intervals for habitat suitability models. Wildlife Society Bulletin 24:347-352.

Bergman, K. 1999. Habitat utilization by *Lopinga achine* (Nymphalidae: Satyrinae) larvae and ovipositing females: implications for conservation. Biological Conservation 88:69-74.

Billings, W.D. 1988. Alpine vegetation. *In* North American Terrestrial Vegetation. M.G. Barbour and W.D. Billings *editors*. Cambridge University Press, Cambridge. pages 391-420.

Brooks, R.P. 1997. Improving habitat suitability index models. Wildlife Society Bulletin 25:163-167.

Carey, D.B. 1994. Patch dynamics of *Glaucopsyche lygdamus* (Lycaenidae): correlations between butterfly density and host species diversity. Oecologia 99:337-342.

Clausen, R.T. 1975. *Sedum* of North America North of the Mexican Plateau. Cornell University Press, Ithaca, New York, USA.

Corns, I.G.W. and R.M. Annas. 1986. Field guide to forest ecosystems of West-Central Alberta. Northern Forestry Centre, Minister of Supply and Services, Canada.

Dennis, R.L.H. and H.T. Eales. 1997. Patch occupancy in *Coenonympha tullia* (Müller, 1764) (Lepidoptera: Satyrinae): habitat quality matters as much as patch size and isolation. Journal of Insect Conservation 1:167-176.

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

Eales, H.T. and R.L.H. Dennis. 1998. Predicting site occupancy for *Coenonympha tullia* (Müller, 1764) (Lepidoptera: Nymphalidae, Satyrinae) using habitat parameters. Entomologist's Gazette 49:3-16.

Förare, J. and C. Solbreck. 1997. Population structure of a monophagous moth in a patchy landscape. Ecological Entomology 22: 256-263.

Forys, E. and S.R. Humphrey. 1999. The importance of patch attributes and context to

the management and recovery of an endangered lagomorph. Landscape Ecology 14:177-185.

Grabherr, G., M. Gottfreid, and H. Pauli. 1994. Climate effects on mountain plants. Nature 369:6480.

Grundel, R., N.B. Pavlovic, and C.L. Sulzman. 1998. The effect of canopy cover and seasonal change on host plant quality for the endangered Karner blue butterfly (*Lycaeides melissa samuelis*). Oecologia 114:243-250.

Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models and observations. Biological Journal of the Linnean Society 42:17-38.

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

Hanski, I., A. Moilanen and M. Gyllenberg. 1996. Minimum viable metapopulation size. The American Naturalist 147:527-541.

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

Haslett, J.R. 1997. Insect communities and the spatial complexity of mountain habitats. Global Ecology and Biogeography Letters 6:49-56.

Hill, J.K., C.D. Thomas and O.T. Lewis. 1996. Effects of habitat patch size and isolation on dispersal by *Hesperia comma* butterflies: implications for metapopulation structure. Journal of Animal Ecology 65:725-735.

Hosmer, D.W. and S. Lemeshow. 1989. Applied Logistic Regression. John Wiley and Sons, Inc., New York, USA.

Keyghobadi, N., J. Roland, and C. Strobeck. *In press*. Influence of landscape on population genetic structure of the alpine butterfly *Parnassius smintheus* (Papilionidae). Molecular Ecology 83.

Keyghobadi, N. *In preparation*. PhD thesis, University of Alberta, Edmonton, Canada.

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

Meglécz, E., G. Nève, K. Pecsenye, and Z. Varga. 1999. Genetic variations in space and time in *Parnassius mnemosyne* (L.) (Lepidoptera) populations in north-east Hungary: implications for conservation. Biological Conservation 89:251-259.

Merrill, T., D.J. Mattson, R.G. Wright, and H.B. Quigley. 1999. Defining landscapes suitable for restoration of grizzly bears *Ursus arctos* in Idaho. Biological Conservation 87:231-248.

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

Murphy, D.D. and B.A. Wilcox. 1986. Butterfly diversity in natural habitat fragments: a test of the validity of vertebrate-based management. *In* Wildlife 2000, Modeling Habitat Relationships of Terrestrial Vertebrates. J.Verner, M.L. Morrison and *editors*. University of Wisconsin Press, Madison, Wisconsin, USA. pages 287-292.

Murphy, D.D., K.E. Freas, and S.B. Weiss. 1990. An environment-metapopulation approach to population viability analysis for a threatened invertebrate. Conservation Biology 4:41-51.

Murphy, D.D., M.S. Menninger, and P.R. Ehrlich. 1984. Nectar source distribution as a determinant of oviposition host species in *Euphydryas chalcedona*. Oecologia 62:269-271.

New, T.R., R.M. Pyle, J.A. Thomas, C.D. Thomas and P.C. Hammond. 1995. Butterfly conservation management. Annual Review of Entomology 40:57-83.

North, M. and J. Greenberg. 1998. Stand conditions associated with truffle abundance in western hemlock/douglas-fir forests. Forest Ecology and Management 112:55-66.

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

Oostermeijer, J.G.B. and C.A.M. van Swaay. 1998. The relationship between butterflies and environmental indicator values: a tool for conservation in a changing landscape. Biological Conservation 86:271-280.

Parmesan, C., N. Ryrholm, C. Stefanescus, J.K. Hill, C.D. Thomas, H. Descimon, B. Huntley, L. Kaila, J. Jullberg, T. Tammaru, W.J. Tennent, J.A. Thomas, and M. Warren. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399:579-583.

Quinn, R.M., K.J. Gaston, and D.B. Roy. 1998. Coincidence in the distributions of butterflies and their foodplants. Ecography 21:279-288.

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

Schwarzwälder, B., M. Lörtscher, A. Erhardt and J. Zettel. 1997. Habitat utilization by the heath fritillary butterfly, *Mellicta athalia* ssp. *celadussa* (Rott.)(Lepidoptera: Nymphalidae) in montane grasslands of different management. Biological Conservation 82:157-165.

Singer, M.C. 1972. Complex components of habitat suitability within a butterfly colony. Science 176:75-77.

Sokal, R.R. and F.J. Rohlf. 1998. Biometry, third edition. W.H. Freeman and Company. New York, USA.

Sutcliffe, O.L., C.D. Thomas, T.J. Yates, and J.N. Greatorex-Davies. 1997. Correlated extinctions, colonizations, and population fluctuations in a highly connected ringlet butterfly metapopulation. Oecologia 109:235-241.

SYSTAT. 1998. SYSTAT 8.0 For Windows, Standard Version. SPSS Inc.

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

Weiss, S.B., D.D. Murphy, and R.R. White. 1988. Sun, slope, and butterflies: topographic determinants of habitat quality for *Euphydryas editha*. Ecology 69:1486-1496.

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

Wiklund, C. and C. Åhrberg. 1978. Host plants, nectar source plants, and habitat selection of males and females of *Anthocharis cardamines* (Lepidoptera). Oikos 31:169-183.

Williams, E.H. 1988. Habitat and range of *Euphydryas gillettii* (Nymphalidae). Journal of the Lepidopterists' Society 42:37-45.

Williams, J.A. 1990. Vegetation of Peter Lougheed Provincial Park. Alberta Recreation and Parks, Kananaskis Country, Operations Branch, Environmental Management, Canmore, Alberta.

Zar, J.H. 1996. Biostatistical Analysis, *third edition*. Prentice Hall, Upper Saddle, New Jersey, USA.

Chapter 6

GENERAL CONCLUSION

"...it may be critical to not only characterize the landscape, but to be able to characterize

the response of individuals to the landscape," (Roitberg and Mangel 1990).

Our ability to define habitat suitability and habitat quality for a species depends on a

thorough understanding of its natural history, in order to adequately identify its resource

requirements (Hanski and Thomas 1994). The goal of this thesis was to quantify habitat

suitability and quality of subalpine and alpine meadows for the butterfly *Parnassius*

smintheus. In pursuit of this goal, meadow characteristics were measured and related to

butterfly occurrence and abundance. Although availability and abundance of resources

contribute to habitat suitability and habitat quality, individuals can mitigate differences in

these through behaviour (Roitberg and Mangel 1997). Simply quantifying required

resources and overlooking the role of behaviour may fail to explain patterns of animal

distribution in the landscape. The behaviour of adult females and larvae were therefore

studied in response to a critical resource, the larval host plant.

Larval *P. smintheus* are monophagous, feeding almost exclusively on lance-leaved

stonecrop, *Sedum lanceolatum*. Adult female and larval behaviours were studied in

relation to the host plant to determine whether females consider the suitability and/or

quality of habitat and oviposition sites for their offspring, and if larvae are able to relocate

from hatching sites onto suitable host plants. Field observations of adult female *P.*

smintheus in Chapter 2 suggest that they do not orientate to the host plant during flight,

instead landing on most suitable nectar plants, including the host plant, in proportion to

their availability. Despite frequent landings and ovipositions off of the host plant, *S.*

lanceolatum does elicit oviposition. In unsuitable habitat females behaved differently than

they did in suitable habitat; females dispersed greater distances (average step length in non-

habitat > 10 m and in habitat ~ 6.5 m) between landing sites and oviposited significantly

less than in suitable habitat. It appears however, that females did not distinguish between

different quality meadows provided that there were some *S. lanceolatum*. They did,

however, detect differences in habitat suitability. The ability of females to recognize non-

habitat and alter their behaviour accordingly, by emigrating from it and retaining eggs, is

critical for their reproductive success. These movement and oviposition behaviours likely

promote residency, or retention, of adult females in suitable meadows and their dispersal

from non-habitat.

Because females oviposit off of the host plant, first-instar larvae must move to find their

own food source. In Chapter 3 larval mobility and search ability were investigated. First-

instar larvae were highly mobile in the laboratory setting. Estimated movement based on

laboratory studies, when applied to known distributions of the larval host plant in suitable

meadows on Jumpingpound Ridge, suggested that larvae are indeed capable of moving

from random locations (or oviposition sites) to a host plant. Late-instar larvae were

released from a host plant at distances that were intended to mimic random oviposition

events by females (1 cm to 16 cm). The distance at which they were released from *S.*

lanceolatum did not affect their search success; most were capable of locating the host

plant in less than 15 minutes. Movements of late-instar larvae were directed towards the

host plant in laboratory bioassays. Experienced larvae searched for the host plant and

directed their movement towards it. Because of the mobility and search-ability of larval *P. smintheus*, the random pattern of ovipositions by females in suitable habitat may not be as costly as first expected. Larvae demonstrated the ability to mitigate oviposition 'errors'. The proximity, abundance and/or spatial pattern of the host plant however, may affect larval search success and ultimately determine suitability or quality of meadows for larval *P. smintheus*.

To determine whether adult females and larvae respond to the abundance and spatial patterning of the host plant, these host plant attributes were measured at female oviposition sites and were also related to larval feeding events in Chapter 4. Although females assessed suitability of meadows for their offspring (Chapter 2), adult females oviposited in random locations within suitable meadows without considering the proximity, density, or spatial arrangement of the host plant (Chapter 4). Larval feeding damage was distributed randomly among available host plants, suggesting that after leaving one plant, larvae do not move directly to the next-nearest host plant to resume feeding. Abundance of both larvae and adult *P. smintheus* were positively correlated with the abundance of the larval host plant; meadows that are of high quality for adults are likely also of high quality for larvae. Although abundance of the larval host plant varies among Jumpingpound Ridge meadows, spatial patterning does not differ among them, nor were there any detectable effects of host plant spatial patterning on adult or larval population size. Abundance of the larval host plant, therefore, is an important measure of habitat quality for *P. smintheus*, whereas host

plant spatial point patterning is not, at least not at the spatial scale over which females

move to oviposit and larvae move to feed on a plant.

Topographical and ecological models at a large scale (Banff National Park and Kananaskis

Country, Alberta) and at a small scale (Jumpingpound Ridge) identified those variables that

were correlated with occurrence and abundance patterns of *P. smintheus*, respectively, in

particular the effects of slope, soil texture and plant community. Ecological models were

an improvement over topographical models – explaining more of the variation in both

occurrence and abundance of *P. smintheus*. Percent sand in the soil and plant community

type were the best independent variables for explaining butterfly occurrence; slope

(correlated with percent sand in the soil) and host plant abundance were the best covariates

for describing butterfly abundance. These may have been correlates of host plant

abundance. Host plant abundance was not measured at the larger-scale and may explain

why the model describing abundance of *P. smintheus* was more successful than the model

relating meadow characteristics to *P. smintheus* occurrence.

Because of the weakness of the occurrence model it is doubtful that coarse landscape

classifications, commonly used for management of natural areas, will adequately protect

suitable habitat for this butterfly, unless larger areas are set aside which would include all

meadow types. Descriptive models from Chapter 5 can be used as a blueprint to create

predictive models of habitat suitability and habitat quality of alpine and subalpine meadows

for *P. smintheus*, particularly if deliberate management strategies such as fire were used to alter vegetation structure (treeline) and composition.

Although models of habitat suitability and quality for *P. smintheus* developed here only partially describe suitable habitat for *P. smintheus*, they have improved our knowledge of *P. smintheus* natural history– providing meaningful information for current population models of *P. smintheus* (Keyghobadi *et al. in press*, Roland *et al. in press*) and future studies of *P. smintheus*. Determining how adult females respond to larval resources is important for understanding the mechanism of adult female oviposition and dispersal, which in turn will help us to understand how males disperse in response to females. Quantifying larval mobility and search ability helped us to better assess the cost of adult female oviposition off of the host plant. By relating both adult female behaviours and larval behaviours to the host plant, they were set in an ecological context, thus improving our ability to understand how meadow characteristics affect their suitability and quality for the alpine butterfly *P. smintheus*. It is clear from this study, and those of other butterfly species, that maintaining viable populations of native Lepidoptera requires consideration of life-history and behavioural information. In Europe and some parts of North America Lepidopteran habitat is disappearing or suffering from degradation caused by anthropogenic fragmentation of the landscape. The province of Alberta is fortunate to be in a position to prevent extirpation of native butterflies provided it initiates a conservation effort founded on ecological studies, which consider not only distribution records of

butterflies but also identify, describe and quantify resources at a scale appropriate to

species of concern.

LITERATURE CITED

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

Keyghobadi, N., J. Roland, and C. Strobeck. *In press*. Influence of landscape on population genetic structure of the alpine butterfly *Parnassius smintheus* (Papilionidae). Molecular Ecology 83.

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

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

Appendix A

Table A-1. Egg laying sites during the female flight path observations in the non-habitat, poor-quality and good-quality meadows (total eggs laid, 49).

Egg laying site	Non-habitat	Poor-Quality (J)	Good-Quality (G)
Anemone patens			1
Antennaria alpina			1
Castilleja sp.		2	
Dryas octopetala		9	
Epilobium angustifolium		1	
Galium boreale		2	2
Grass	2	1	5
Dead Grass		1	4
Hedysarum sulphurescens		2	
Oxytropis sericea		1	1
Potentilla diversifolia			1
Potentilla fruticosa			5
Sedum lanceolatum			2
Selaginella densa			1
Tolmachevia integrifolia		1	
Ground		2	1
Rock			1

Appendix B

Spatial Point Pattern Analysis: Ripley's K-function

The methods selected for quantifying the characteristics of spatial point patterns of *S. lanceolatum* in this paper include univariate and bivariate versions of Ripley's K-function analysis. Ripley's Univariate K-function analysis is used to identify spatial patterns of one type of event (or point). Like the estimation of variance, Ripley's K-function is a second-order analytical method (Diggle 1983, Boots and Getis 1988) which calculates the variance of distance measurements for all combinations of pairs of points. The expected number of other events within distance t of an arbitrary point ($E[N(t)]$) divided by the intensity of the spatial point pattern (λ, or the number of points, n, divided by the study area, A), is the second-order cumulative function $K(t)$, Ripley's K-function (Ripley 1976):

$$K(t)=\frac{E[N(t)]}{\lambda}$$

(2)

If distribution data were generated from a random process in the study area, as the distance, t, increases from an arbitrary point, the probability of encountering a neighbouring point would increase exponentially (Diggle 1983):

$$K(t)=\pi t^{2}$$

(3)

Edge effects exist for events within the study area which have their neighbouring circle of radius t outside the study area boundaries. Previous studies have included an edge

correction in the calculation of $\dot{K}(t)$, by weighting the proportion of the circle centered at i with radius t in the study area (Andersen 1992):

$$\hat{K}(t)=\frac{A}{n^2}\sum_i^n\sum_j^n\frac{I_t(u_{ij})}{w_{ij}}$$

(4)

where A is the size of the study area; n is the total number of events considered; u_{ij} is the distance between the events i and j; w_{ij} is the edge correction term, equal to the proportion of the circle, centered at i with radius t, in the study area; and $I_t(u_{ij})$ is equal to 1 if u_{ij} is less than t and 0 otherwise. Diggle (1983) provides formulae for the value of w_{ij} when the study plot is a rectangle or a circle. For other shapes this value has to be calculated numerically (Andersen 1992). There are some problems with this method of edge correction (see discussions by Getis & Franklin 1987, Haase 1995, Dale and Powell *in preparation*). Calculations for the edge correction term for the Ripley's K-function analysis were modified to meet the definition of Haase (1995): the $K(t)$ estimates assume that the area outside the study area has a point density and distribution pattern similar to that within the study area, closest to the edges, and generates x, y coordinates of points lying outside the study area. Points lying near the edge with circles radius t lying outside the study area now have points within radius t of them for estimates of $K(t)$, thereby eliminating the need of the edge correction term (w_{ij}) in Equation 3. Known spatial patterns were generated (clustered, random and regular) in the S+ spatial statistics program (Kaluzny *et al.* 1998), and were run through the calculations. Results adequately detected

the departure of the spatial point pattern from complete spatial randomness.

To determine if the pattern observed is significantly different from random, maximum and minimum envelopes were generated using Monte Carlo simulations. Ninety-five percent confidence envelopes were determined by the 2.5 % tails of the estimates of $\hat{K}(t)$ at each distance t for one hundred simulations, of the same number of points placed at random on the sampling area. Where the observed $K(t)$ lay outside the confidence envelopes the spatial point pattern was considered to differ significantly from the null hypothesis of complete spatial randomness. To improve visual interpretation of the calculations, $L(t)$ was plotted against t. $L(t)$ is the square root transformed and standardized $K(t)$. The expected value of $L(t)$ for complete spatial randomness approximates zero at each distance t:

$$\hat{L}(t)=\sqrt{\frac{\hat{K}(t)}{\pi}}-t \qquad (5)$$

$L(t)$ greater than the confidence envelope indicates departure from complete spatial randomness in the direction of clustering of events, $L(t)$ less than the confidence envelopes suggests over-dispersion or regular spacing of events and values of $L(t)$ lying within the confidence envelopes indicate that the observed spatial pattern does not differ significantly from complete spatial randomness (Fig. B-1).
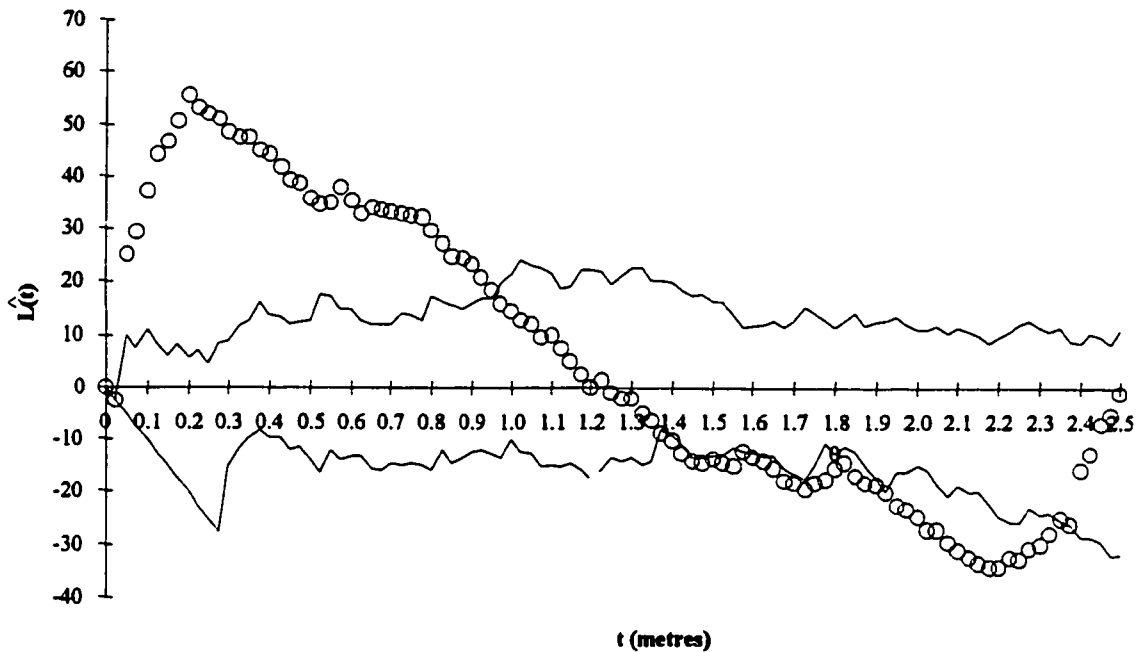
Fig. B-1. A graphical representation of Ripley's Univariate K-function analysis. The open circles represent the *L(t)* estimates for the observed spatial pattern of *Sedum lanceolatum* plants in one plot. The solid lines represent the 95% confidence envelopes from the Monte-Carlo simulations. From distance, *t*, 0.05 m to approximately 0.95 m the spatial pattern of *Sedum lanceolatum* is significantly different from random in the direction of clustering, from 0.95 m to 1.4 m *L(t)* lies within the confidence envelopes and indicates that the spatial pattern appears random, and from 1.4 m to 2.4 m the *L(t)* lies below the confidence envelopes because the spatial pattern is significantly different from random, in the direction of regularity.

Ripley's Bivariate K-function

If data have been gathered in the same region for more than one type of event (or point),

such as two types of host plant, the bivariate version of Ripley's K-function can be used to

determine if the observed spatial point pattern of one type of point is associated with the

spatial point pattern of another type of point (Diggle 1983). The null hypothesis for

Ripley's Bivariate K-function is that the two types of points are independent of one another

(the two types of points do not interact) at a range of distances, t. Rejection of the null

hypothesis at a given distance, t, indicates that the two types of points have a positive

(aggregated) association or a negative (segregated) association. $K_{12}(t)$ and $K_{21}(t)$ are

estimates of the number of type 2 events within radius t of a type 1 event and the number of

type 1 events within radius t of a type 2 event, respectively.

$$\hat{K}_{12}(t) = \frac{A}{(n_1 n_2)} \sum_{i=1}^{n1} \sum_{j=1}^{n2} \frac{I_t(u_{ij})}{(w_{ij})}$$

(6)

$$\hat{K}_{21}(t) = \frac{A}{(n_1 n_2)} \sum_{i=1}^{n1} \sum_{j=1}^{n2} \frac{I_t(v_{ij})}{(w_{ji})}$$

(7)

Where $n1$ and $n2$ are the number of type 1 and type 2 events, respectively, A is the area of

the study plot; I_t is a counter variable; u_{ij} is the distance from the ith type 1 event to the jth

type 2 event; v_{ij} is the distance from the ith type 2 event to the jth type 1 event; and w_{ij} is

the proportion of the circle, centered at i with radius t, in the study region. When you

combine the counter variable and the distance variables, I_t and u_{ij} in Equation 5 or I_t and v_{ij}

in Equation 6, it is equal to 1 if u_{ij} or v_{ij} is less than t and 0 otherwise. $L(t)$ is the bivariate

association of the two species, and square-root transforms and standardizes $K(t)$ as in the

Ripley's Univariate K-function, where the expected value of $L(t)$ for complete spatial

randomness approximates zero at each distance t (Diggle 1983). Calculations for the edge

correction term for the bivariate Ripley's K-function analysis were modified to meet the

definition of Haase (1995), where the K_{12} (t) and $K_{21}(t)$ estimates assume that the area

outside the study area has a point density and distribution pattern similar to that of the

study area closest to the edges and generates x, y coordinates of points lying outside the

study area. Points lying near the edge with circles radius t lying outside the study area now

have points within radius t of them for estimates of K_{12} (t) and $K_{21}(t)$, therefore; the edge

correction term (w_{ij}) can be dropped from Equations 5 and 6.

$$\hat{L}(t) = \sqrt{\frac{n_2 \hat{K}_{12}(t) + n_1 \hat{K}_{21}(t)}{\pi(n_1 + n_2)}} - t \qquad (8)$$

To determine if the pattern observed is significantly different from the random null

hypothesis, maximum and minimum envelopes were generated from Monte Carlo

simulations. Ninety-five percent confidence envelopes were determined by the 2.5 % tails

of the estimates of $L(t)$ at each distance t from one hundred random shufflings of the labels

(type 1 and type 2), of the same number of points in the same position. Unlike the Ripley's

Univariate K-function, this version of the Ripley's Bivariate K-function does not compare

the observed point pattern to one of complete spatial randomness by randomly tossing the same number of points on the study area. Rather, it holds the underlying pattern of points (*e.g.*, the x, y coordinates of *S. lanceolatum* plants) constant and randomly shuffles labels (*e.g.*, presence of larval feeding damage or absence of larval feeding damage) amongst the observed points (in Andersen 1992 this method was referred to as "a test of random marking"). Where the observed $L(t)$ lies outside the confidence envelopes the bivariate spatial point pattern was considered to differ significantly from the null hypothesis, thus indicating association (departure from independence) between the two types of points. $L(t)$ greater than the confidence envelope indicates that the two types of points are positively associated (aggregated) given the underlying spatial arrangement of points and $L(t)$ less than the confidence envelopes suggests that the two types of points are negatively associated (over-dispersed or regular) given the underlying spatial arrangement of points (Fig. B-2). The program used to estimate Ripley's Univariate and Bivariate K-functions is Potemkin free software, and a copy can be obtained on the Internet at:
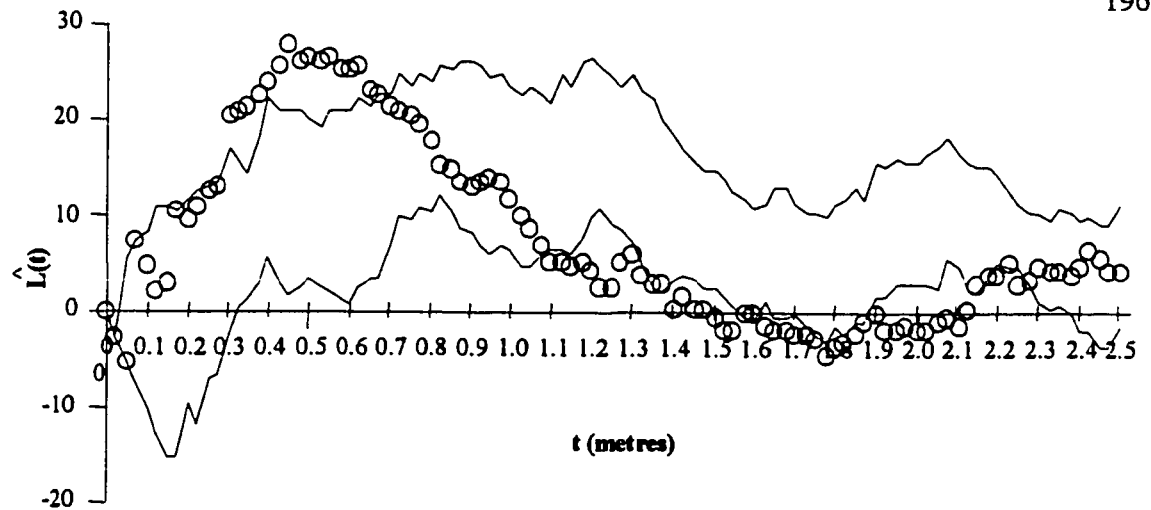
ftp://www.biology.ualberta.ca/pub/jbrzusto/potemkin/potsrc.zip.

Fig. B-2. A graphical representation of Ripley's Bivariate K-function analysis. The open circles represent the $L(t)$ estimates for the observed bivariate association of *Sedum lanceolatum* plants with larval feeding damage and *Sedum lanceolatum* plants without larval feeding damage, for one plot. The solid lines represent the 95% confidence envelopes from the Monte-Carlo simulations. From distance, t, 0.3 m to approximately 0.6 m the spatial pattern of plants with and without larval feeding damage are positively associated; from 0.6 m to 1.1 m and from 2.2 m to 2.5 m the spatial pattern of plants with and without larval feeding damage do not appear to interact; and from 1.1 m to 2.1 m the spatial pattern of plants with and without larval feeding damage are negatively associated, given the underlying spatial pattern of *S. lanceolatum*.

LITERATURE CITED

Andersen, M. 1992. Spatial analysis of two-species interactions. Oecologia 91:134-140.

Boots, B.N. and A. Getis. 1988. Point pattern analysis. Sage Publications, Newbury Park, California, USA.

Dale, M.R.T. and R.D. Powell. *In preparation*. Characterizing point patterns in plant ecology.

Diggle, P.J. 1983. Statistical analysis of spatial point patterns. Academic Press, New York, USA.

Getis, A. and J. Franklin. 1987. Second-order neighbourhood analysis of mapped point patterns. Ecol. 68: 473-477.

Haase, P. 1995. Spatial pattern analysis in ecology based on Ripley's K-function: introduction and methods of edge correction. Journal of Vegetation Science 6:575-582.

Kaluzny, S.P., S.C. Vega, T.P. Cardoso, and A.A. Shelly. 1998. S+ Spatial Stats: user's manual for Windows and Unix. Springer-Verlag, New York, USA.

Ripley, B.D. 1976. The second-order analysis of stationary point processes. Journal of Applied Probabilities 13:255-266.