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

by

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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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Table of Contents

List of Tables

List of Figures

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).

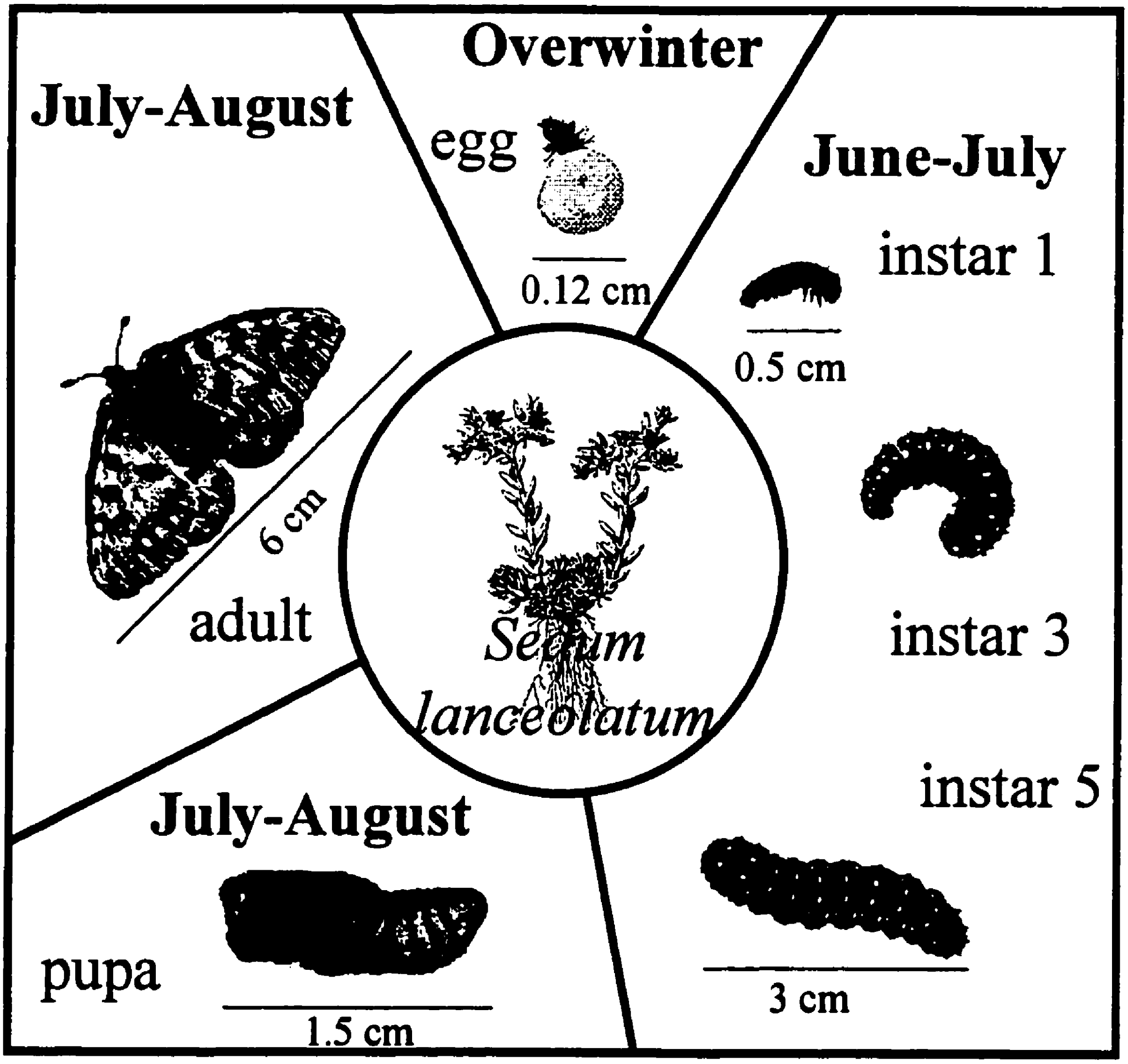

Fig. 1-1. Schematic life-cycle and phenology of *Parnassius smintheus* on Jumpingpound Ridge. The drawing of the larval host plant, *Sedum lanceolatum*, is taken from Clausen (1975).

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

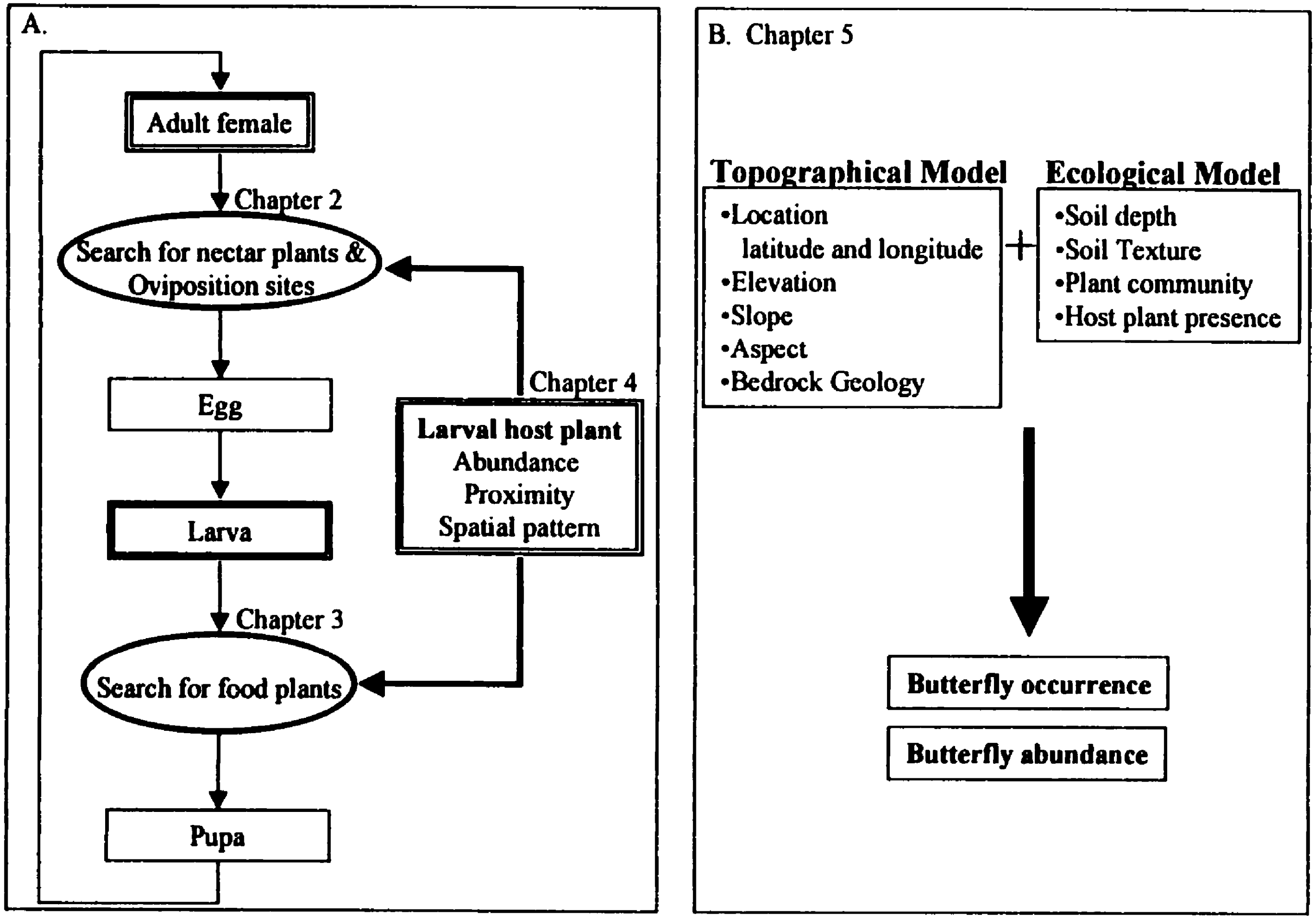

Fig. 1-2. Outline of thesis. A. Investigating how adult females and larvae of the alpine butterfly, *Parnassius smintheus* respond to the larval host plant, *Sedum lanceolatum*. B. Using both topographical and ecological characteristics of meadows to describe the patterns of occurrence and abundance 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.

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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.

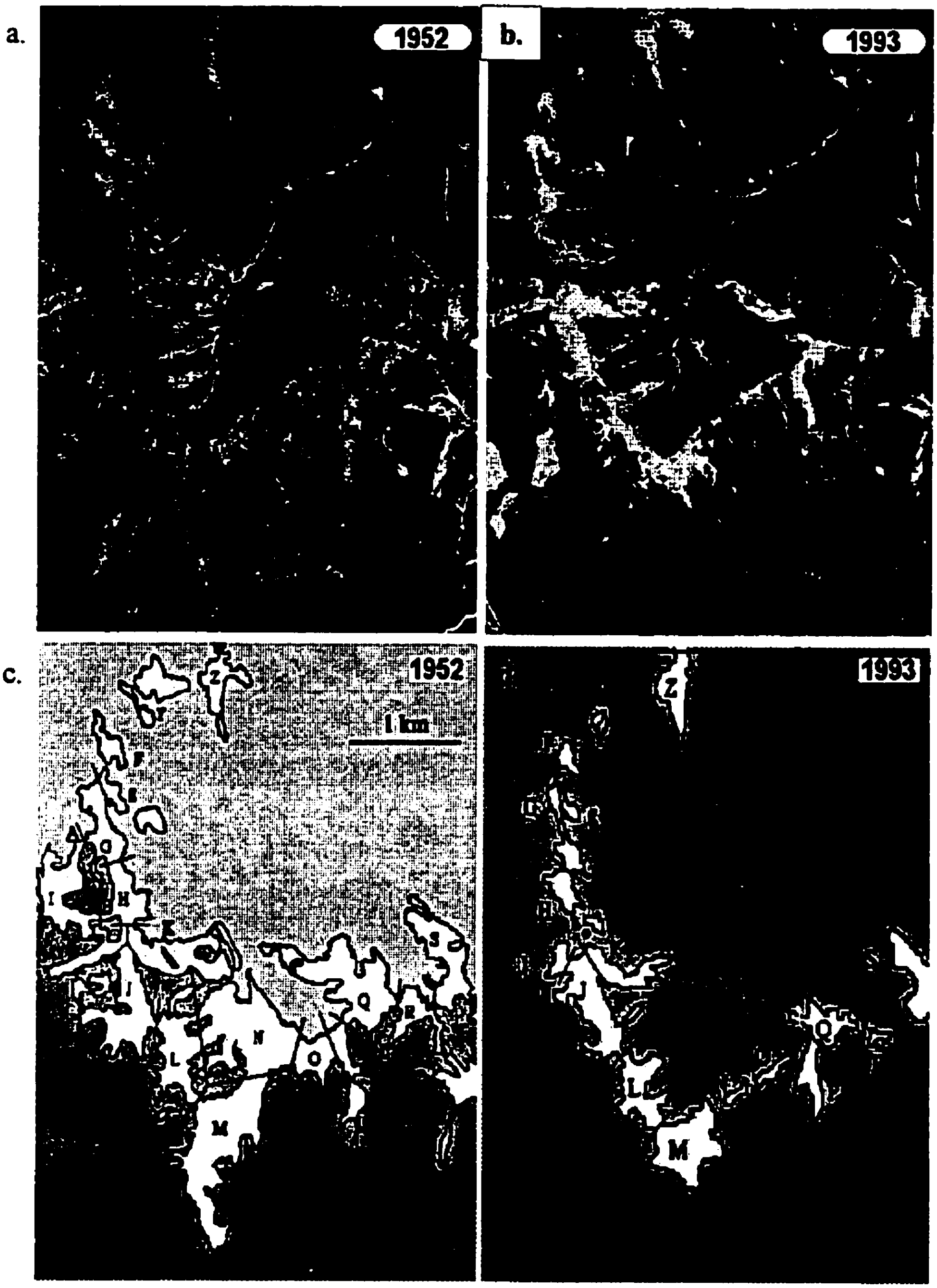

Fig. 2-1. Rise in treeline over the past four decades is evident from air photos taken on Jumpingpound Ridge, Kananaskis Country, Alberta (50°57'N, 114°55'W) in 1952 (a) and 1993 (b). Treeline (or meadow perimeters), as interpreted from the air photos, are represented by the lines for 1952 (c) and 1993 (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):

$$P_x = \frac{O_x}{L_x} \tag{1}$$

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.

	Lag 1 step		**Lag 2 steps**		**Lag 3steps**	
Meadow	**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

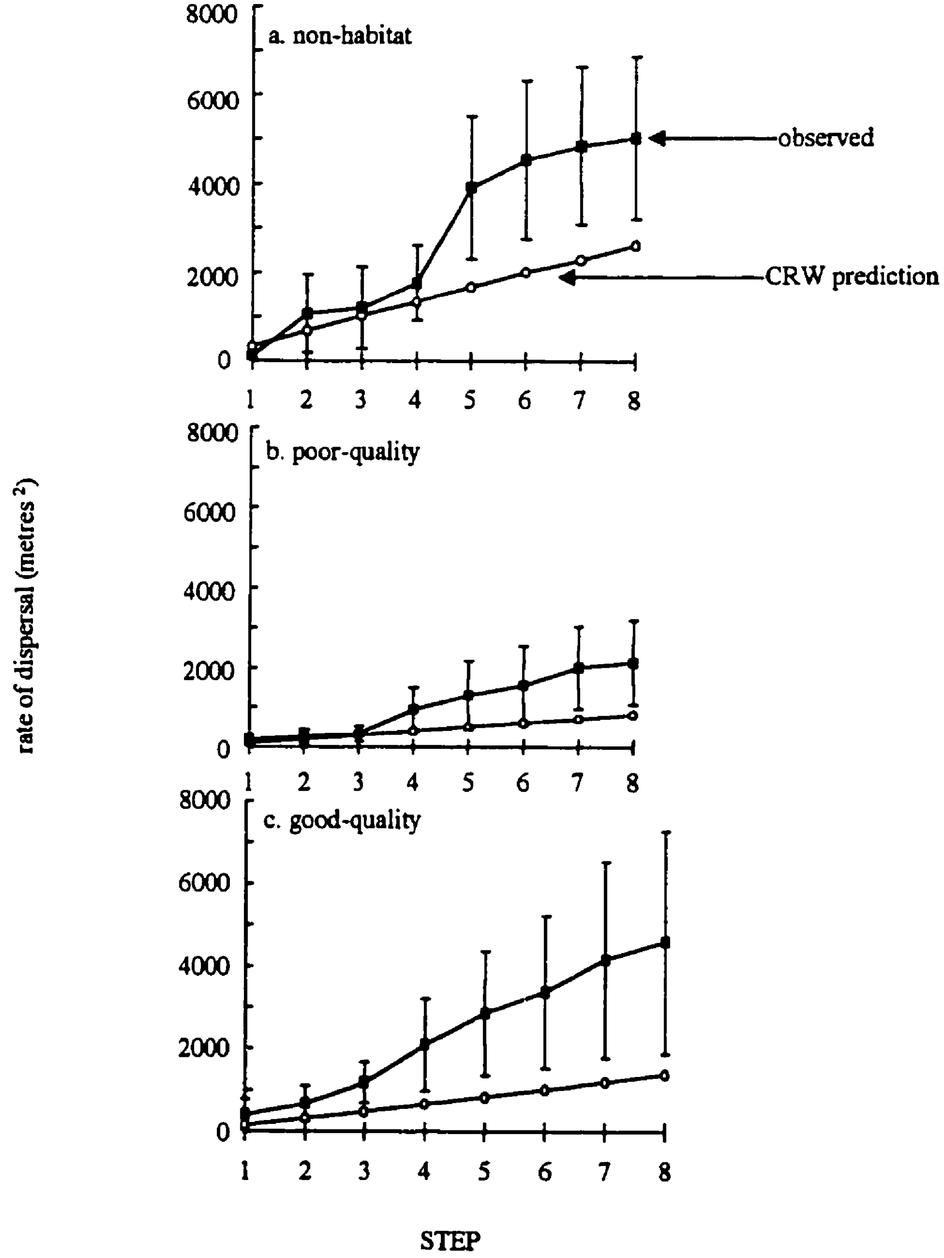

Fig. 2-2. Observed mean net displacement (rate of dispersal) with standard error bars and the expected mean net displacement squared from the Correlated Random Walk Model for the non-habitat meadow (a), the poor-quality meadow (b), and the good-quality meadow (c). Females exceeded the CRW model predictions after 4, 6 and 2 steps in the non-habitat, poor-quality, and good-quality meadows, respectively.

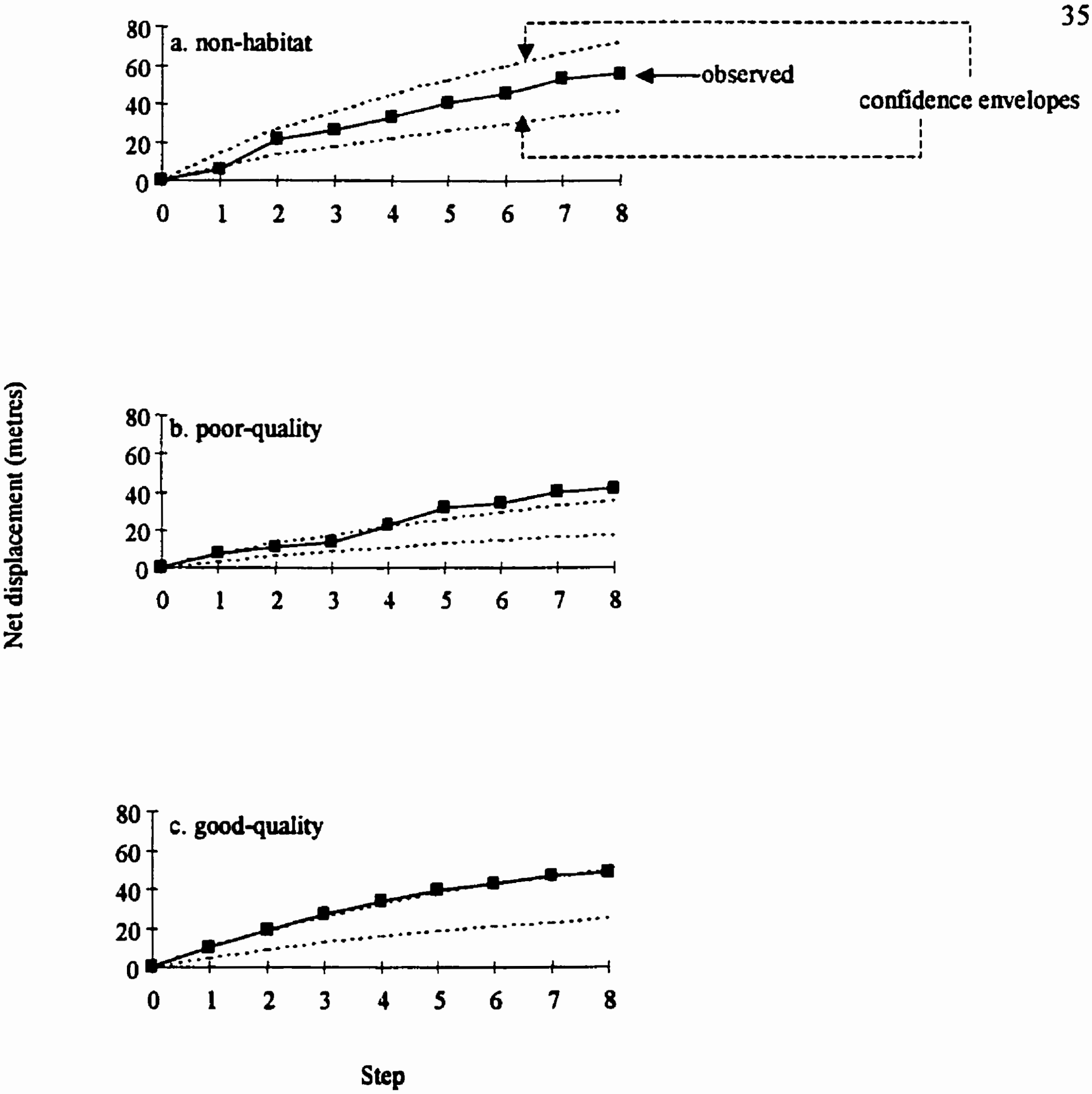

Fig. 2-3. Observed mean net displacement (m) of female *P. smintheus* plotted with 95% confidence envelopes from simulated flight paths for: (a) the non-habitat meadow; (b) the poor-quality meadow; and, (c) the good-quality meadow. Where the observed net displacement is greater than the upper confidence 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.

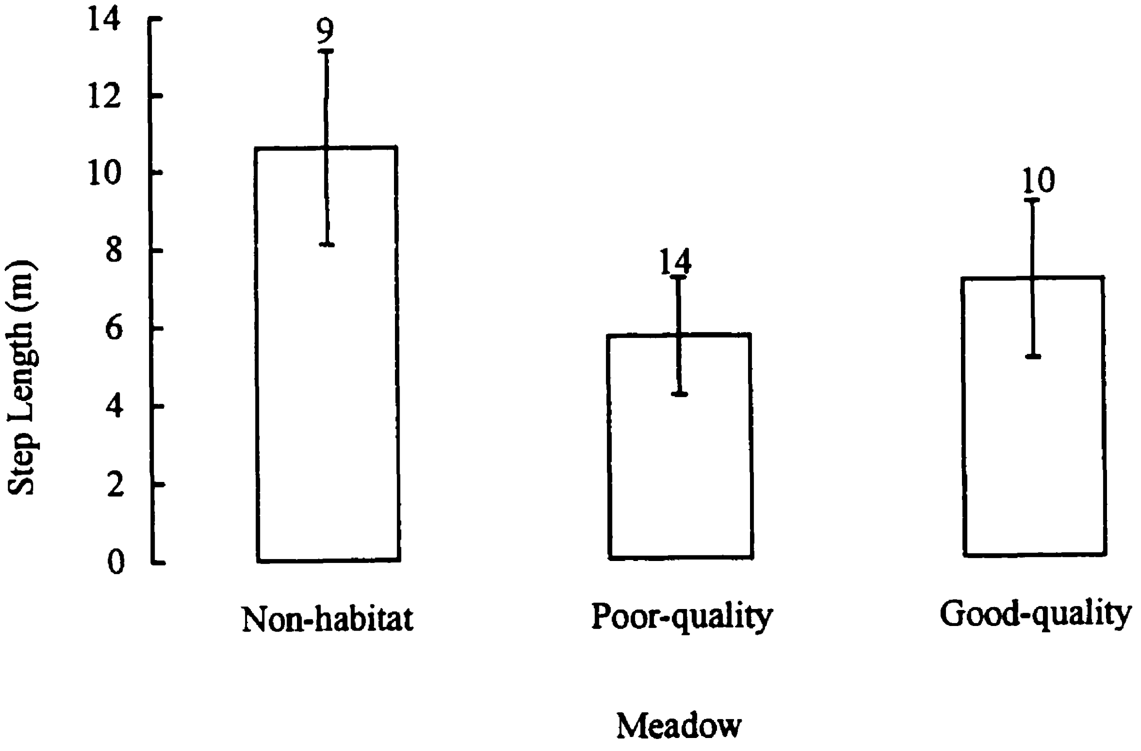

Fig. 2-4. The mean step length (m) for female *P. smintheus* released in the three meadow habitats, calculated from the mean step lengths of the first eight steps of each female. The number of females observed in each of the treatments is recorded at the top of the standard error bars. There was no significant 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.

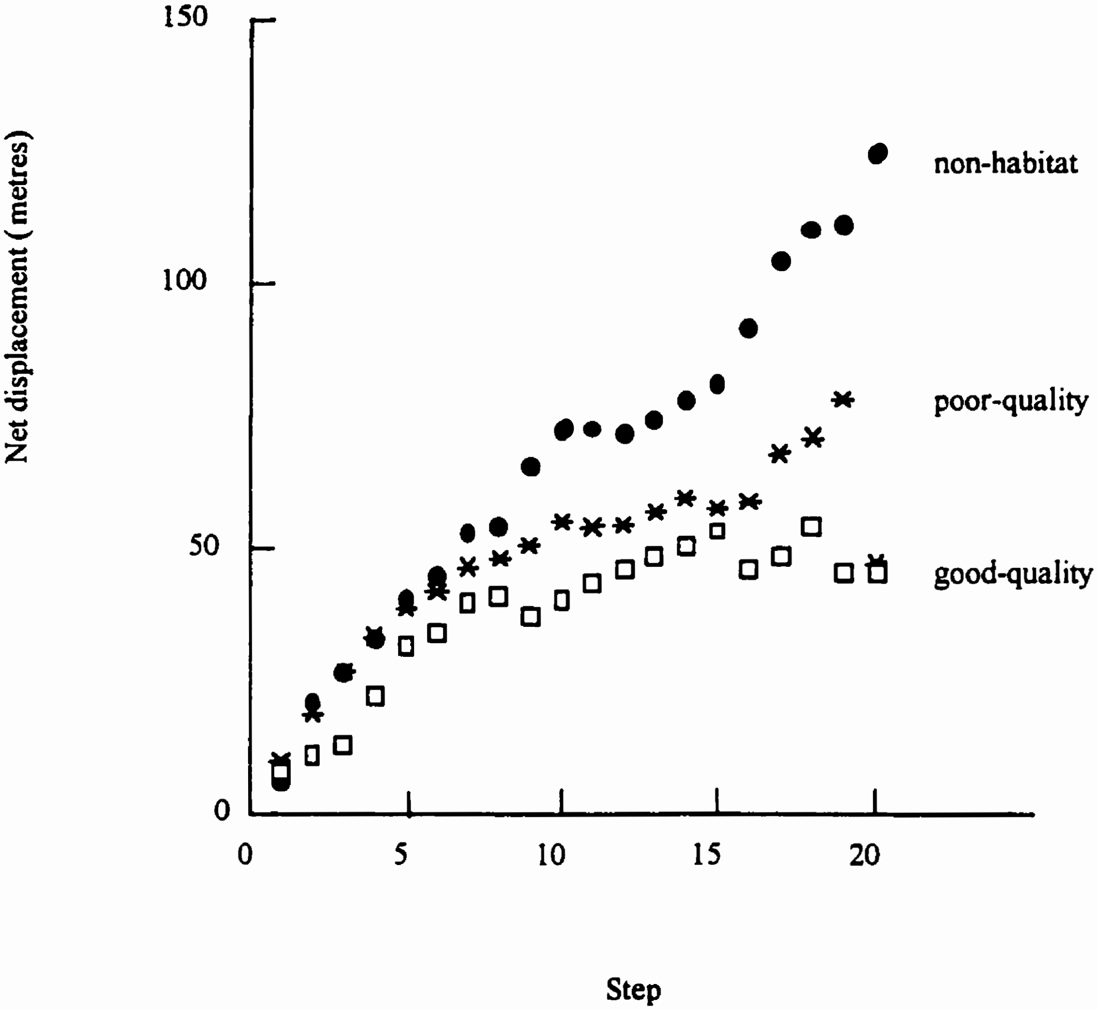

Fig.2-6. The mean net displacements (m) of female *P. smintheus* released in the three meadow habitats. The sample sizes for the different habitats after 8 and 20 steps are: non-habitat, 9 and 6; poor-quality, 14 and 8; and good-quality, 10 and 5. There was no significant effect of habitat quality after 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).

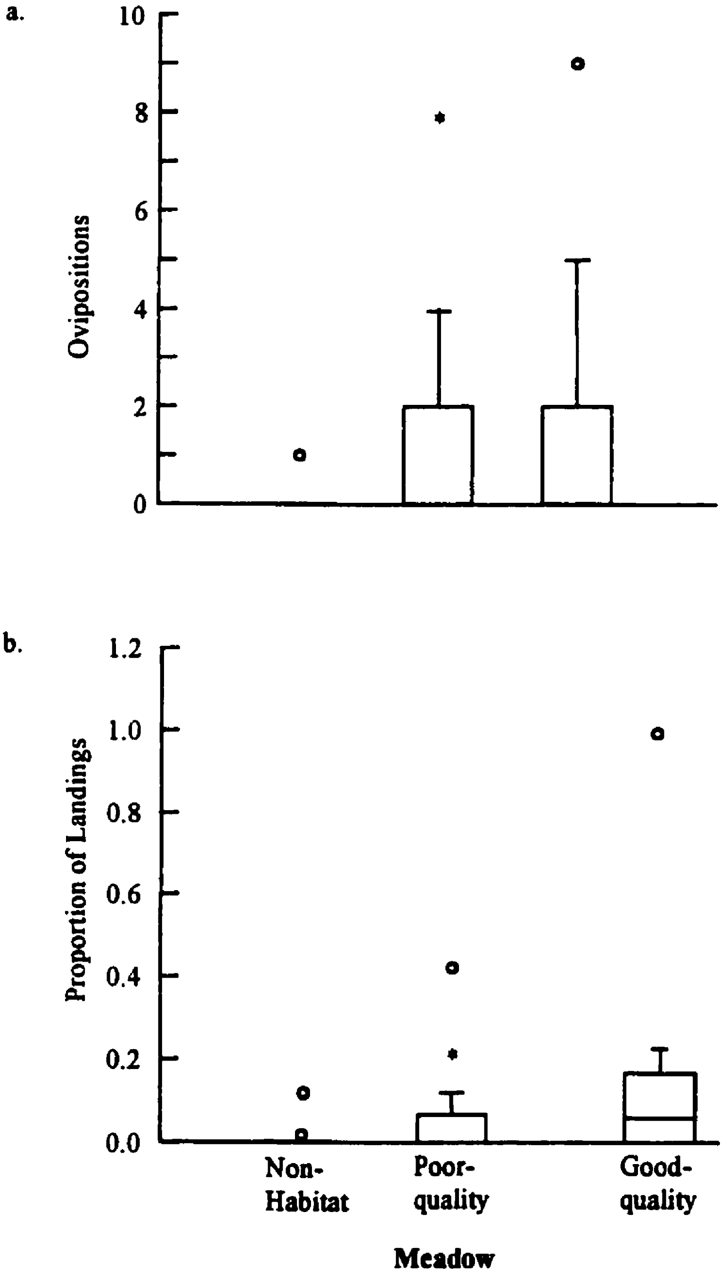

Fig. 2-7. Box and whisker plots for: (a) the number of ovipositions observed in the three meadows during flight path observations; and, (b) the proportion of landings which resulted in ovipositions. There was no significant effect of habitat quality on the number of ovipositions observed (p=0.07) nor on the proportion of landings which resulted in ovipositions (p=0.09). * and o are outliers and extreme outliers.

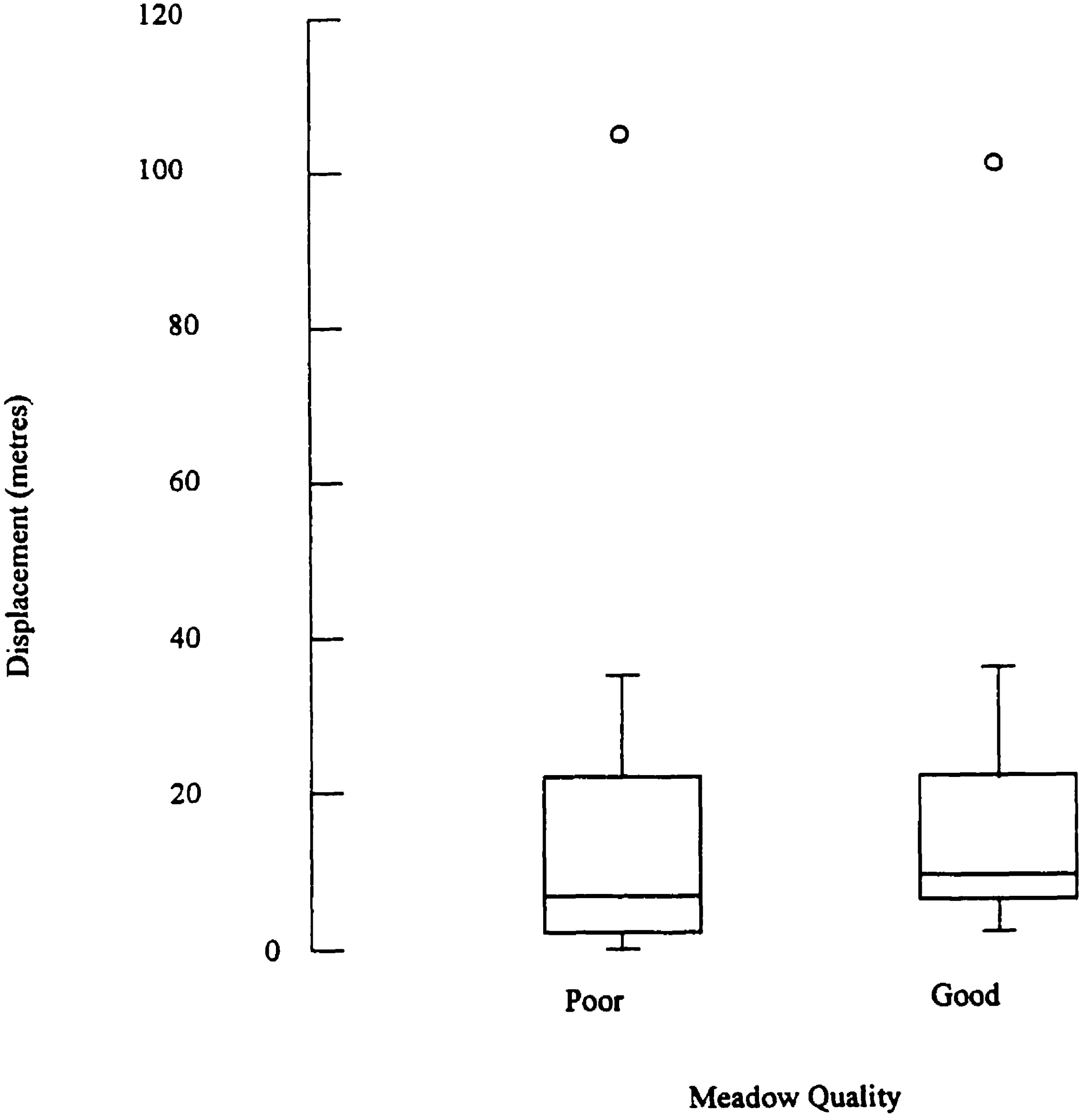

Fig. 2-8. Box and whisker plots of net displacement (m) between successive ovipositions in the two butterfly meadow treatments. There was no significant effect of habitat quality on displacement between ovipositions; p=0.93.

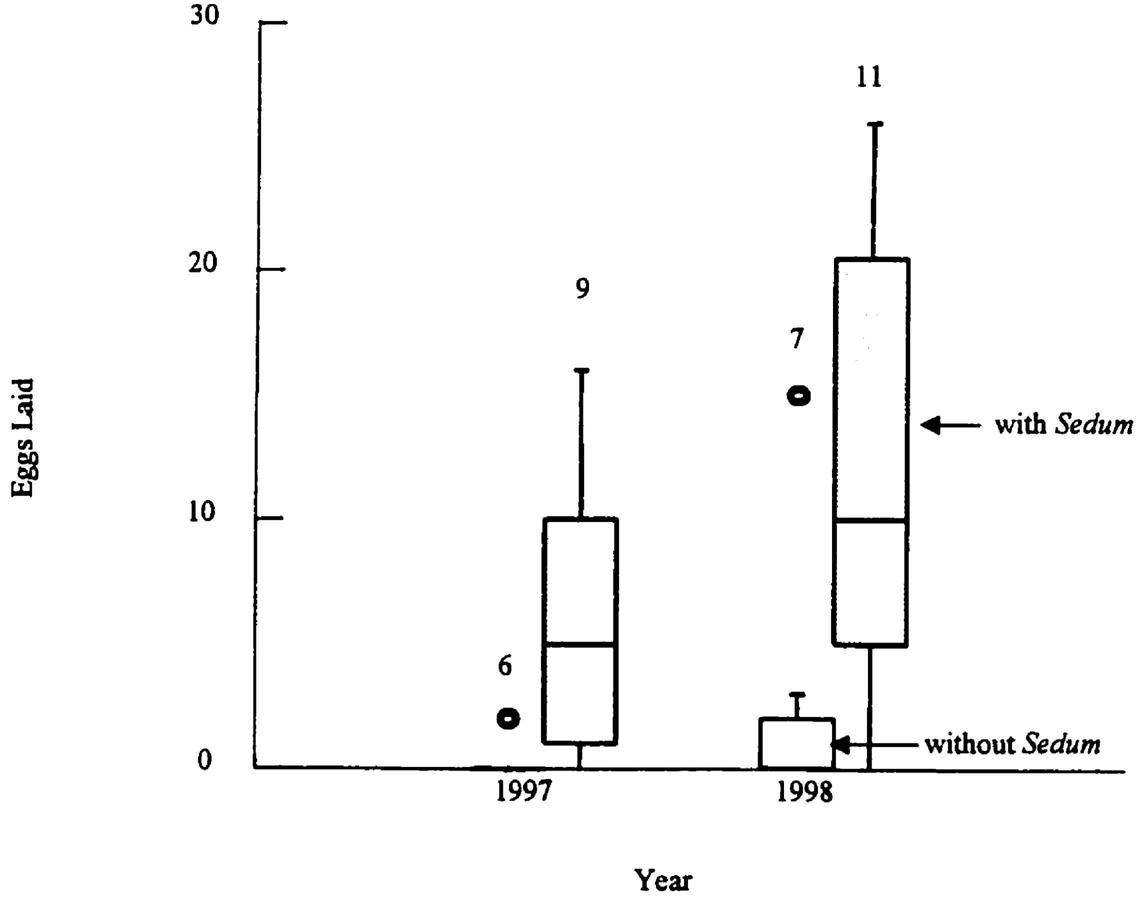

Fig. 2-9. Box and whiskêr plots of number of eggs laid in 1997 and 1998 for females caged for 24 hour with *Sedum lanceolatum* (stippled) and without *S. lanceolatum* (empty). Sample sizes are indicated above the plots. There was a significant effect of *S. lanceolatum* presence in both 1997 (p=0.009) 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).

	Parnassius apollo	***Parnassius smintheus***	
Egg laying Site		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*).

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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).

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

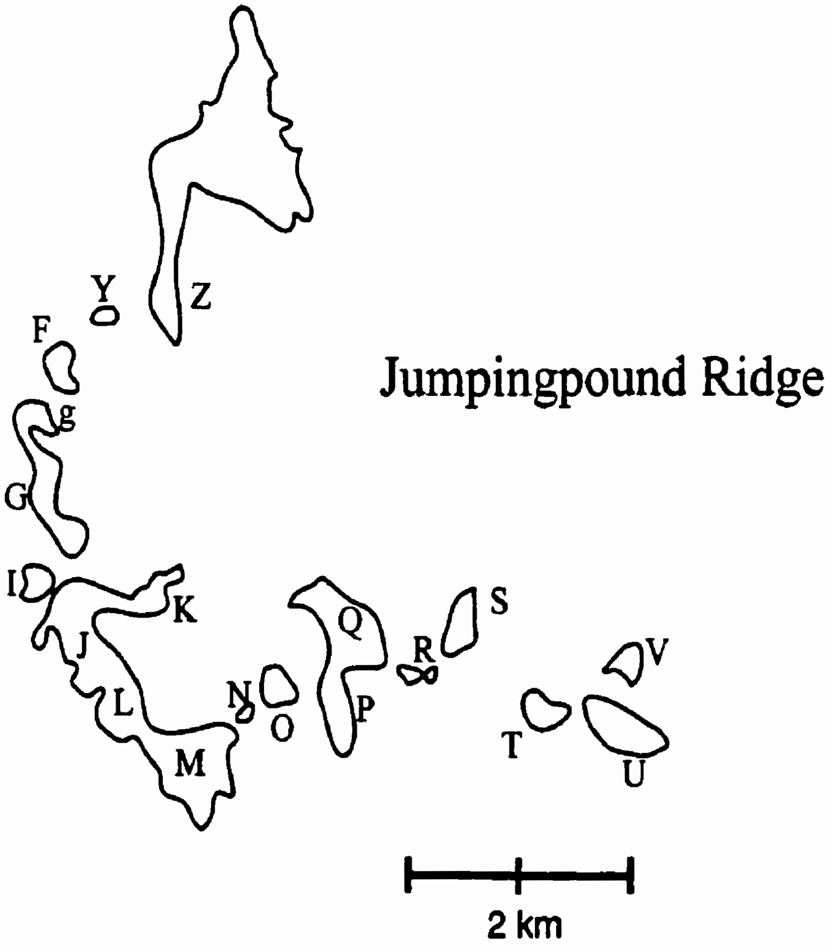

Fig. 3-1. Meadows on Jumpingpound Ridge (50 °57'N, 114°55' W). Meadows above treeline have each been assigned a letter and are separated from one another by different distances through forest.

(*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

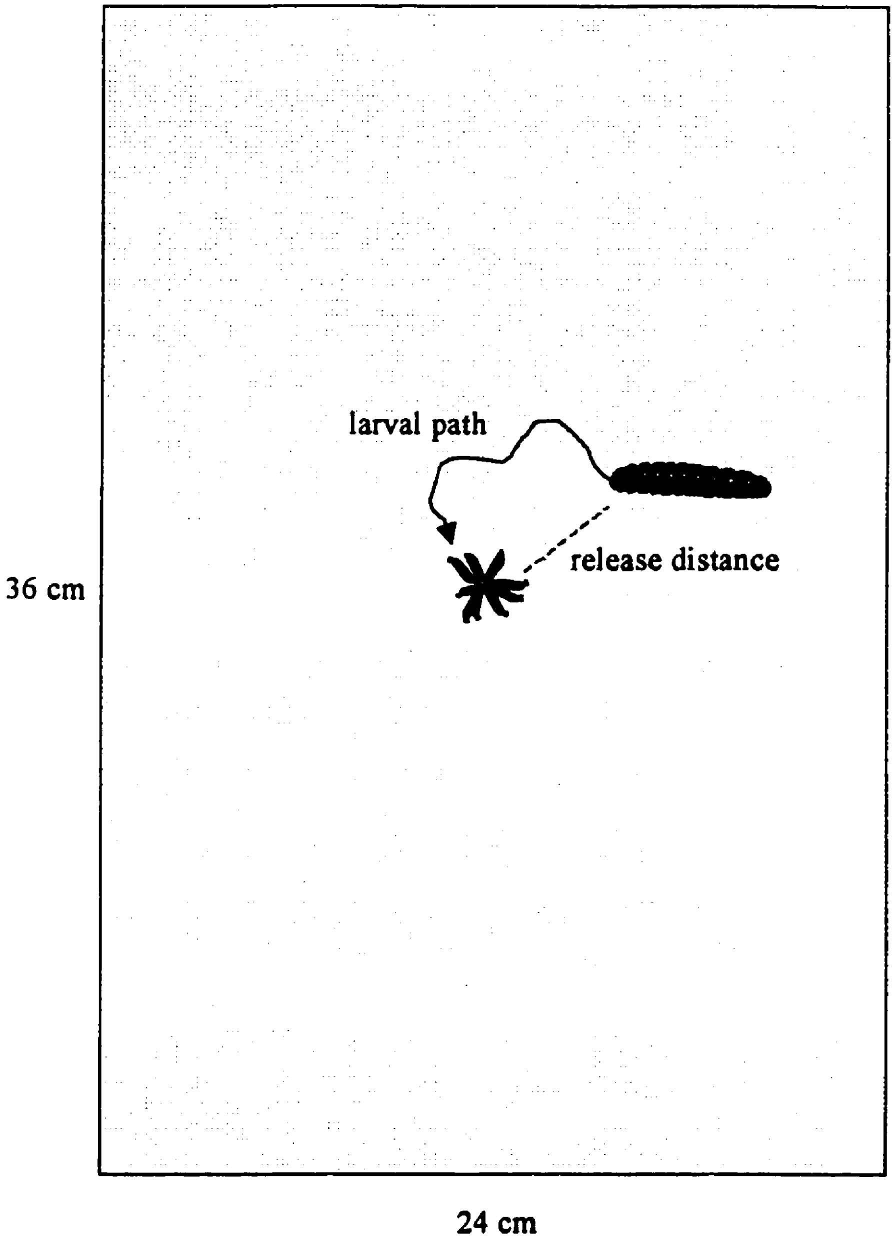

Fig. 3-2. Experimental set-up for late-instar larval search ability experiments. The container was lined with coarse soil, 1 cm deep. The solid line represents the larval search path tracing and the dotted line represents the release distance. Larvae were released at 1, 2, 4, 8, 16 and 32 cm from the host plant, *Sedum lanceolatum*.

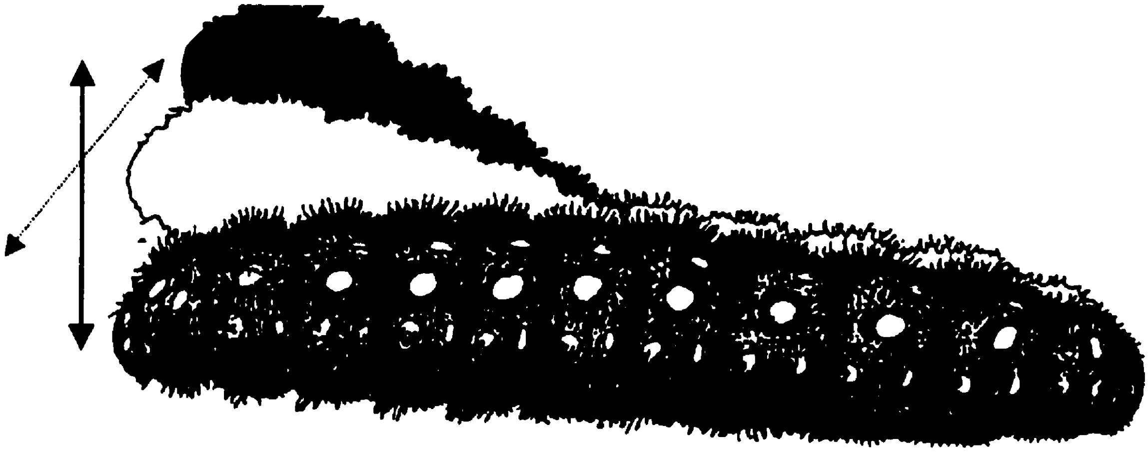

Fig. 3-3. Head-wave behaviour exhibited by late-instar *P. smintheus* larvae. The head and first few segments of the larval body are raised above the substrate moved right or left, or both, and then lowered back down to the substrate. Original black and white sketch of *P. smintheus* larvae is from Bird *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).

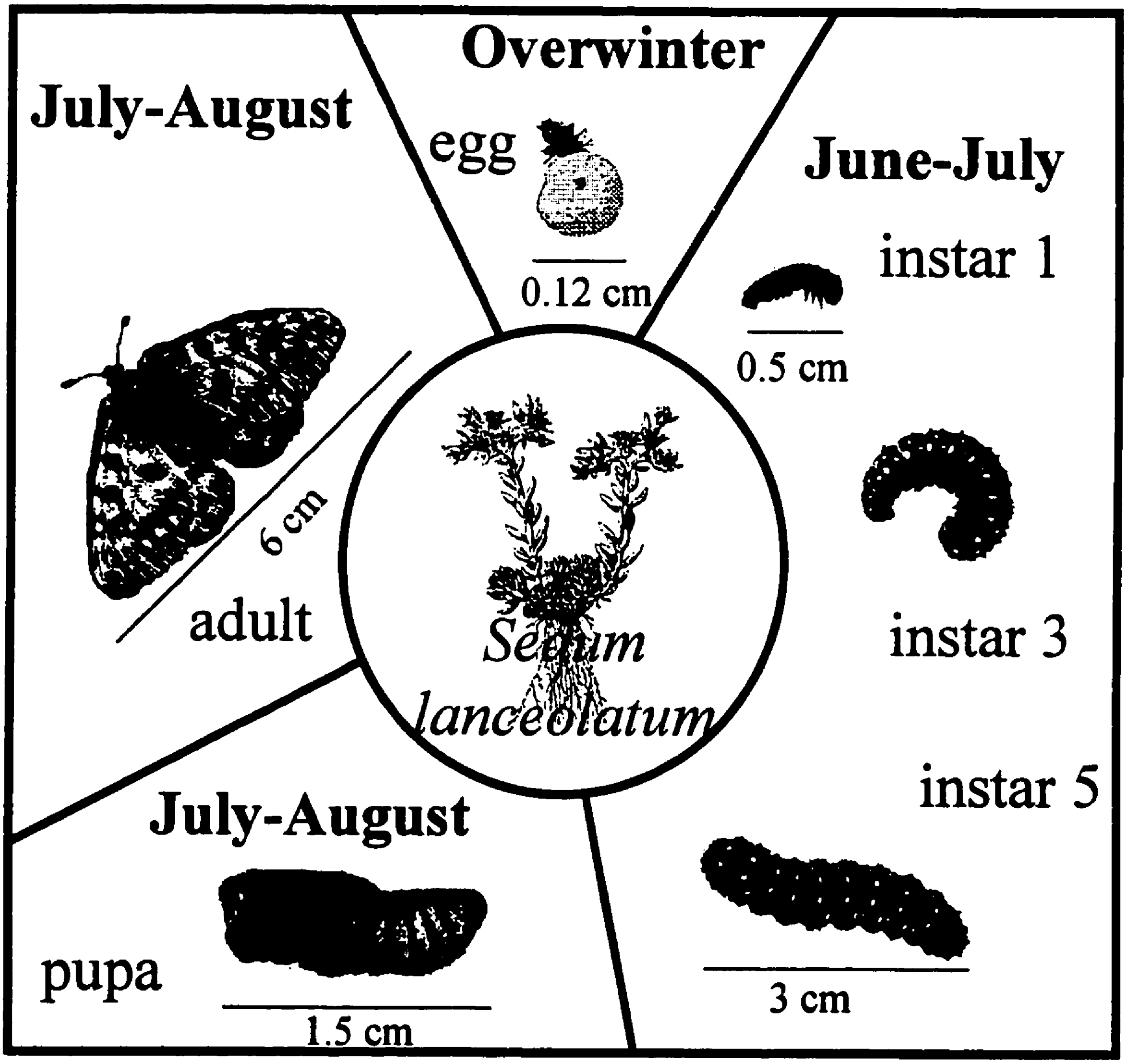

Fig. 3-4. Schematic life-cycle and phenology of *Parnassius smintheus* on Jumpingpound Ridge. The drawing of the larval host plant, *Sedum lanceolatum*, is taken from Clausen (1975).

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

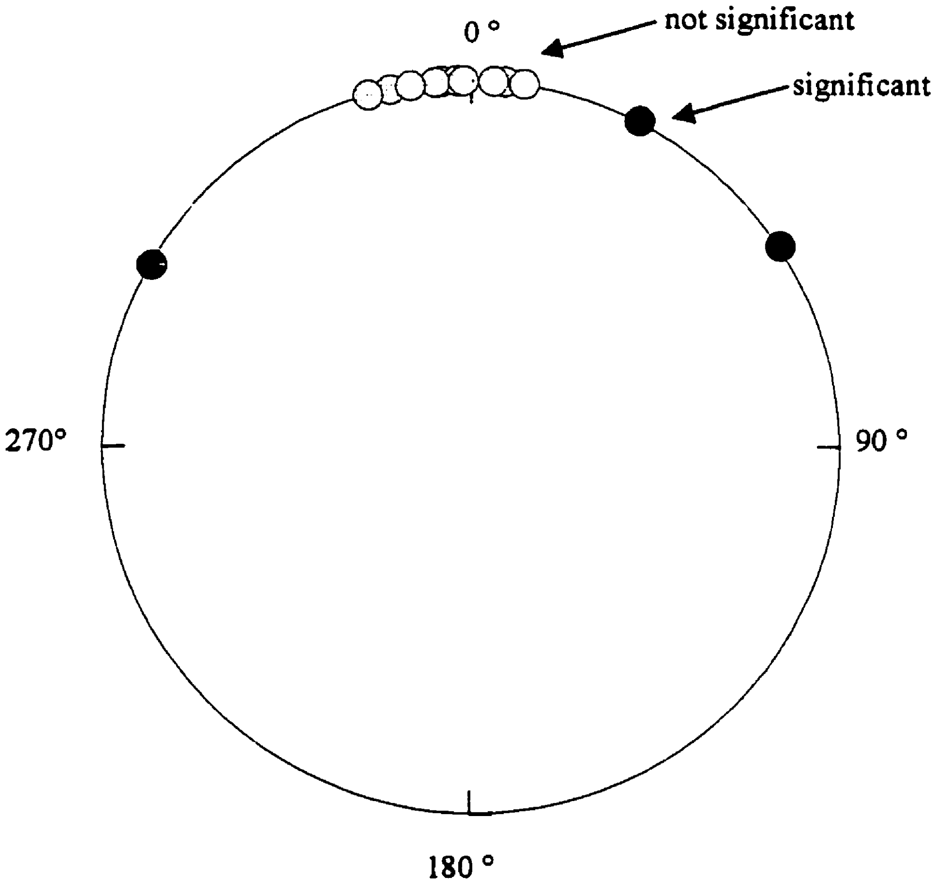

Fig. 3-5. Median turn angles (degrees) summarize turning behaviour of individual first-instar larvae. The solid and open circles represent median turn angles which do differ significantly from zero ($p<0.05$) and median turn angles which do not differ significantly from zero, respectively.

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).

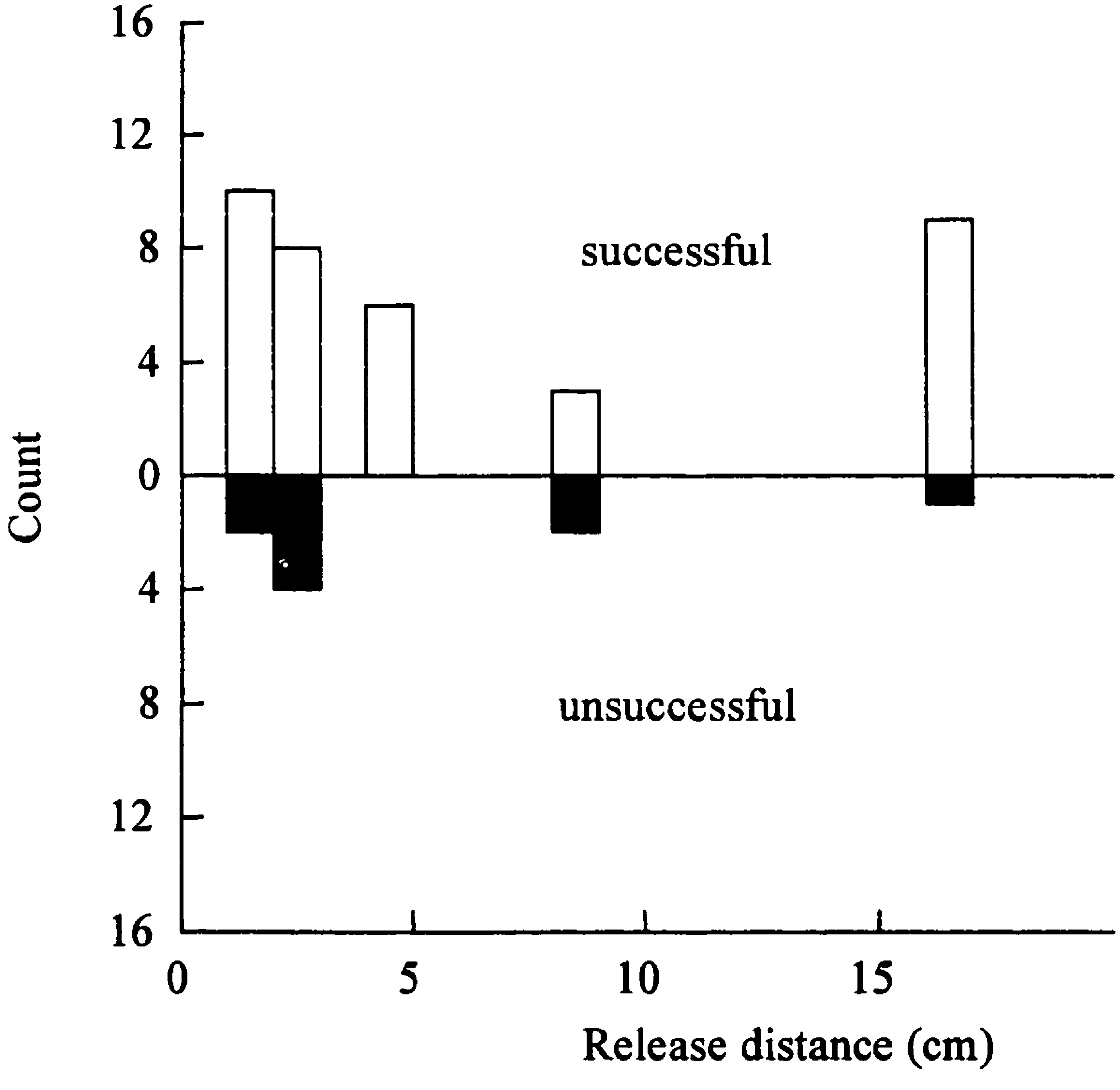

Fig. 3-6. The results of individual late-instar larval searches. Larvae were released at 1, 2, 4, 8 and 16 cm from the host plant. There was no significant effect of release distance on search outcome (p=0.48).

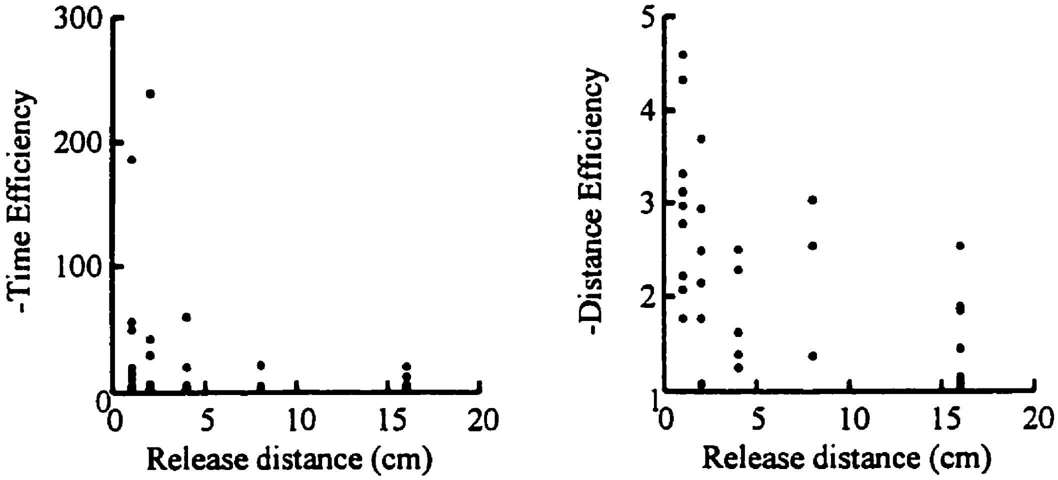

Fig. 3-7. The negative time and distance efficiencies of larval search behaviour released at different distances (cm) from the host plant. Larger values indicate poor search efficiency and smaller values, good search efficiency.

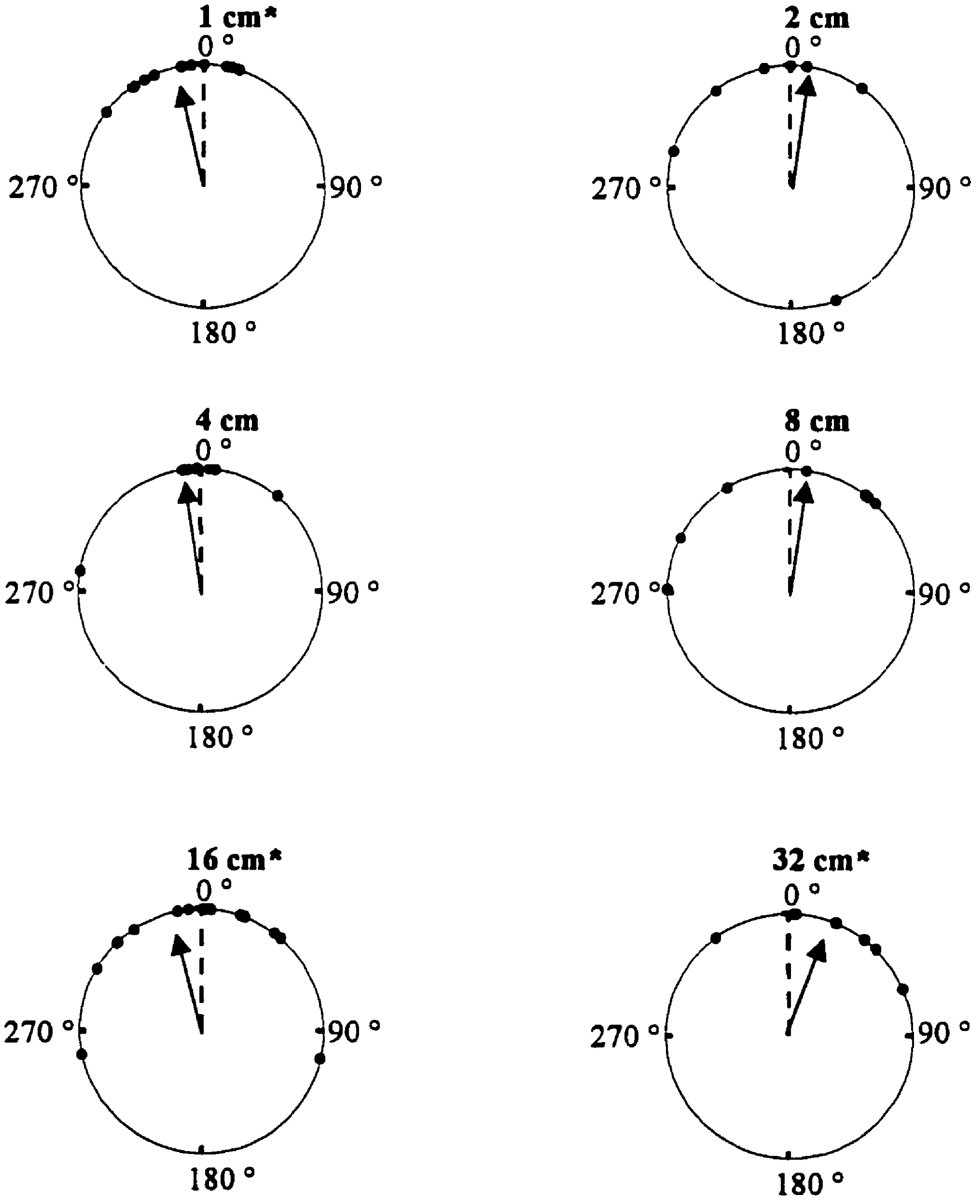

Fig. 3-8. The direction of the first move of all larvae relative to the host plant (solid circles). The median angle of larval directionality is indicated by the arrow for each release distance (1, 2, 4, 8, 16 and 32 cm). The dashed line represents the straight line between the release site and the host plant, and * indicates significant departure from straight line direction to the host plant, $p<0.05$.

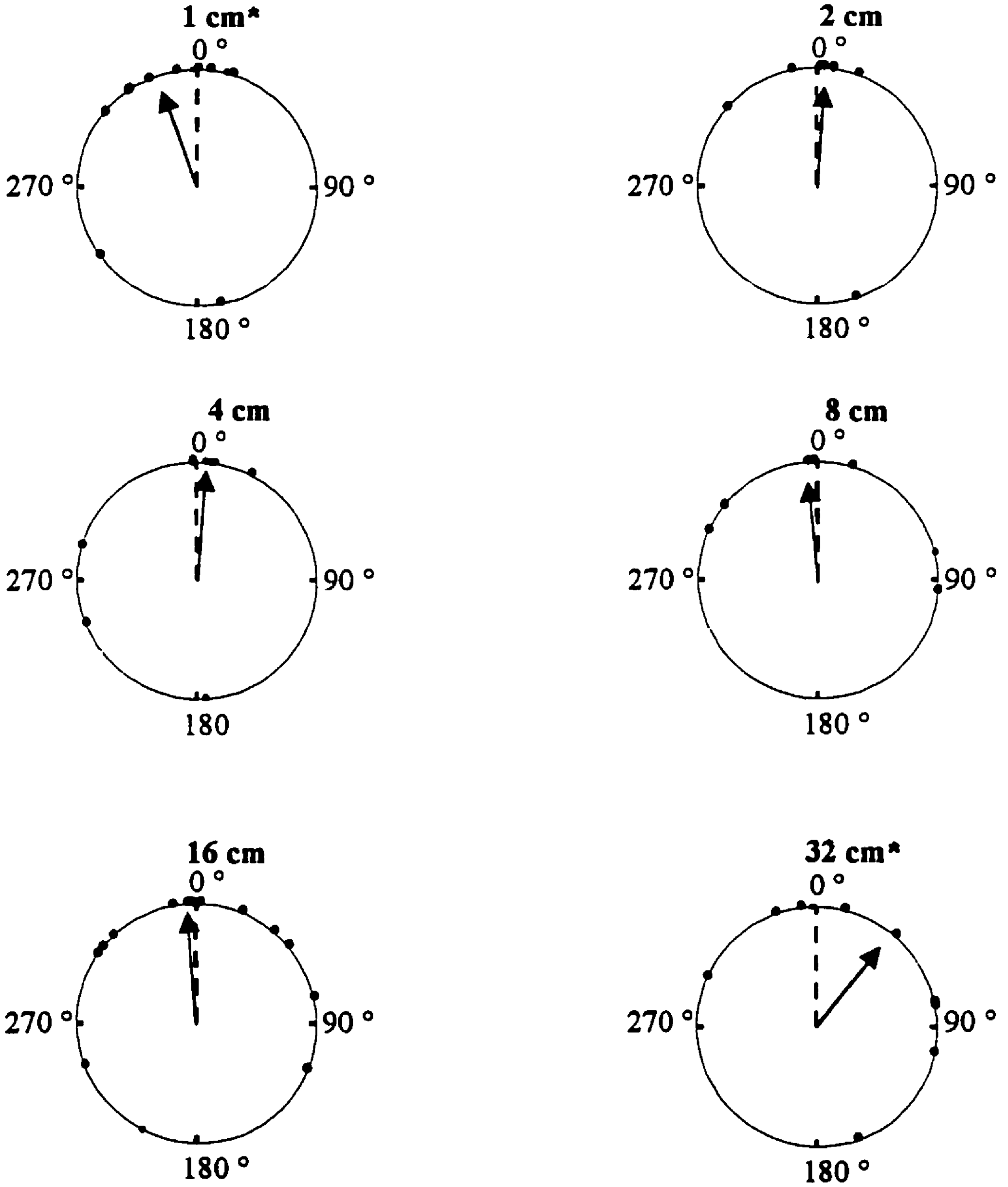

Fig. 3-9. The direction of the second move of all larvae relative to the location of the host plant (solid circles). The median angle of larval directionality is indicated by the arrow for each release distance (1, 2, 4, 8, 16 and 32 cm). The dashed line represents the straight line between the end of 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).

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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

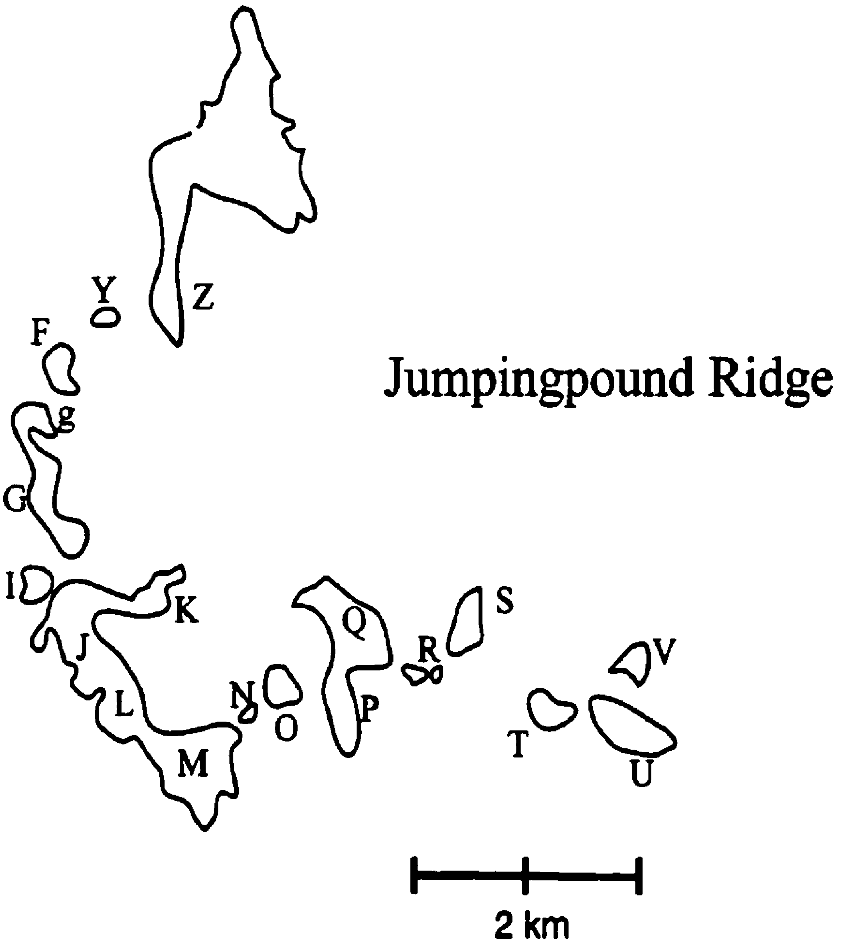

Fig. 4-1. Meadows on Jumpingpound Ridge, Alberta (50 °57'N, 114°55' W). Meadows above treeline have each been assigned a letter and are separated from one another by different distances through forest.

(*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

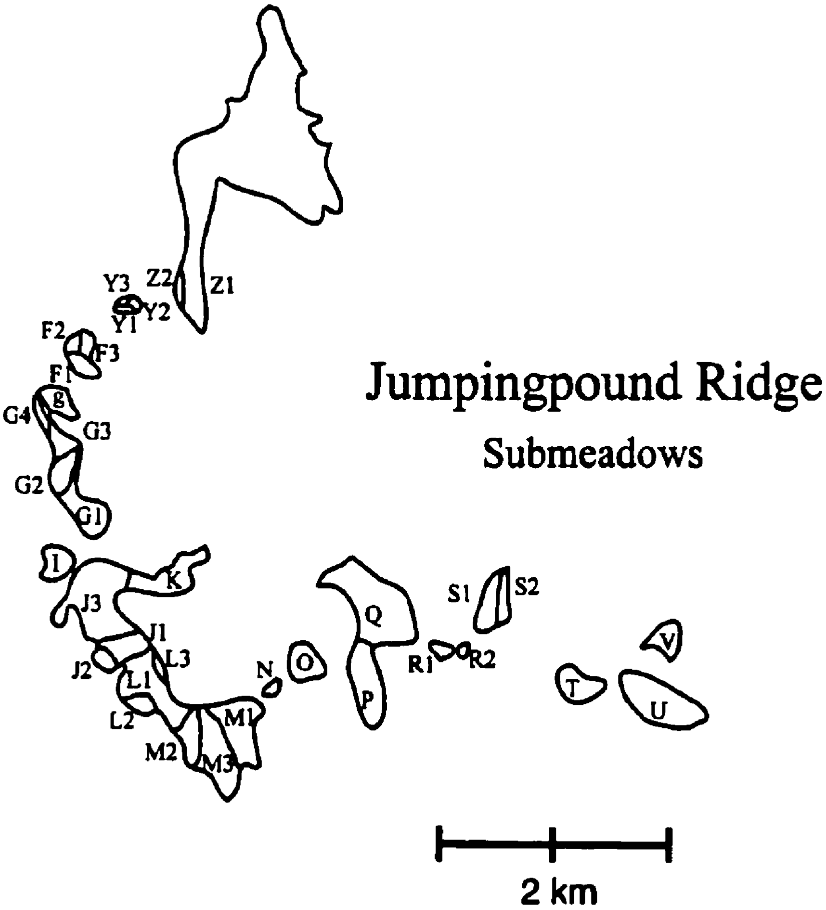

Fig. 4-2. Subdivided meadows on Jumpingpound Ridge. Divisions were determined based on aspect and general plant community.

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,

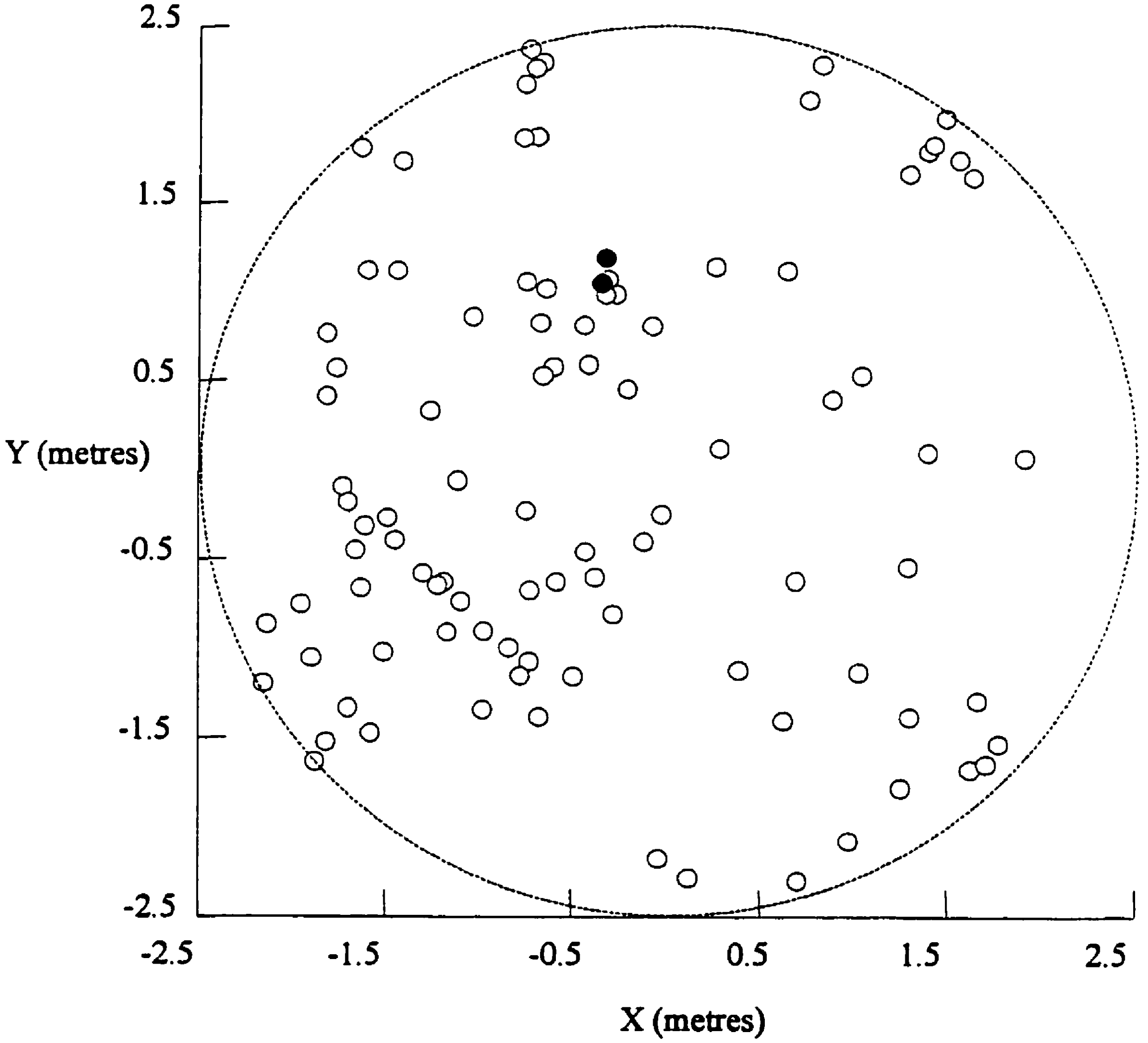

Fig. 4-3. All mapped locations of *Sedum lanceolatum* plants within a 2.5 metre radius study plot (dashed line). The open circles represent the plants without larval feeding damage and the filled circles represent plants with larval feeding damage.

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.

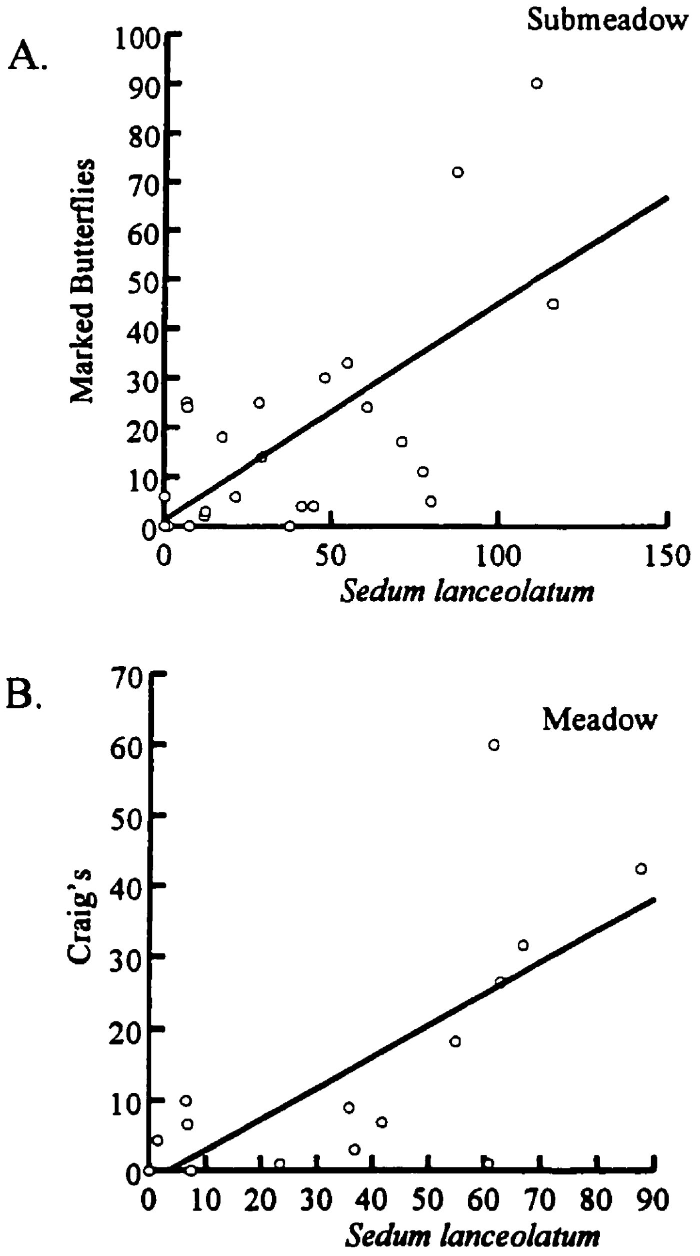

Fig. 4-4. Effect of *Sedum lanceolatum* abundance on the population indices of *Parnassius smintheus* (number of marked butterflies for the submeadows and Craig's estimate for the meadows). The linear regression line for submeadow-scale (a) and meadow-scale (b) are both significant at $p<0.005$.

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			

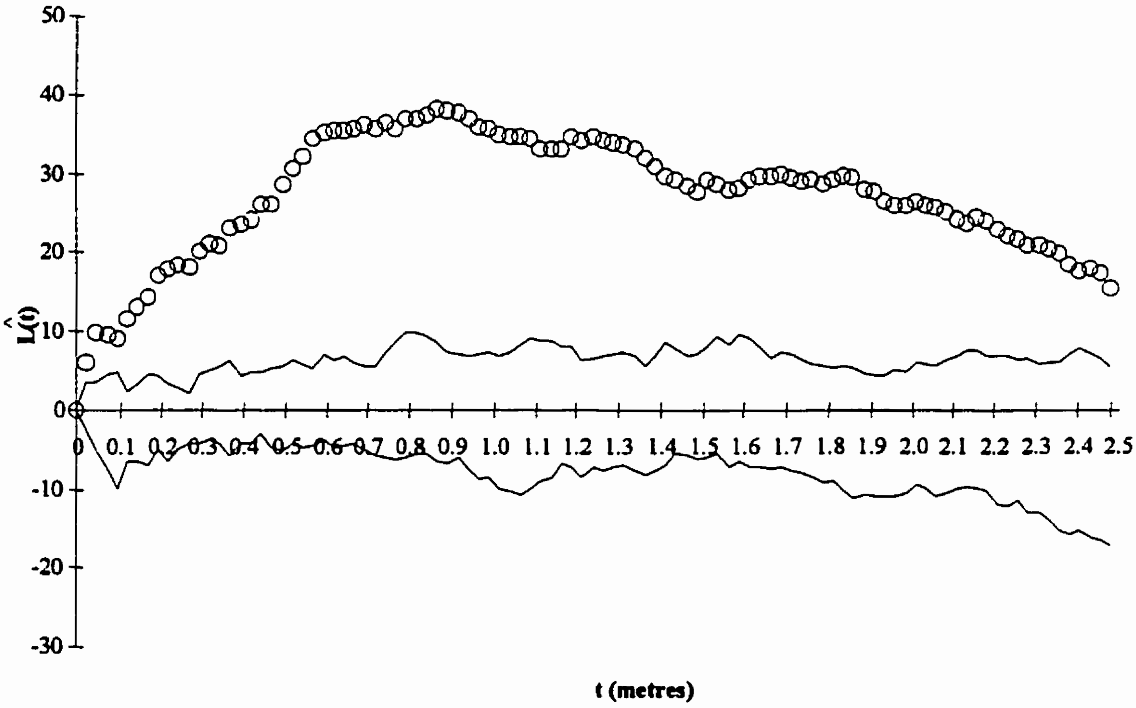

Fig. 4-5. Graphical representation of Ripley's Univariate K-function analysis demonstrating a clustered spatial point pattern at all distances of *t*, metres. The open circles represent the $\hat{L}$(t) estimates for the observed spatial pattern of *Sedum lanceolatum* plants in one plot. The solid lines 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.

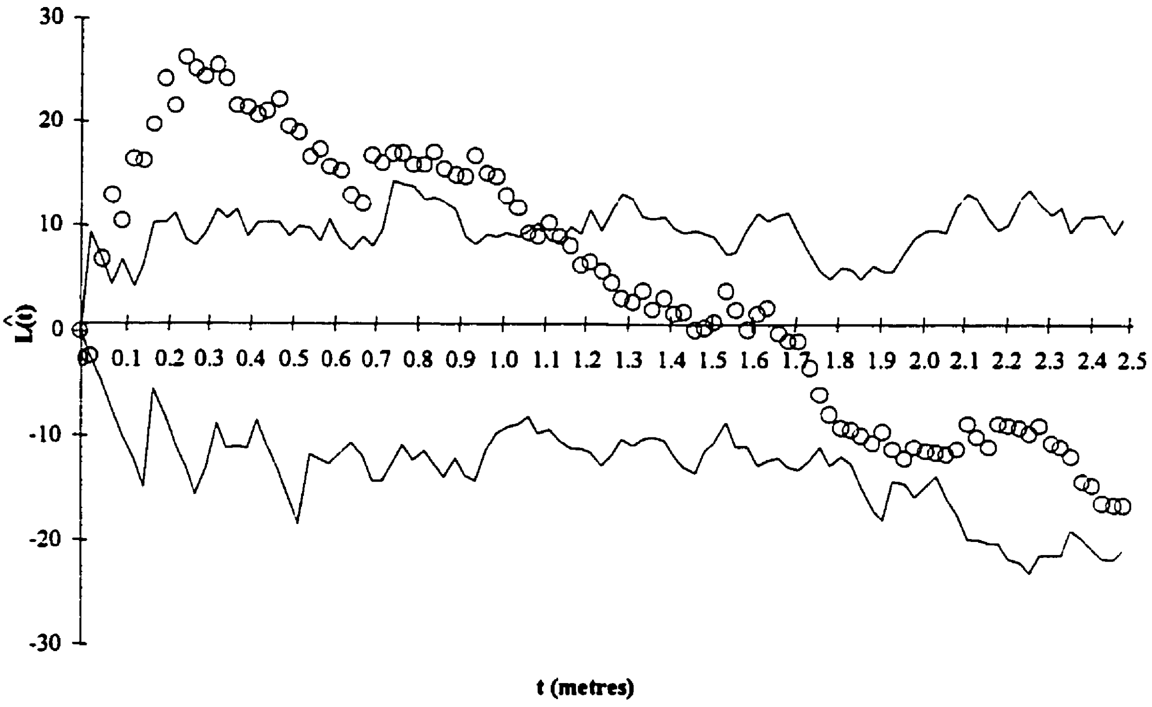

Fig. 4-6. Graphical representation of Ripley's Univariate K-function analysis demonstrating clustered spatial point patterns at small distances of *t* and seemingly random patterns at larger distances of *t*. The open circles represent the $\hat{L}$(t) estimates for the observed spatial pattern of *Sedum 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, $p<0.5 \times 10^{-9}$, McFadden's $\rho^2=0.32$). 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

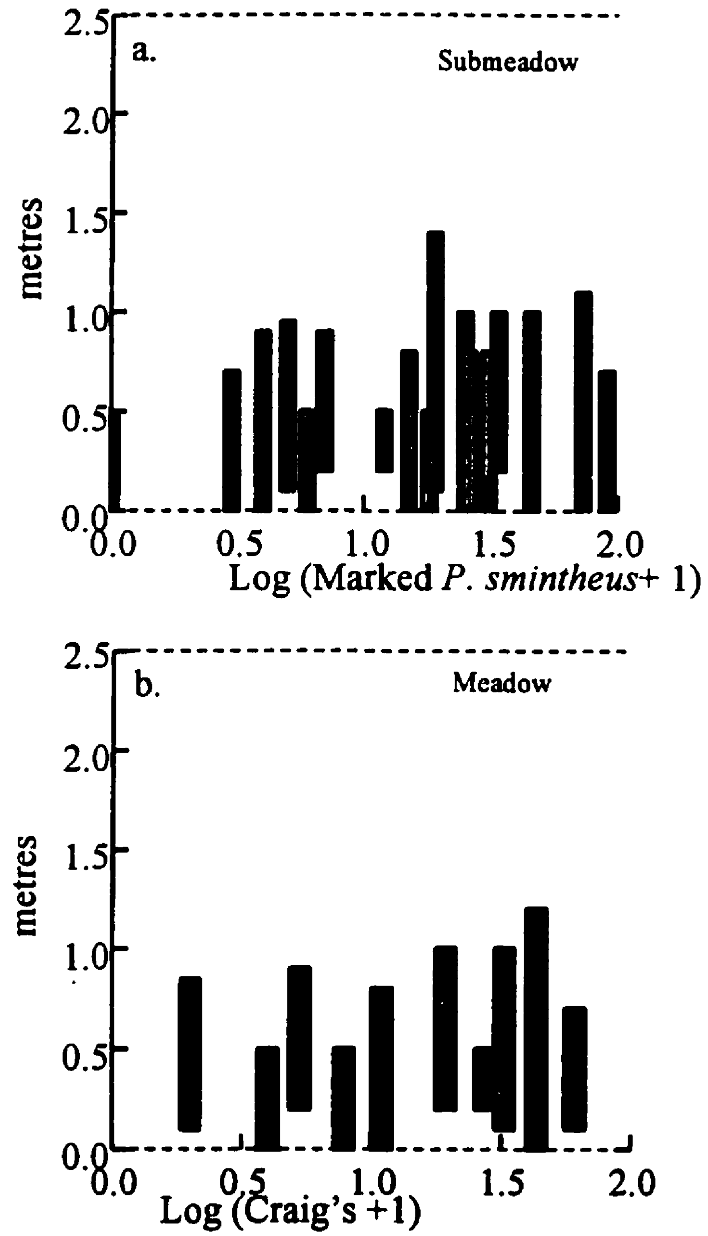

Fig. 4-7. Results from the Ripley's Univariate K-function analyses, are summarized for all plots in Jumpingpound Ridge (a) submeadows and (b) meadows with different population sizes of *P. smintheus*. The bars represent the range, in metres, over which *S. lanceolatum* plants exhibited spatial point 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.

				F-test: linear vs. additive model			
Scale	Model	Residual df	Residual Deviance	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

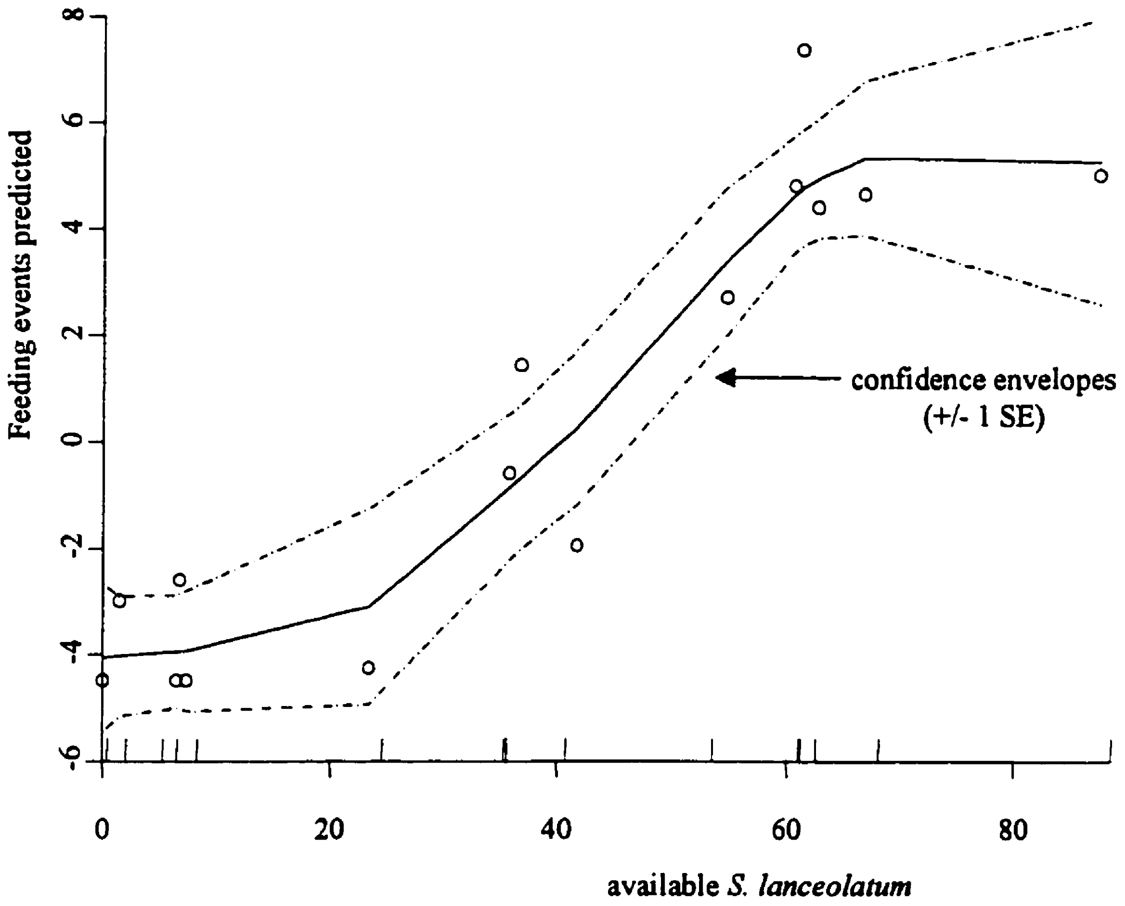

Fig. 4-8. Generalized additive model (spline-fit) predicting the amount of *S. lanceolatum* plants with feeding damage from the number of available *S. lanceolatum* plants in 5 m diameter plots, at the meadow-level. The confidence envelopes outline the estimated function (+/-) one standard error.

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)
$\mathbf{F}_b$	13	8	11(0.4-1.4)
$\mathbf{g}_a$	7	1	highly variable
$\mathbf{G}_b$	13	8	12(1.1-2.5)
$\mathbf{I}_a$	6	5	5(0-2.5)
$\mathbf{J}_d$	13	8	13(0-0.7)
$\mathbf{K}_a$	9	5	8(0-1.4)
$\mathbf{L}_d$	6	2	5(0-0.8)
$\mathbf{M}_b$	11	6	highly variable
$\mathbf{O}_a$	3	1	3(1.6-2.5)
$\mathbf{P}_a$	0		
$\mathbf{Q}_a$	3	3	3(0-2.5)
$\mathbf{R}_b$	8	1	highly variable
$\mathbf{S}_c$	1	1	1(0-2.5)
$\mathbf{T}_a$	0		
$\mathbf{U}_a$	0		
$\mathbf{V}_a$	0		

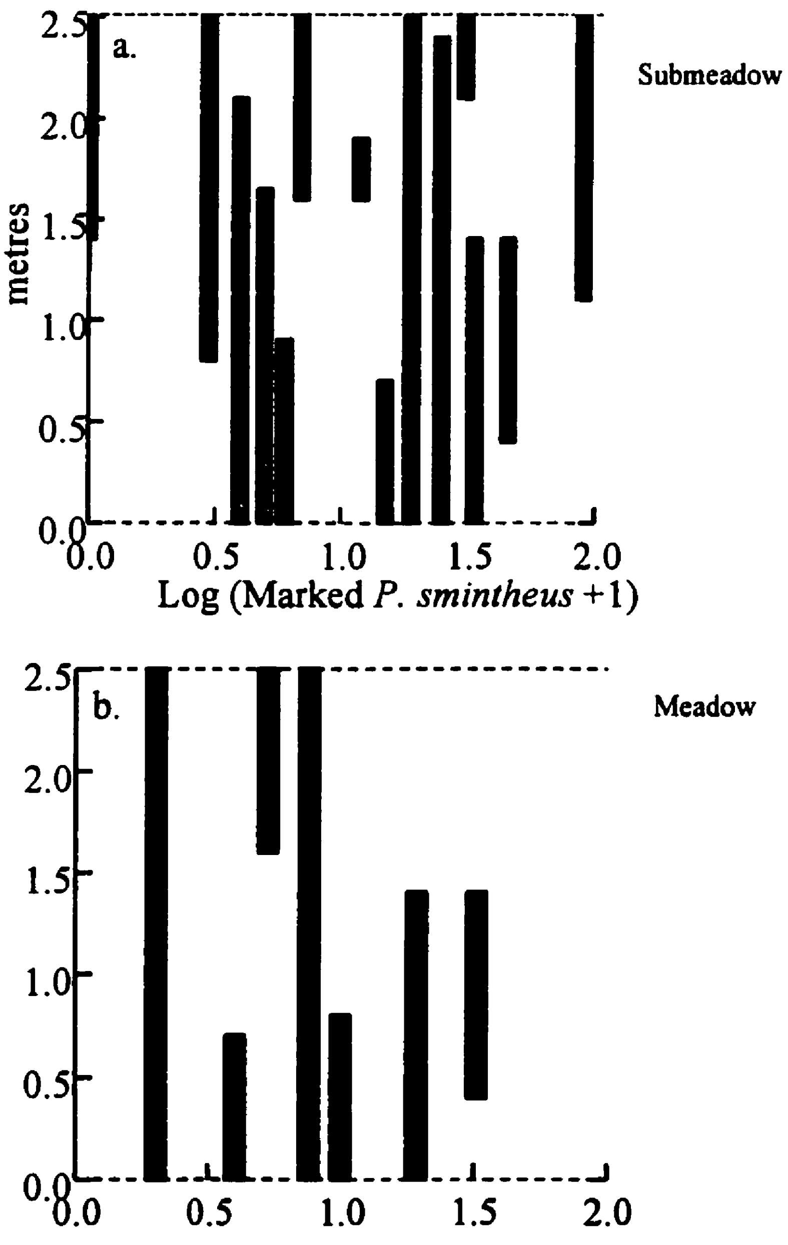

Fig. 4-9. Results from the Ripley's Bivariate K-function analyses, are summarized for all plots in Jumpingpound Ridge (a) submeadows and (b) meadows with different population sizes of *P. smintheus*. The bars represent the range, in metres, over which the spatial pattern of *Sedum lanceolatum* plants with and without feeding damage appeared independent. The broken line represents distances over which Ripley's K-function was estimated.

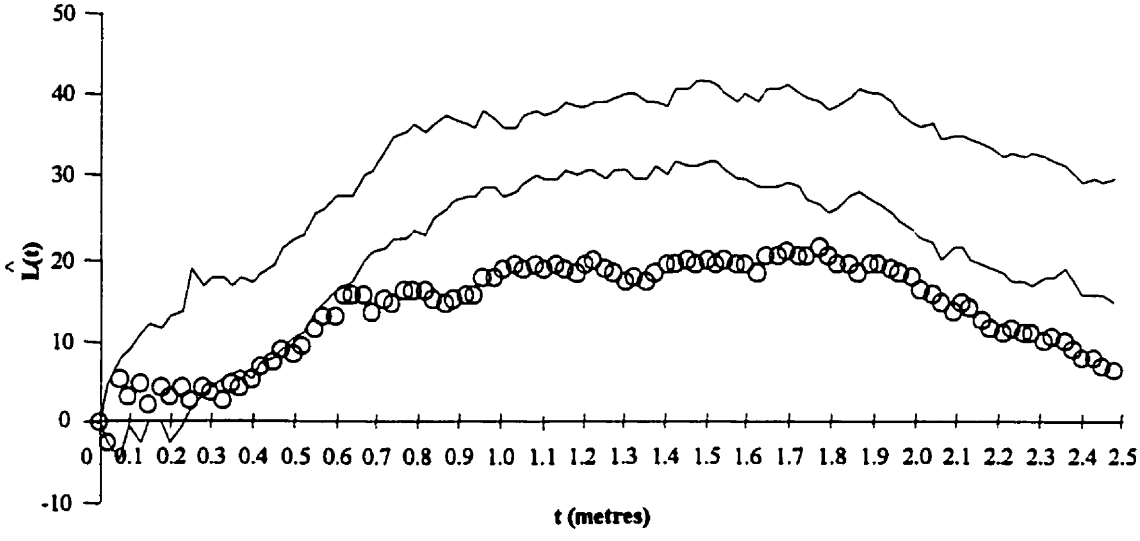

Fig. 4-10. Graphical representation of Ripley's Bivariate K-function analysis. The open circles represent the $\hat{L}(t)$ estimates for the observed bivariate association between the patterns of *Sedum lanceolatum* plants with larval feeding damage and *S. lanceolatum* plants without larval feeding damage, for one plot. The solid lines represent the 95% confidence envelopes from the Monte-Carlo simulations. The overall $\hat{L}(t)$ would lie within these confidence envelopes. From distance, *t*, 0.5 m to approximately 2.5 m the observed estimate of $\hat{L}(t)$ indicates a positive association between the spatial patterns of *S. lanceolatum* plants with and without larval feeding damage. However, the observed estimates of $\hat{L}(t)$ 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*.

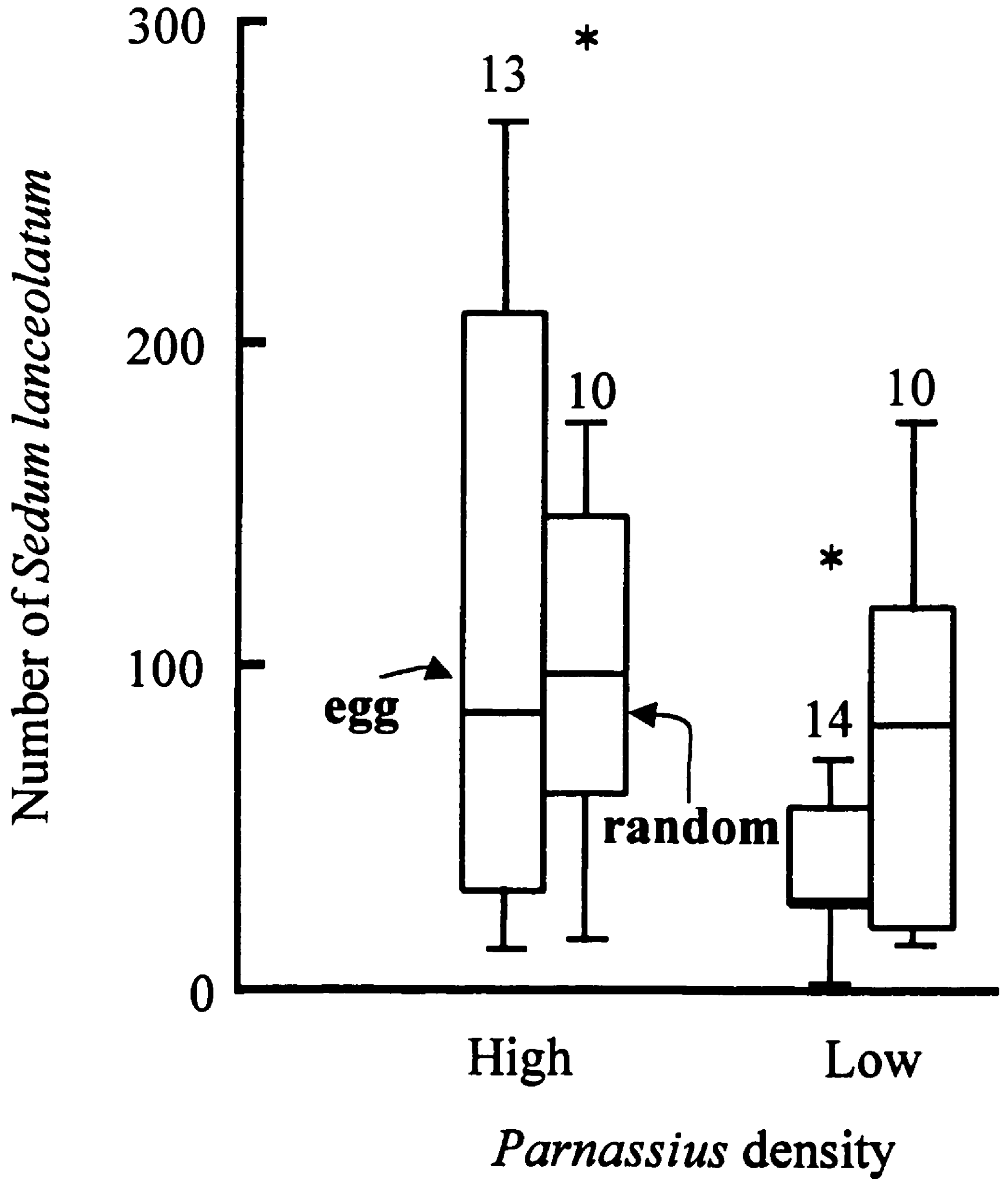

Fig. 4-11. Box and whisker plots of the number of *Sedum lanceolatum* plants within a 2.5 metre radius of oviposition sites and random sites in the high- and low-density meadows. The line in the box represents the median number of *S. lanceolatum* plants. Numbers at the tops of the boxes indicate the 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).

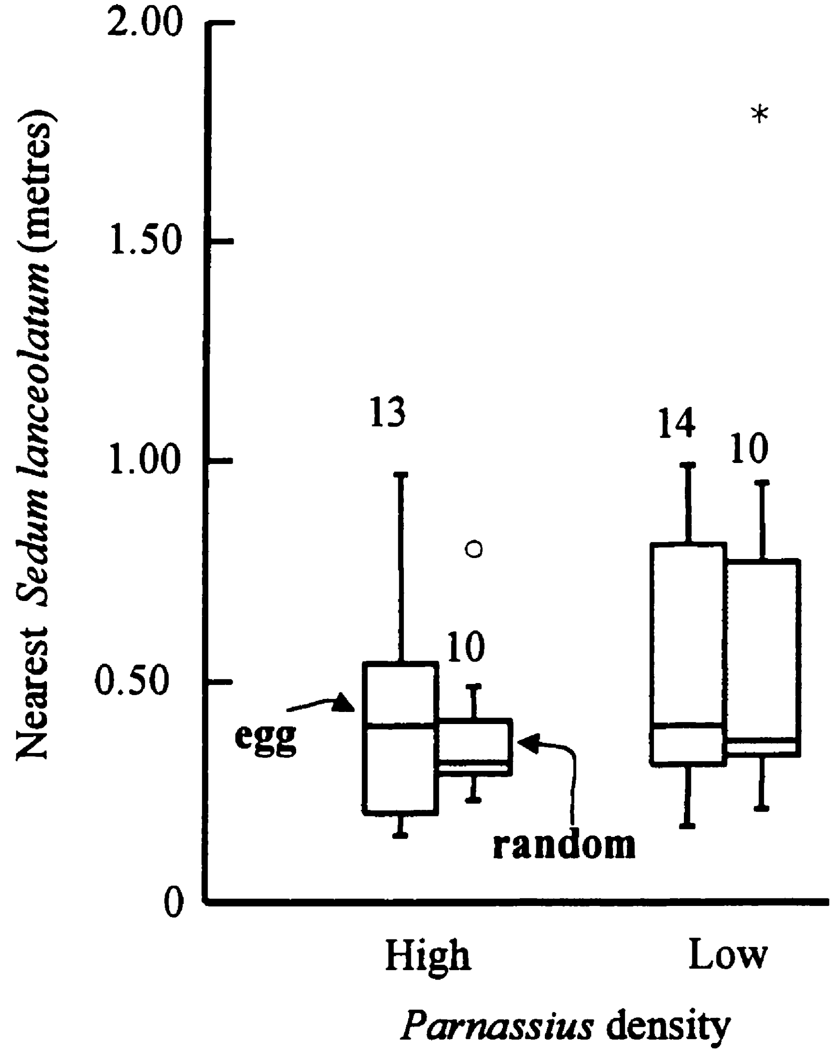

Fig. 4-12. Box and whisker plots of the distance to the nearest *Sedum lanceolatum* plant from oviposition sites and random sites in the high- and low-density meadows. Numbers at the tops of the boxes indicate the number of plots sampled. There were no significant differences detected within meadows ($p>0.05$). * and ° are outliers.

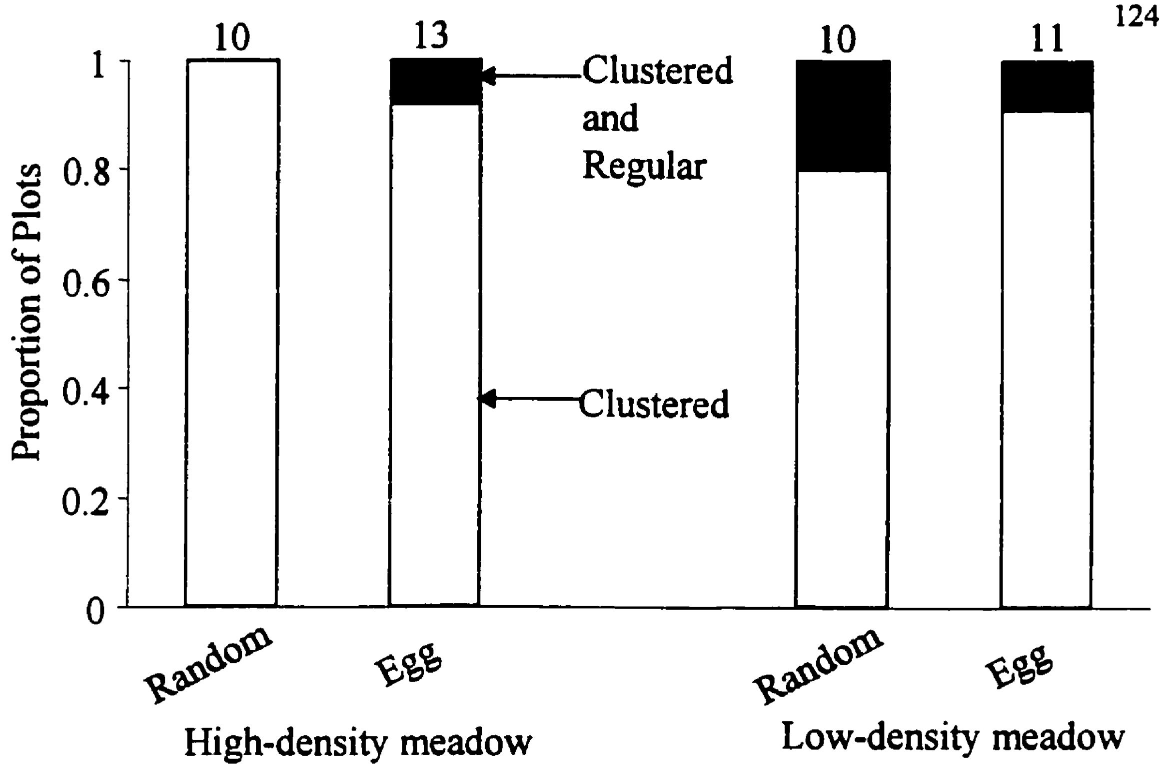

Fig. 4-13. The proportion of random and egg-laying plots where the spatial patterning of *S. lanceolatum* plants was: **clustered** at all distances (0 m to 2.5 m) or **clustered** at small distances and **regular** at larger distances in the high- and low-density quality meadows on Jumpingpound Ridge. 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

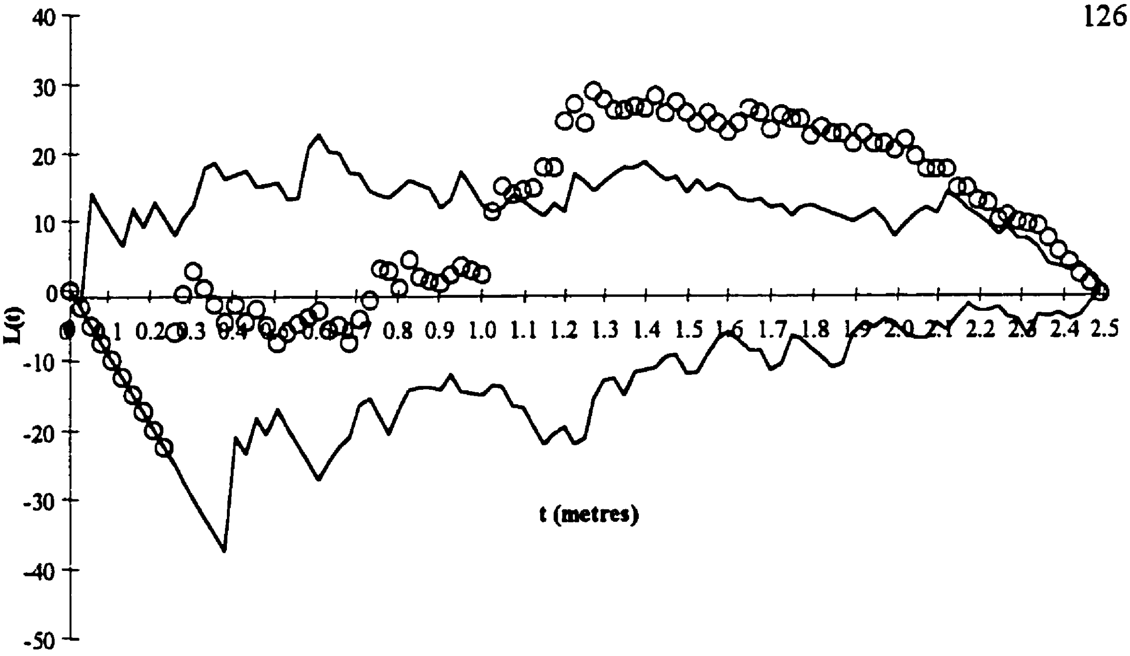

Fig. 4-14. Graphical representation of the modified version of Ripley's Univariate K-function analysis. The open circles represent the $\hat{L}$(t) estimates for the observed spatial pattern of *Sedum lanceolatum* plants from the centre, of one plot. The solid lines represent the 95% confidence envelopes from the Monte-Carlo simulations. From distance, *t*, 1.1 m to approximately 2.4 m the observed estimate of $\hat{L}$(t) indicates that the spatial pattern of *S. lanceolatum* is clustered. Notice how $\hat{L}$(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 $\hat{L}$(t) from the lower confidence envelope to randomness.

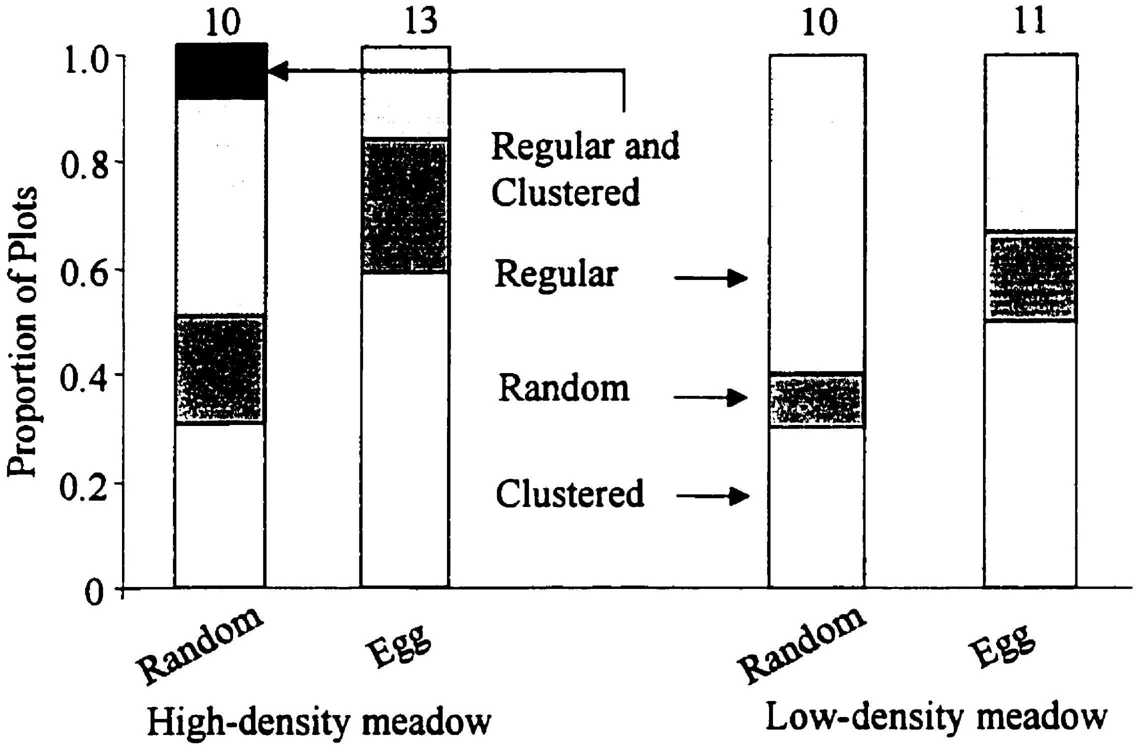

Fig. 4-15. Results from the modified Ripley's Univariate K-function. The proportion of plots where the spatial pattern of *Sedum lanceolatum*, around the centre of the random plots and the egg laying site in the oviposition plots, appears **random** or diverges from complete spatial randomness in the 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.

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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

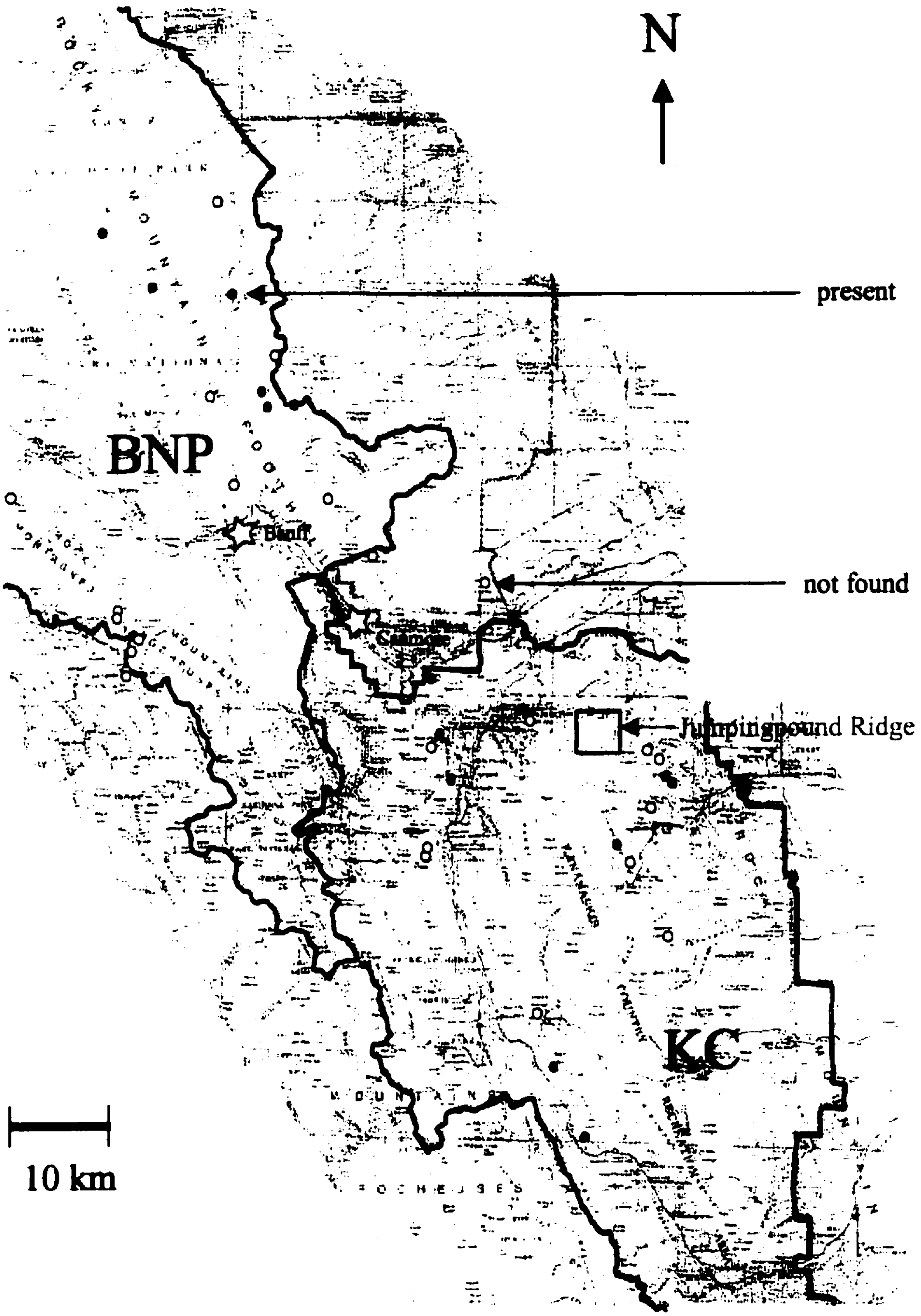

Fig. 5-1. Large-scale study sites in Banff National Park (BNP) and Kananaskis Country (KC), Alberta, where *P. smintheus* were present or not found. The perimeters of the park boundary and recreation area are outlined in black. Jumpingpound Ridge (red square) is the location of the small-scale study.

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*

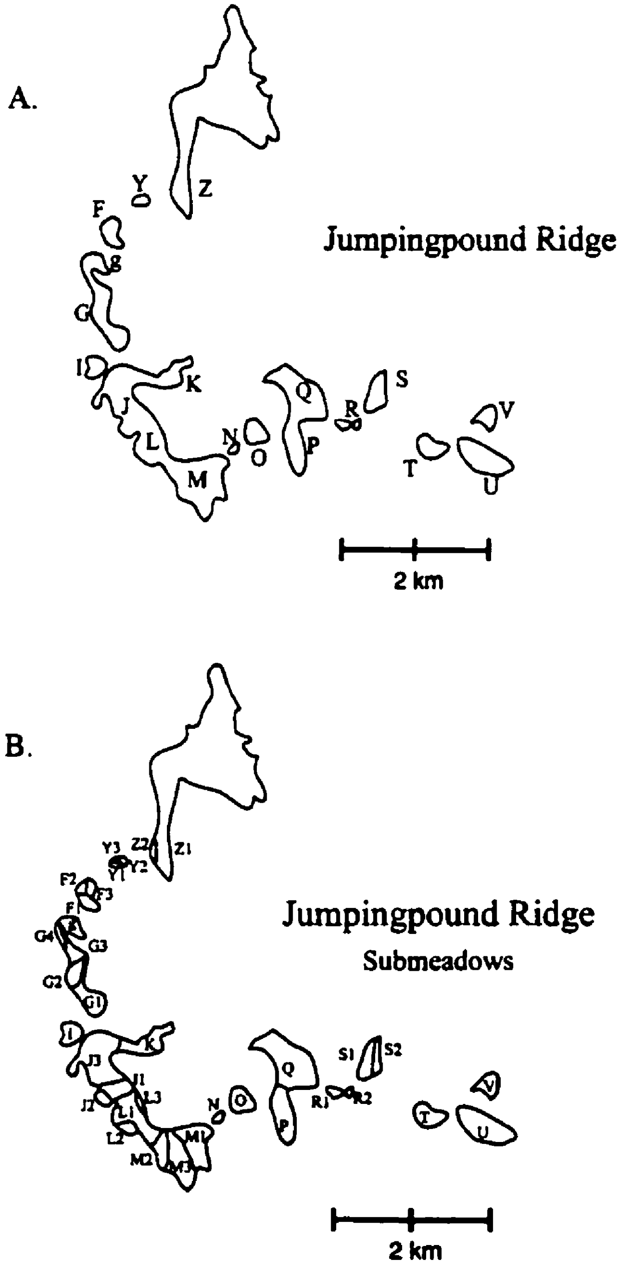

Fig. 5-2. Meadows (a) and submeadows (b) on Jumpingpound Ridge, Kananaskis Country, Alberta (50 °57'N, 114°55' W).

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.

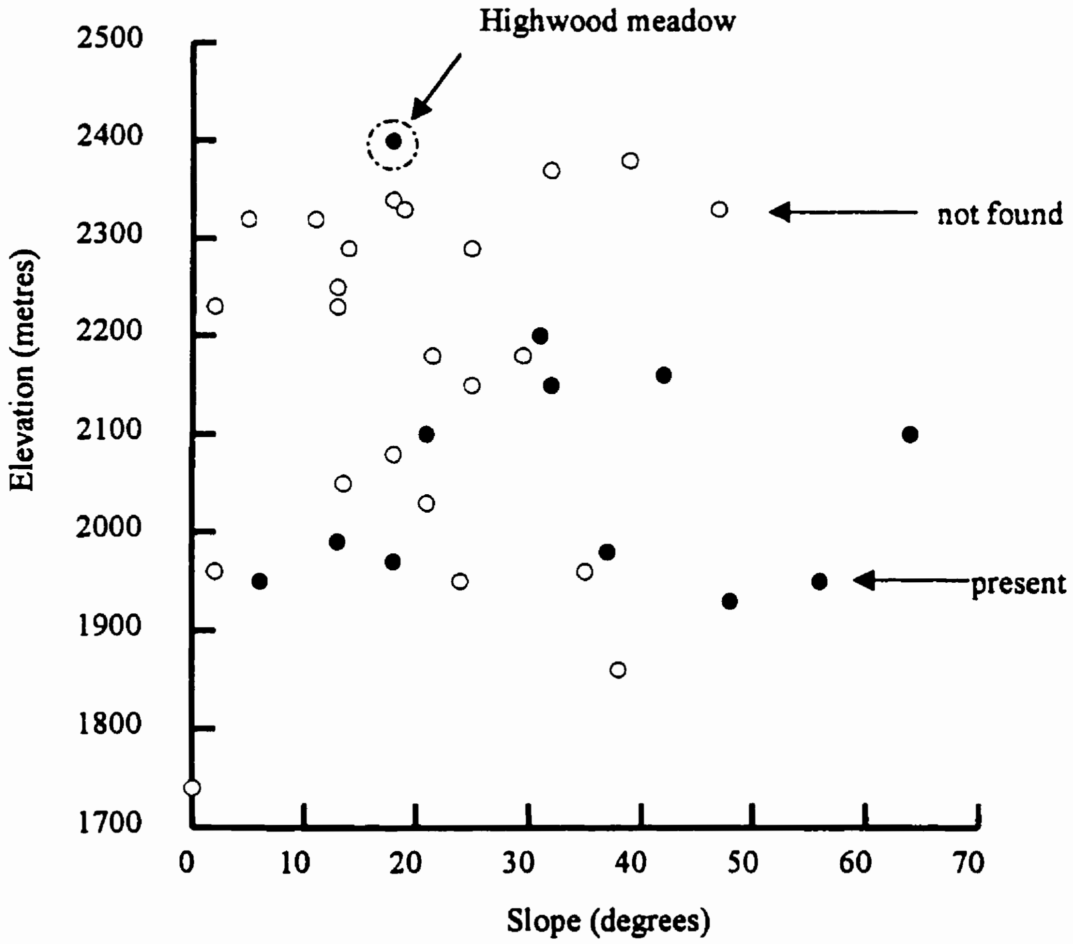

Fig. 5-3. A scatterplot of *P. smintheus*-present and *P. smintheus*-not found sites for the two significant topographical predictor variables of *P. smintheus* occurrence, slope (degrees) and elevation (metres).

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.

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

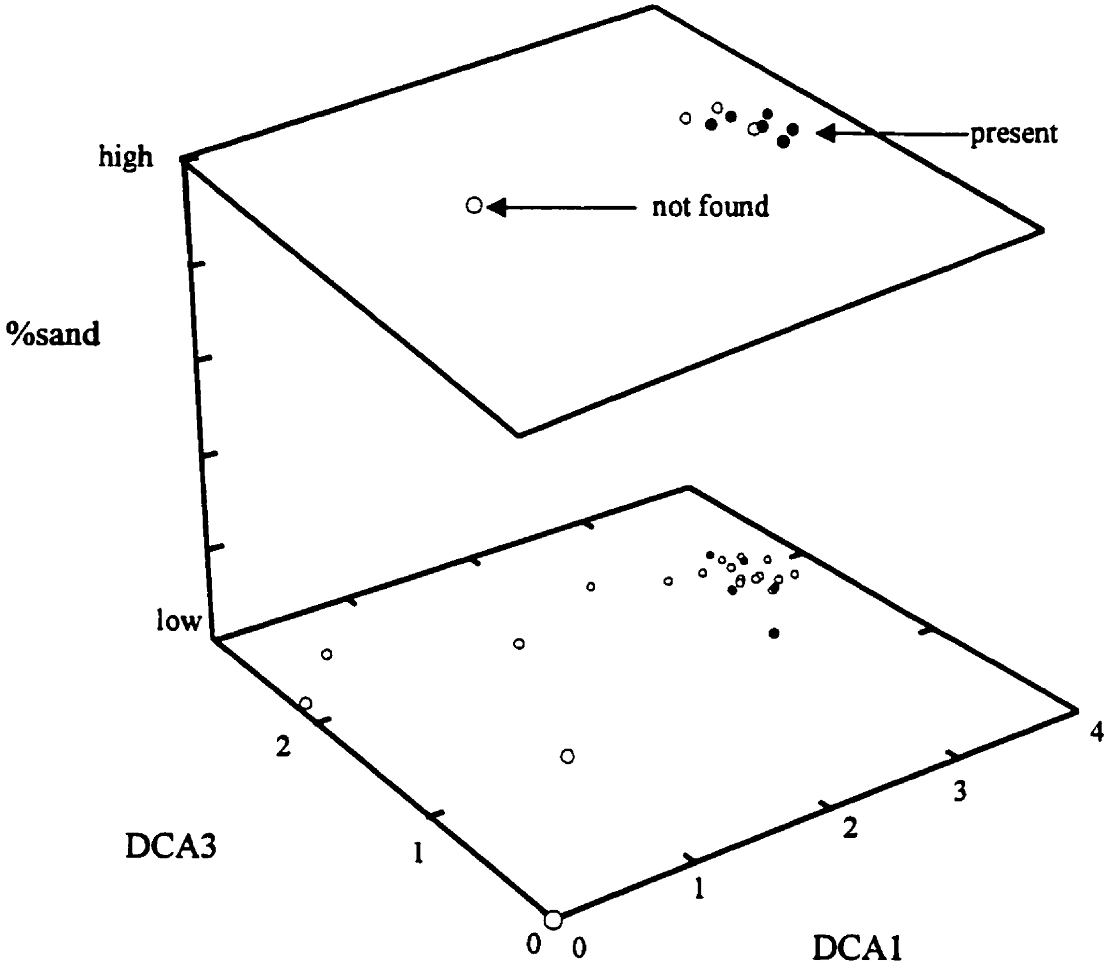

Fig. 5-4. Scatterplot of *P. smintheus*-present and *P. smintheus*-not found sites for the three significant ecological predictor variables of *P. smintheus* occurrence: two plant community axes (DCA1 and DCA3), and the binary variable for percent sand in the soil.

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 $\rho^2 < 0.2$ for the coarse topographcial model and McFadden's $\rho^2 > 0.2$ 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 (*Lupinus 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.

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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.

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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):

$$K(t)=\frac{E[N(t)]}{\lambda} \qquad (2)$$

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):

$$K(t)=\pi t^2 \qquad (3)$$

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 $\hat{K}(t)$, by weighting the proportion of the circle centered at *i* with radius *t* in the study area (Andersen 1992):

$$\hat{K}(t)=\frac{A}{n^2}\sum_{i}^{n}\sum_{j}^{n}\frac{I_t(u_{ij})}{w_{ij}} \tag{4}$$

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 $\hat{K}(t)$ 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 $\hat{K}(t)$, 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 $\hat{K}(t)$ 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, $\hat{L}(t)$ was plotted against t. $\hat{L}(t)$ is the square root transformed and standardized $\hat{K}(t)$. The expected value of $\hat{L}(t)$ for complete spatial randomness approximates zero at each distance t:

$$\hat{L}(t)=\sqrt{\frac{\hat{K}(t)}{\pi}}-t \tag{5}$$

$\hat{L}(t)$ greater than the confidence envelope indicates departure from complete spatial randomness in the direction of clustering of events, $\hat{L}(t)$ less than the confidence envelopes suggests over-dispersion or regular spacing of events and values of $\hat{L}(t)$ lying within the confidence envelopes indicate that the observed spatial pattern does not differ significantly from complete spatial randomness (Fig. B-1).

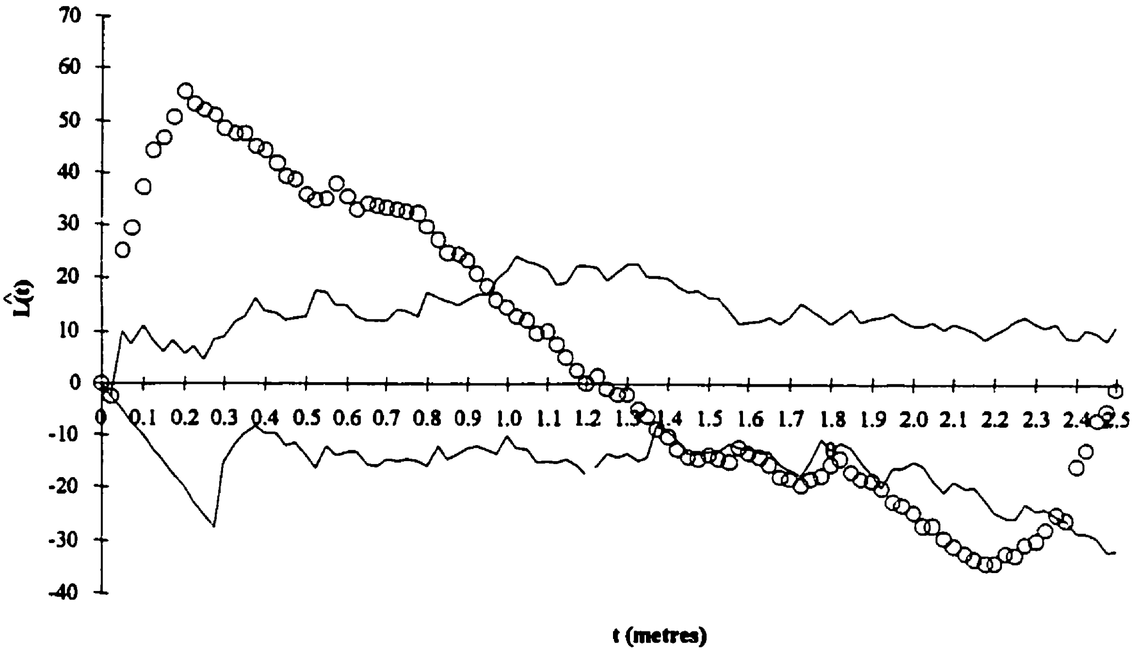

Fig. B-1. A graphical representation of Ripley's Univariate K-function analysis. The open circles represent the $\hat{L}(t)$ estimates for the observed spatial pattern of *Sedum lanceolatum* plants in one plot. The solid lines represent the 95% confidence envelopes from the Monte-Carlo simulations. From 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 $\hat{L}(t)$ lies within the confidence envelopes and indicates that the spatial pattern appears random, and from 1.4 m to 2.4 m the $\hat{L}(t)$ 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. $\hat{K}_{12}(t)$ and $\hat{K}_{21}(t)$ 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.

$$\hat{K}_{12}(t)=\frac{A}{(n_1n_2)}\sum_{i=1}^{n1}\sum_{j=1}^{n2}\frac{I_t(u_{ij})}{(w_{ij})} \tag{6}$$

$$\hat{K}_{21}(t)=\frac{A}{(n_1n_2)}\sum_{i=1}^{n1}\sum_{j=1}^{n2}\frac{I_t(v_{ij})}{(w_{ji})} \tag{7}$$

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. $\hat{L}(t)$ is the bivariate association of the two species, and square-root transforms and standardizes $\hat{K}(t)$ as in the Ripley's Univariate K-function, where the expected value of $\hat{L}(t)$ 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 $\hat{K}_{12}(t)$ and $\hat{K}_{21}(t)$ 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 $\hat{K}_{12}(t)$ and $\hat{K}_{21}(t)$, therefore; the edge correction term (w_{ij}) can be dropped from Equations 5 and 6.

$$\hat{L}(t)=\sqrt{\frac{n_2\hat{K}_{12}(t)+n_1\hat{K}_{21}(t)}{\pi(n_1+n_2)}}-t \tag{8}$$

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 $\hat{L}(t)$ 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 $\hat{L}(t)$ 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. $\hat{L}(t)$ greater than the confidence envelope indicates that the two types of points are positively associated (aggregated) given the underlying spatial arrangement of points and $\hat{L}(t)$ 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**.

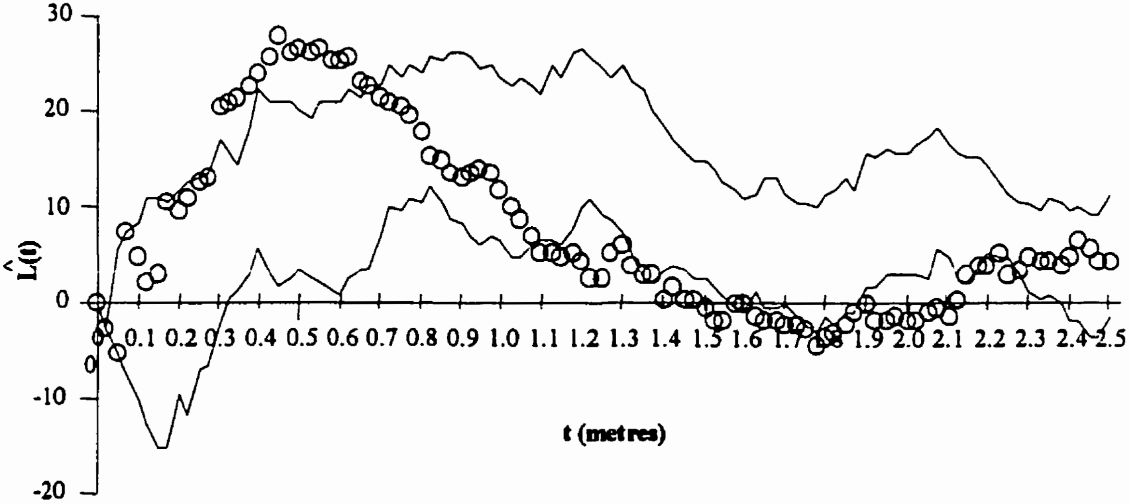

Fig. B-2. A graphical representation of Ripley's Bivariate K-function analysis. The open circles represent the $\hat{L}(t)$ estimates for the observed bivariate association of *Sedum lanceolatum* plants with larval feeding damage and *Sedum lanceolatum* plants without larval feeding damage, for one plot. 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*.

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